CORRIGENDA

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The following pages should be substituted for pages 611 to 623 which constitute Contribution Number E-6, "Seasonal and Areal Distribution of Gulf of Maine Coastal Zooplankton, 1963", by Kenneth Sherman.

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E-6

SEASONAL AND AREAL DISTRIBUTION OF GULF OF MAINE COASTAL ZOOPLANKTON, 1963

By

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ABSTRACT

Gulf of Maine coastal waters were sampled for zooplankton on single cruises during the winter, spring, summer and fall, 1963. Areal and seasonal variations were found in zooplankton volumes, major group occurrences and species composition. Three areas - the western, central and eastern Gulf - showed differing patterns of relative zooplankton abundance, with highest volumes occurring in the western sector, moderate volumes in the central area and lowest volumes in the eastern area.

Major zooplankton groups were more numerous in the western Gulf during winter, spring and fall. In summer, zooplankton groups were found in a variable pattern throughout each of the sampling areas. Larval forms were most numerous during spring and summer, indicating widespread breeding during these periods.

Copepods were the most numerous group of zooplankters encountered. Twenty-two species were present of which eight - *Calanus finmarchicus, Centropages typicus, Metridia lucens, Pseudocalanus minutus, Acartia longiremis, Oithona similis, Temora longicornis,* and *Tortanus discaudatus* - were most numerous. Six species were more abundant in the western area then in the eastern sector during all seasons. *Calanus finmarchicus* was more abundant in the east than the west in spring and *P. minutus* reached maximum numbers in the central area during summer. The fluctuations in seasonal and areal distribution of zooplankton volumes, major groups, and species are discussed in relation to previous studies and possible causes of variation.

INTRODUCTION

As part of a research program on the relation between environmental factors and availability of immature herring, *Clupea harengus* L., the Bureau of Commercial Fisheries Biological Laboratory, Boothbay Harbor, Maine, initiated a study of the Gulf of Maine coastal zooplankton. Research has provided information regarding seasonal and annual changes in zooplankton distribution and abundance.

In his classic work, Bigelow (1926) was first to describe the Gulf of Maine zooplankton. He characterized the dominant forms as the "Calanus Community" and showed that this endemic assemblage of zooplankters underwent seasonal pulsations in standing crop, progressing from a winter minimum to a spring-summer maximum, and was augmented annually by intrusions of northern and southern immigrant forms. Subsequent studies of Fish and Johnson (1937) and Redfield (1941) acknowledged the permanence of Bigelow's calanoid community, and the occurrence of immigrant species. Reports on endemic copepod species have been published by Fish (1936*a*, *Calanus finmarchicus;* 1936*b* *Pseudocalanus minutus;* 1936*c* *Oithona similis;* 1955 *Microsetella norvegica*) and Redfield (1941, Calanoid species). Information regarding immigrant zooplankters was presented by Redfield (1939) for populations of the pteropod *Limacina retroversa* and by Redfield and Beale (1940) for several chaetognath species. Recently, Colton, *et al.* (1962) reported on the periodic intrusions of oceanic copepods into the inner reaches of the Gulf.

In the earlier works of Bigelow (1926) and Fish and Johnson (1937), lower mean-annual-volumes of zooplankton were reported east of the centrally located Penobscot Bay area than to the west of this region. Recent information, provided by staff members of the Boothbay Harbor Laboratory, suggests that this difference in areal distribution along the Maine coast is not limited to zooplankton. During 1962, it was observed that mean length of two-year-old herring was greater in the area west of Penobscot Bay than to the eastward (Watson, J.E., unpublished data). Erythrocyte antigen frequencies

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of young herring were found to differ east and west of Penobscot Bay (Sindermann, 1962). A discontinuity of the myxosporidian parasite, *Kudoa clupeidae*, was observed in small herring with infestations occurring west of Penobscot Bay but not to the eastward (Sindermann, 1961). Also, differences in spawning time of herring occur east and west of Penobscot Bay, as evidenced by the occurrence of larvae ($\leq$ 9 mm standard length) east of Penobscot Bay two to three weeks earlier than larvae of the same size found to the westward (Graham, J.J., personal communication). In view of these findings, sampling was undertaken to determine whether differences in the composition and relative abundance of zooplankters occurred along the Maine coast.

METHODS

This report is based on the examination of 71 zooplankton samples collected from Gulf of Maine coastal waters during four seasonal cruises of the research vessel, *Rorqual*. Station locations and periods of collection are given in Table 1. Zooplankton samples were collected with a Gulf III sampler (Gehringer, 1962), fitted with an eight-inch nose cone and monel netting (aperture width 0.37 mm). All tows were of 30-min duration, taken during daylight hours, from 20 m to the surface in an oblique manner, with 10 min of towing at the surface and at depths of 10 and 20 m. A calibrated flow meter, affixed to the tail section of the Gulf III, was used to determine the amount of water strained. In addition, a U.S. Navy Electromagnetic Underwater Log, mounted on the keel of the *Rorqual*, measured the distance traversed during each tow. Analyses of the variation in the amount of water strained as determined by meter readings and Electromagnetic Log values indicated no significant differences in amount of water strained (Graham, J.J., unpublished data). For cruises 1 and 7, meter readings were used to calculate the amount of water strained, and for cruises 4 and 5, Electromagnetic Log readings were used. The average 30-min tow covered a distance of three nautical miles and filtered approximately 200 m^3 of water. Towing speed was maintained at approximately 6 knots.

TABLE 1. STATION LOCATIONS AND PERIODS OF COASTAL ZOOPLANKTON COLLECTIONS, *Rorqual* CRUISES 1, 4, 5 AND 7, 1963.

Station number	Position		Sampling periods, 1963			
	Lat.	Long.	*Rorqual* 1 5-16 Jan.	*Rorqual* 4 25 May- 2 June	*Rorqual* 5 10-22 July	*Rorqual* 7 11-20 Oct.
1.	42°43'	70°30'	X	X	X	X
2.	42°51'	70°43'	X	X	X	X
3.	42°56'	70°41'		X	X	X
4.	43°08'	70°23'		X	X	X
5.	43°17'	70°30'	X	X	X	X
6.	43°24'	70°12'		X	X	X
7.	43°39'	70°09'		X	X	X
8.	43°35'	69°52'	X	X	X	X
9.	43°42'	69°42'			X	X
10.	43°48'	69°29'	X	X	X	X
11.	43°51'	69°26'		X	X	X
12.	43°46'	69°06'	X	X	X	X
13.	43°48'	68°47'		X	X	X
14.	43°57'	68°93'	X	X	X	X
15.	44°02'	68°14'	X	X	X	X
16.	44°17'	68°07'	X	X	X	X
17.	44°10'	67°53'	X	X	X	X
18.	44°27'	67°50'		X	X	X
19.	44°27'	67°18'	X	X	X	X
21.	44°34'	67°19'	X	X	X	X
Number of stations sampled			12	19	20	20

In the laboratory, displacement volumes of all samples were taken. Ctenophores, large coelentrate remains (>2 cm long), and all fish larvae were removed from the samples and not included in the final volume determinations. Samples containing large quantities of ctenophores and medusae were not included in the analyses, due to the filtration error introduced by mesh clogging. Zooplankton samples were split into aliquots ranging from a half to a sixty-fourth, depending on the mass of the sample, and sorted into major taxonomic groups. Copepods were identified to species and the numbers of copepods and other zooplankters, per 100 m^3 of water strained were calculated.

RESULTS

Zooplankton Volumes

Seasonal and areal distributions of zooplankton volumes were compared. Abundance estimates are considered to be minimal, as use of a 0.37 mm mesh aperture limited sampling to the larger zooplankters. Also, tows were limited to the upper 20 m, and were taken only during daylight hours. To examine differences in areal distribution, the coastal region was divided into three areas, a central area located in the vicinity of Penobscot Bay, an eastern area extending from Mt. Desert Island to Grand Manan Island, and a western area from Casco Bay to Cape Ann. The areas, station locations, and sampling periods are shown in Fig. 1.

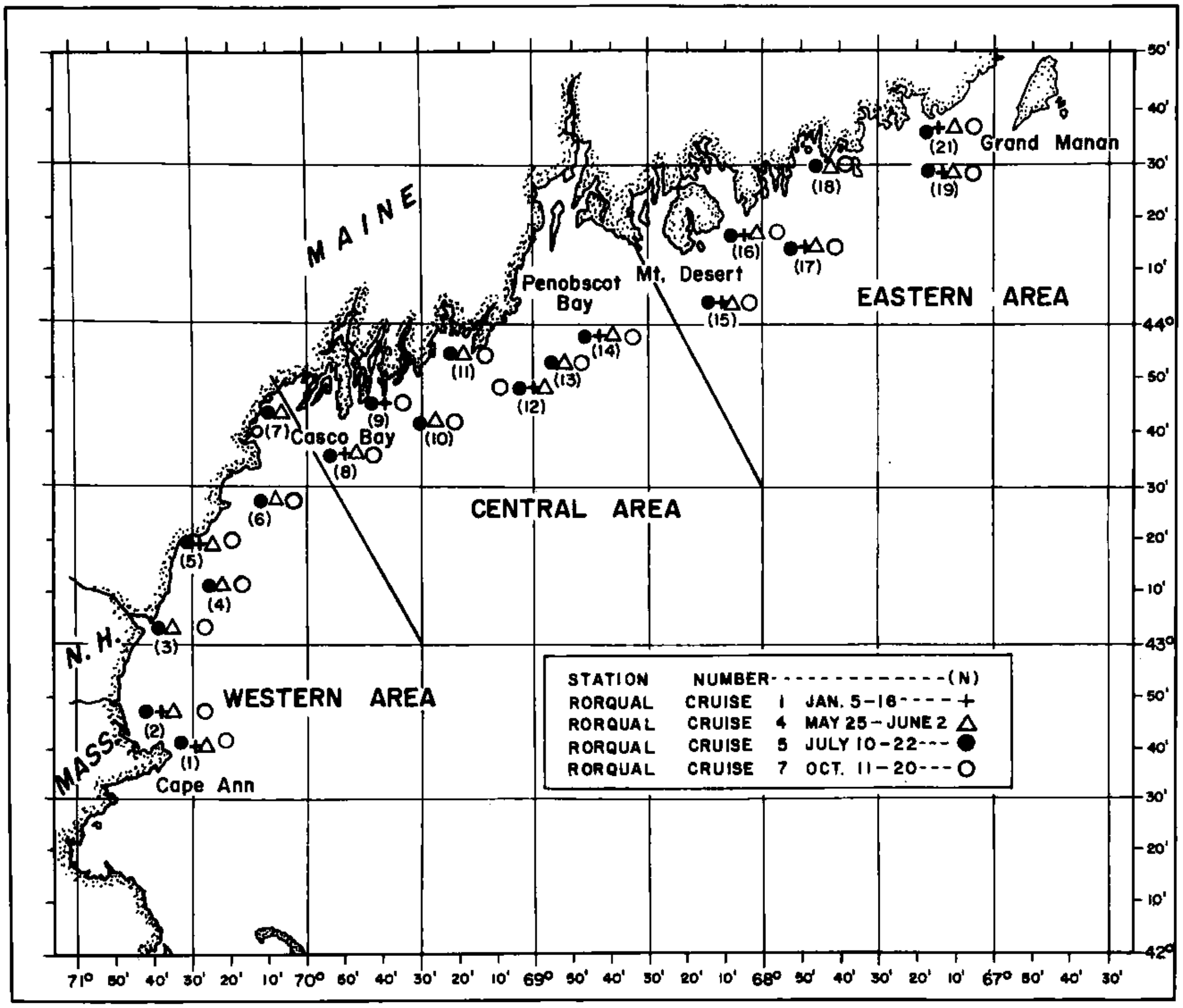

Fig. 1. Zooplankton sampling areas, station locations and periods of collections.

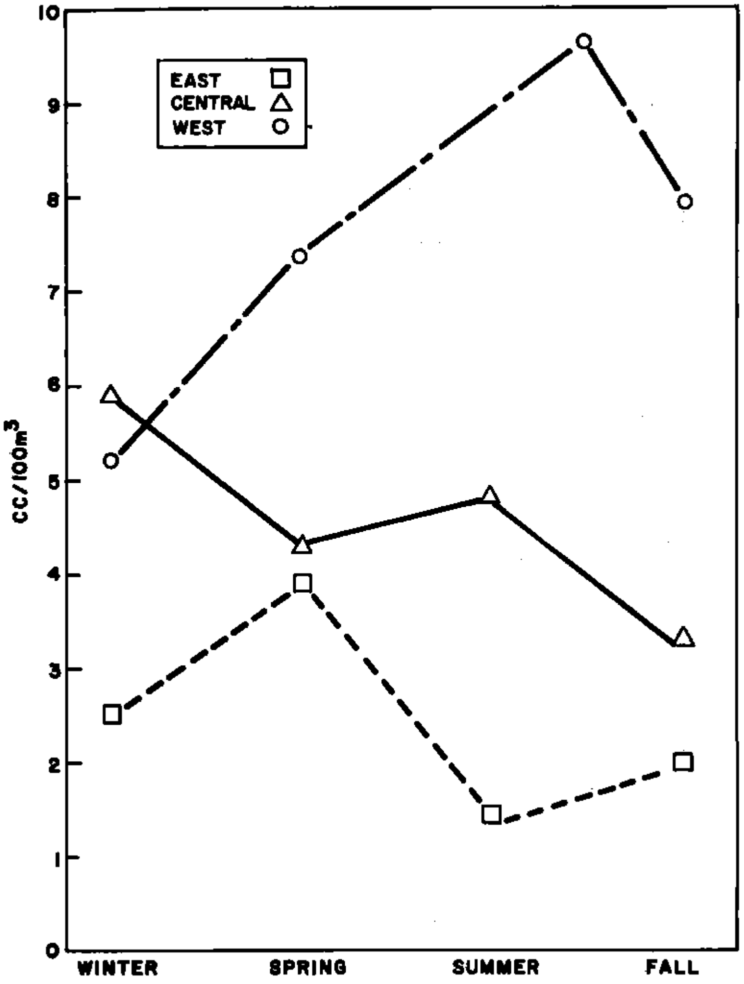

Fig. 2. A comparison of average zooplankton volumes per 100 m^3 of water strained among seasons for each of the three areas.

A comparison of average zooplankton volumes among areas for each of the four seasons is given in Fig. 2. Significant differences among areas ($H=19.159$, $P < .01$) were found using the Kruskal-Wallis analysis of variance (Siegel, 1956). In the eastern area the displacement volumes were the lowest encountered, ranging from a spring high of 3.9 cc/100 m^3 to a summer low of 1.4 cc/100 m^3. An intermediate range of values was found in the central area, ranging from a winter high of 5.9 cc/100 m^3, to a fall low of 3.2 cc/100 m^3. The greatest seasonal change in mean volumes occurred in the western area with values progressing from a winter low of 5.2 cc/100 m^3 to a summer high of 9.6 cc/100 m^3.

Zooplankton Groups

The percentage composition of the zooplankton groups encountered on each of the seasonal cruises is presented in Fig. 3. Copepods were the dominant zooplankters during each of the seasons, reaching a fall and winter high of 91% of the total zooplankton and declining to 45% in summer. Of the other planktonic forms found, nine--pteropods, chaetognaths, decapod larvae, cladocerans, brachyuran larvae, tunicates (appendicularians), cirripeds, and fish and crustacean eggs--constituted greater than 1% of the total zooplankton. The spring and summer decline in percentage composition of copepods was associated with the increase of other abundant (> 1% of the total zooplankton) groups; from two in winter to five in spring and seven in summer (Fig. 3). The breeding period of many species during warmer months was evidenced by the abrupt rise in decapod larvae in spring, and fish eggs and crustacean eggs during summer. Cirripeds occurred in swarms during spring, but diminished in summer with the onset of substrate attachment. Brachyuran and pelecypod larvae occurred during the summer and fall periods only. The fall decrease in the number of abundant zooplankton groups present indicated that the zooplankton population was approaching the winter minimum.

To examine the areal distribution of the dominant zooplankton groups, the mean number of zooplankters per 100 m^3 of water was determined for each of the three areas and for each of the seasonal cruises. Differences in areal distribution were plotted for major groups only (>100/100 m^3). During the winter period, copepods were the dominant zooplankters in all areas (Fig. 4A), but were more numerous in the western than in the eastern area.

In spring as in winter, copepods were the dominant zooplankters, increasing in numbers from a group mean of 645/100 m^3 in winter to 5,575/100 m^3 in spring (Fig. 4B). The spring rise in copepods was accompanied by increases in numbers of other major groups - decapod larvae, cladocerans, pteropods, cirriped larvae and tunicates. All major groups, with the exception of cirriped larvae, decreased in numbers from west to east (Fig. 4B).

An increase in the number of major groups was evident during the summer period (Fig. 4C). As in the preceding two seasons, copepods were the dominant zooplankters, with the greatest number (9,853/100 m^3) present in the western sector. Decapod and brachyuran larvae were also more numerous in the western area than in the east. The central area was characterized by a number of dominant

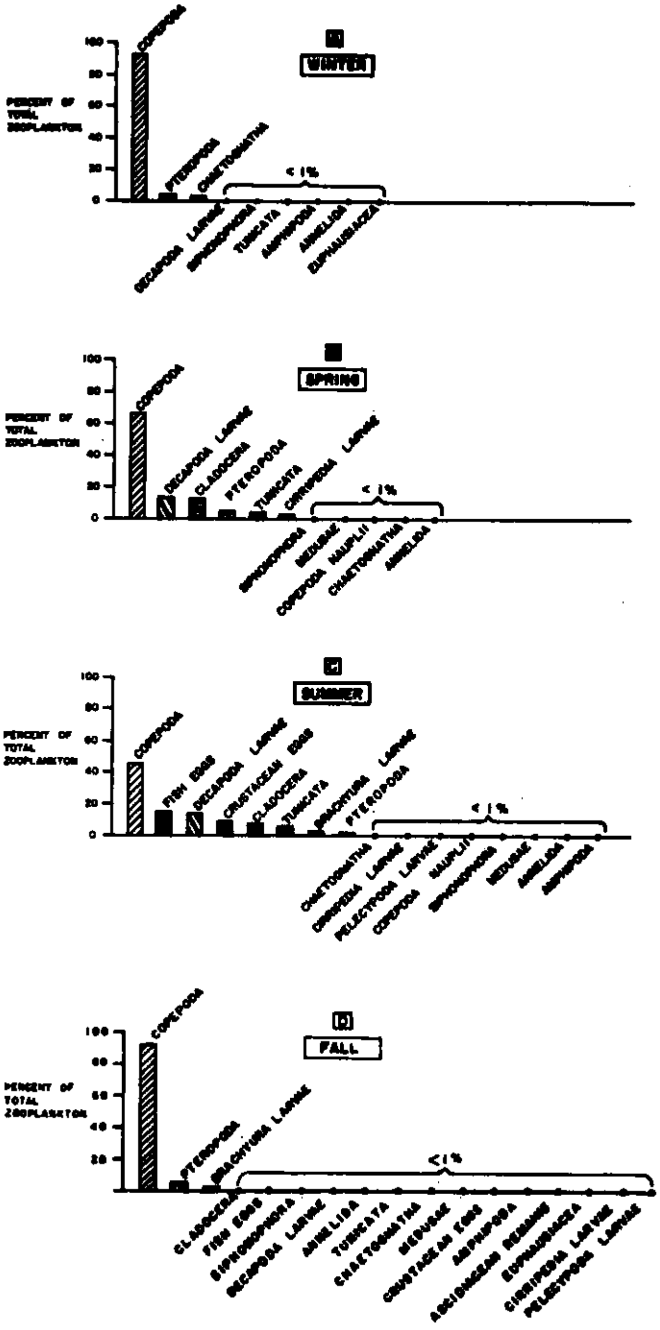

Fig. 3. Percentage composition of the zooplankton groups encountered on each of the seasonal cruises.

forms; cladocerans, pteropods, chaetognaths and fish eggs. Tunicates and crustacean eggs were more numerous in the eastern area.

During fall, fewer major groups of zooplankters were found than in summer, with a reduction from nine to four (Fig. 4D). Fish and crustacean eggs were also markedly reduced in numbers, from a summer high of 4,625/100 m^3 and 2,721/100 m^3, respectively, to less than 100/100 m^3. As in the preceding seasons, copepods were the dominant zooplankters in all areas, with the greatest number

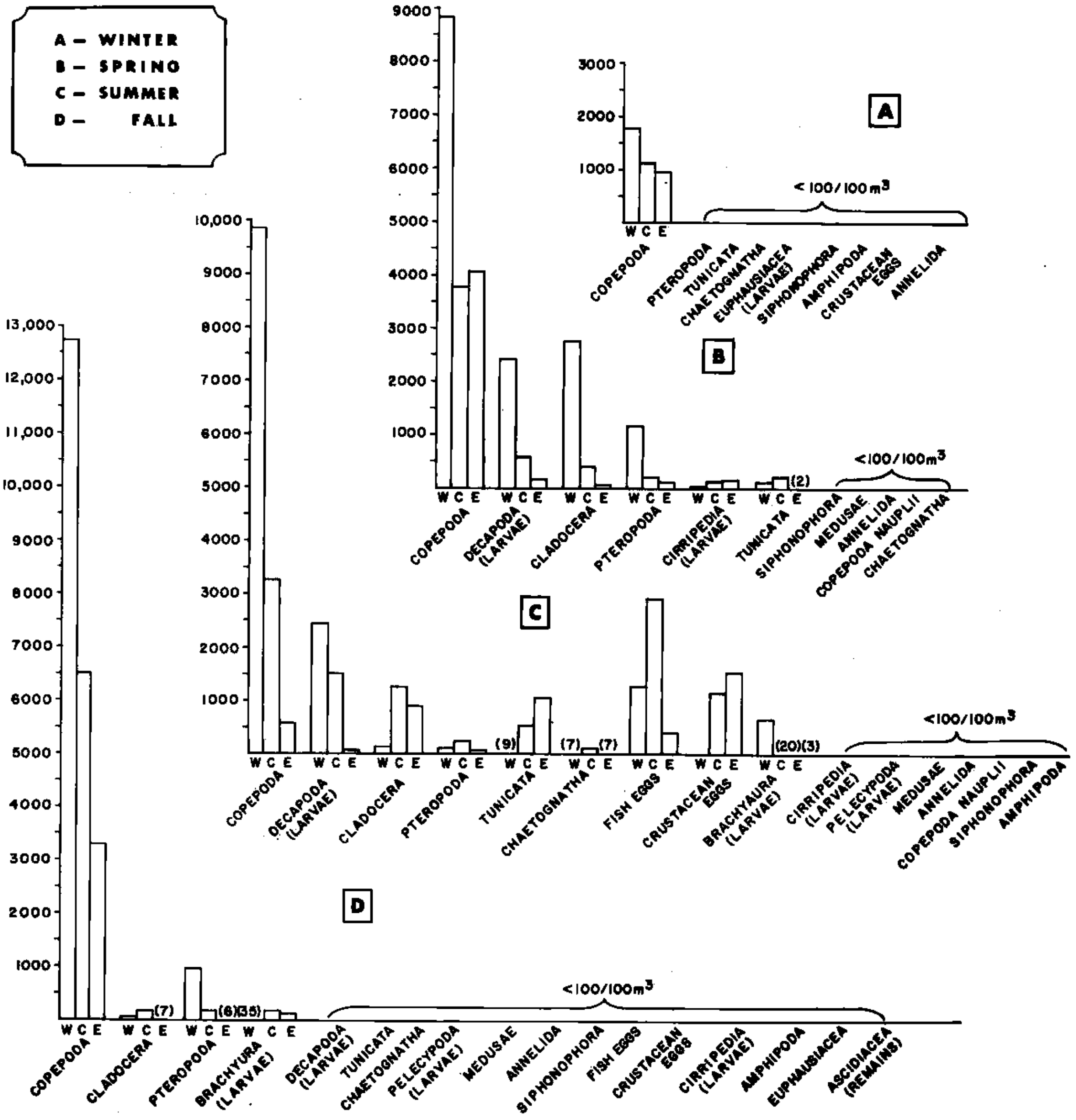

Fig. 4. Bar graph represents the mean number per 100 m^3 of water strained of the dominant zooplankton groups present in each of the three areas-west, central and east-during winter, spring, summer and fall.

(12,744/100 m^3) occurring in the western sector. Other groups more numerous in the western than in the eastern area were cladocera and pteropods. Of the four major groups, only one, brachyuran larvae, was more numerous in the central area. The low abundance of fish eggs, crustacean eggs, and larvae of other groups, indicated that the widespread breeding, characteristic of the summer period, was over and that the zooplankton population was approaching the winter minimum.

Copepod Species Occurrence

Copepods were the dominant zooplankters during all seasons. Species encountered are listed in Table 2. They have been arranged into two groupings; the common forms, those species exceeding

TABLE 2. COPEPOD SPECIES ENCOUNTERED DURING THE 1963 ZOOPLANKTON SAMPLING.

	Mean number/100 m^3	
	Common species >50/100 m^3	Less numerous species <50/100 m^3
Acartia longiremis (Lilljeborg)	204	
Calanus finmarchicus (Gunnerus)	1446	
Centropages typicus Kroyer	2308	
Metridia lucens Boeck	411	
Oithona similis Claus	141	
Pseudocalanus minutus (Kroyer)	398	
Temora longicornis (Muller)	160	
Tortanus discaudatus (Thomson and Scott)	76	
Acartia clausi Giesbrecht		3.17
Aetidius armatus Boeck		0.197
Calanus hyperboreas Kroyer		0.70
Candacia armata (Boeck)		3.21
Centropages hamatus (Lilljeborg)		0.704
Euchaeta norvegica Boeck		0.845
Eurytemora sp.		2.51
Oithona plumifera Baird		0.113
Oithona spinirostris Claus		23.00
Pleuromamma robusta (Dahl)		0.028
Pleuromamma xiphias Giesbrecht		0.028
Rhincalanus nasutus Giesbrecht		0.098
Scolecithricella minor Brady		0.042

a mean value of 50/100 m^3 for all cruises, and the less numerous species, with a mean value of <50/100 m^3 for all cruises. Of the eight common species, *Centropages typicus* was the dominant copepod, followed by *Calanus finmarchicus*, *Metridia lucens*, *Pseudocalanus minutus*, *Acartia longiremis*, *Temora longicornis*, *Oithona similis* and *Tortanus discaudatus* (Fig. 5).

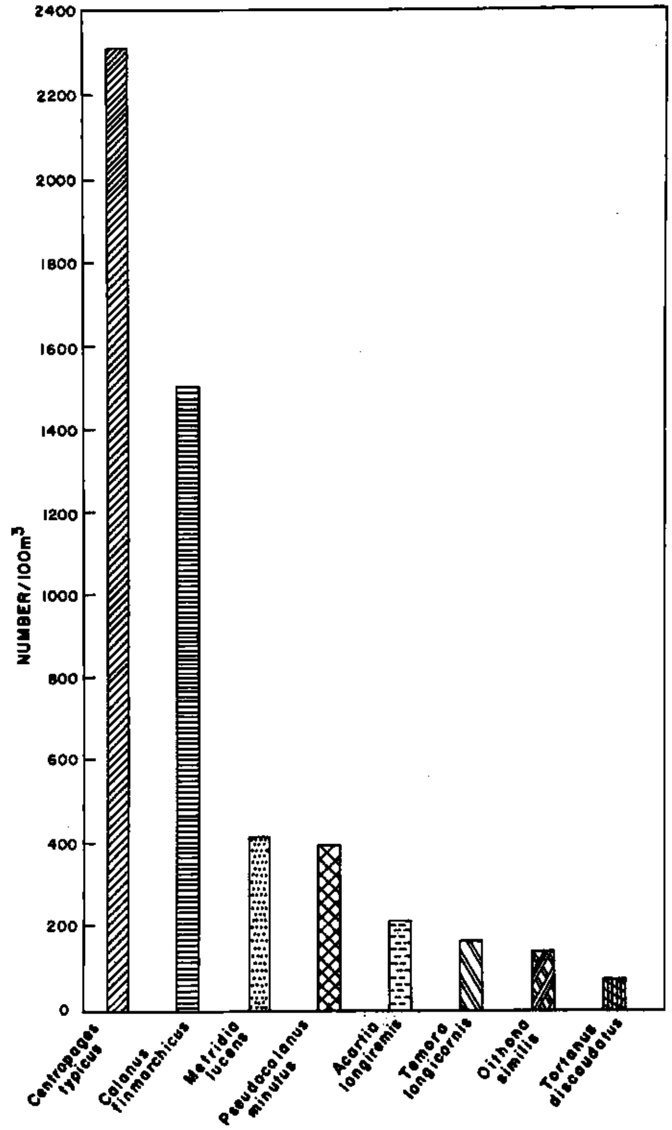

Fig. 5. Bar graph represents the mean number per 100 m^3 of water strained of eight commonly occurring copepod species during 1963.

Six of the eight commonly occurring species declined in abundance from west to east during all seasons (Fig. 6A to F). Differing patterns of occurrence were shown by two species, *C. finmarchicus*, and *P. minutus*, with the former species more abundant in the eastern area than in the western sector during spring and the latter reaching maximum numbers in the central area during summer (Fig. 6G and H).

Seasonal variability in species occurrence was observed among the eight common species. Five reached peak numbers in summer; *C. finmarchicus, M. lucens, O. similis, P. minutus* and *T. discaudatus*. Of the remaining three, *A. longiremis* was most numerous during spring, and *C. typicus* and *T. longicornis* reached peak numbers in the fall (Table 3).

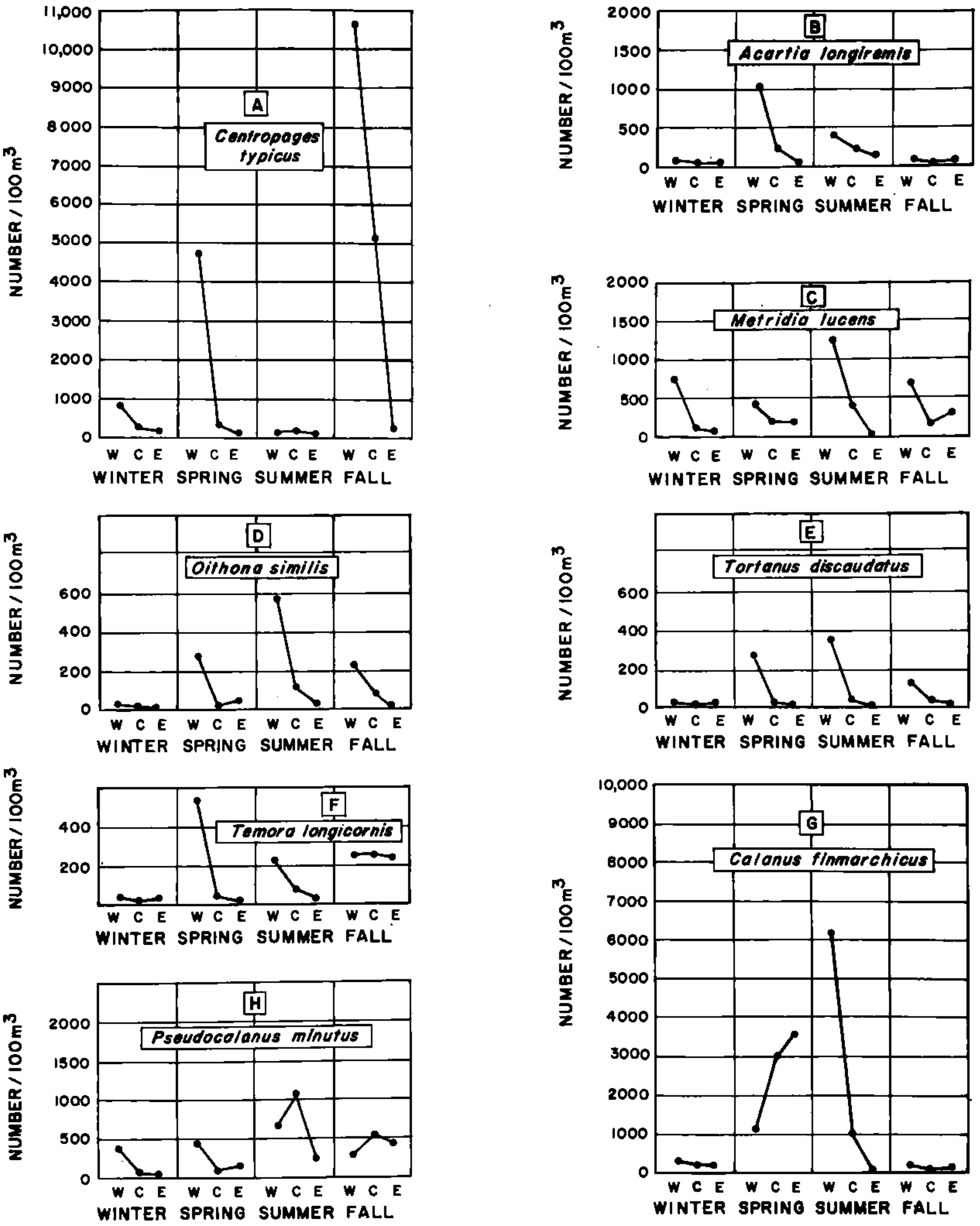

Fig. 6. The areal and seasonal variation in numbers per 100 m^3 of water strained of the eight commonly occurring copepod species.

TABLE 3. SEASONAL PERIODS OF MAXIMUM ABUNDANCE OF THE COMMONLY OCCURRING COPEPOD SPECIES.

Species	Winter 5-16 Jan.	Spring 25 May-2 June	Summer 10-22 July	Fall 11-20 Oct.
Acartia longiremis		0		
Calanus finmarchicus			0	
Centropages typicus				0
Metridia lucens			0	
Oithona similis			0	
Pseudocalanus minutus			0	
Temora longicornis				0
Tortanus discaudatus			0	

TABLE 4. SEASONAL AND AREAL OCCURRENCE OF THE LESS NUMEROUS COPEPOD SPECIES.

Species	Winter (+)			Spring (0)			Summer (X)			Fall (Ø)		
	west	central	east	west	central	east	west	central	east	west	central	east
Aetidius armatus	+											
Acartia clausi				0		0				Ø		
Calanus hyperboreas			+									
Candacia armata	+	+	+						X	Ø		
Centropages hamatus				0						Ø		
Euchaeta norvegica		+								Ø		
Eurytemora sp.				0			X	X	X	Ø		
Metridia longa											Ø	Ø
Oithona plumifera					0							
Oithona spinirostris	+	+			0	0			X	Ø		
Pleuromamma robusta						0						
Pleuromamma xiphias			+									
Rhincalanus nasutus			+									
Scolecithricella minor								X				

The less common species presented interesting patterns of occurrence (Table 4). Of the 14 species found, 8 occurred only during a single season. In winter 4 species, considered to be oceanic in origin, were found - *Aetidius armatus, Calanus hyperboreas, Pleuromamma xiphias*, and *Rhincalanus nasutus*. All but *A. armatus* occurred only in the eastern area. Other seasonally occurring species were: *Oithona plumifera*, and *Pleuromamma robusta*, present only during the spring, *Scolecithricella minor*, found in summer and *Metridia longa* present only in fall. Species occurring in more than a single season were: *Acartia clausi, Candacia armata, Centropages hamatus, Euchaeta norvegica, Eurytemora* sp. and *Oithona spinirostris*.

DISCUSSION

A comparison of mean displacement volumes for each of the areas and seasons revealed different patterns of abundance. The highest values for all seasons were found in the western area. The lowest values occurred in the eastern sector, and intermediate volumes in the central area. Based on data collected during the warmer months (April-October), Bigelow (1926), Fish and Johnson (1937) also found that the region west of Penobscot Bay was consistently higher in zooplankton volumes than the relatively "barren" area to the eastward, from Mt. Desert to the Bay of Fundy. The progression from a winter low to a summer high in the western area is also in agreement with Bigelow (1926); Fish and Johnson (1937) and Redfield (1941). In addition these authors have indicated a late summer reduction in volumes, followed by a short-lived fall increase. During 1963, this fall increase was not apparent in the western or central areas. However, a slight increase in zooplankton volumes occurred in the eastern area.

The seasonal variations of volumes in the central and eastern areas are not compatible with the findings of Bigelow (1926) or Fish and Johnson (1937). However, Redfield (1941) showed that the "Seguin" sector of the Gulf, an area comparable to the central area, had only moderate plankton volumes in summer which declined in fall, increased in winter, declined in spring and increased in summer. The present pattern of seasonal variability in volumes in the central area is in agreement with the description given by Redfield for 1933 data. The increase in volumes, however, from summer to fall of 1934, reported by Redfield (1941), indicated that annual variations can be expected in the central area. In the eastern area, the winter-spring increase in volumes although of a lesser magnitude than the western sector, is in agreement with previous reports. However, the summer decline observed in this region has not previously been reported. Future sampling is planned for this region to examine these results more closely.

Major zooplankton groups showed a seasonal variation both in numbers and areal distribution. Most of the groups were more numerous in the western sector than in the eastern. The most notable exceptions occurred during the summer period when six groups - cladocerans, pteropods, tunicates, chaetognaths, fish eggs and crustacean eggs - were more numerous in the central and eastern areas. The significance of this shift in areal distribution is not known. However, it was found that considerable breeding during the warmer months occurs in the northeastern sector of the Gulf of Maine eddy, as evidenced by the presence of large numbers of fish and crustacean eggs occurring in the central and eastern areas. The general southwesterly movement of surface waters in this eddy (Bigelow, 1926; Bumpus, 1960) may be one of the factors contributing to the concentration of zooplankton in the western area in the period succeeding the peak summer breeding.

Bigelow (1926): Fish and Johnson (1937) indicated that copepods were the most numerous and comprised the greatest volume of zooplankters occurring in Gulf of Maine waters. These investigators also found that volumes of zooplankton were consistently higher west of Penobscot Bay than east of this region. It would follow then, that most of the endemic copepod population would also decrease in abundance from west to east. Fish (1936 *a, c*) reported this decrease for the copepods *Calanus finmarchicus* and *Oithona similis* and noted two breeding stocks for each species - one located east of Penobscot Bay and the other, the principal breeding grounds, to the west.

The decrease in numbers from west to east of all but two species of the commonly occurring copepods found during the present study confirms the conclusions reached by earlier investigators. The apparent exceptions were the species, *Calanus finmarchicus* and *Pseudocalanus minutus*. In this regard, Fish (1936*a*) has shown that successive broods of *C. finmarchicus* produced in the western Gulf were transported initially to the outer Gulf and then to the inner reaches of the eastern and central areas by the upper waters of the Gulf of Maine eddy. These circulation features were thought to be the mechanism for transporting large numbers of *C. finmarchicus* to other areas of the Gulf from the principal western breeding area during spring and summer (Fish, 1936*a*). The large numbers of *C. finmarchicus* found in the eastern area during spring may have resulted from this type of current transport.

The large numbers of *Pseudocalanus minutus* found in the central area during summer is not entirely unexpected. Fish (1936*b*) reported the presence of three stocks of *P. minutus* for: 1) the outer Gulf, 2) the western coastal area, 3) the region east of Mt. Desert to the Bay of Fundy. He indicated that in early spring, the western brood became widely dispersed, and that in late summer, the larger part of the *P. minutus* population originated in waters of the outer Gulf. The presence of large numbers of *P. minutus* in the central area during late summer could have been related to the inshore movement of the Gulf of Maine eddy in this area during the late summer period. Copepod length frequency data could provide additional information regarding the origin of copepod populations and future effort will be directed toward providing this information.

Although occurring in relatively small numbers, immigrant zooplankton species have provided an insight into the origin and along-shore movements of the mixed waters of the Gulf of Maine eddy system (Bigelow, 1926; Fish and Johnson, 1937; Redfield, 1939, 1941; Colton, *et al.*, 1962). The presence of *Calanus hyperboreas*, *Pleuromamma xiphias*, and *Rhincalanus nasutus*, in the eastern area only during winter is in agreement with Redfield (1939, 1941), who reported the indraft of oceanic water from the Nova Scotian banks into the Gulf of Maine during winter.

In a discussion of the environmental characteristics of the Gulf of Maine, Bigelow (1927) concluded that the wide seasonal variations in temperatures of the Gulf are due to... "its geographic location to the leeward of the continent and to the vigorous land climate. Only in a much smaller degree is it influenced by warm or cold currents flowing into it". He further indicated that the wide seasonal variation in salinity characteristic of the Gulf is due to local conditions,..."the water freshening at the season of the spring freshet and then gradually salting again as this inrush of river water is incorporated by the mixings and churnings caused by the tides, winds, and waves". In this regard, it would appear that a great salinity influence on coastal waters would be exerted by the Penobscot Bay area.

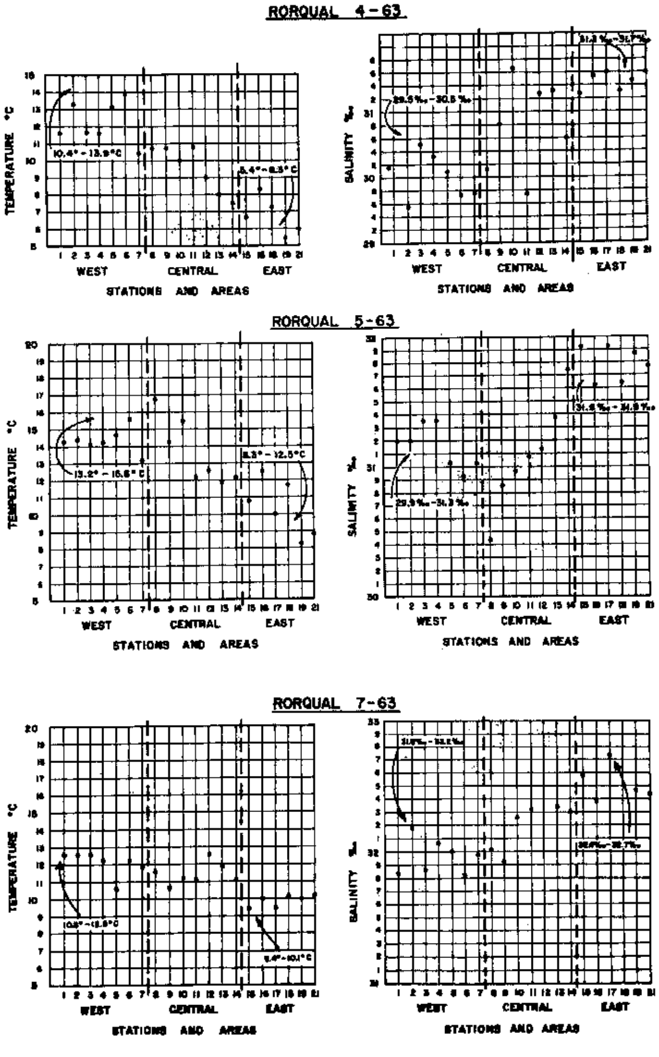

Fig. 7. Areal distribution of surface salinities and temperatures, *Rorqual* cruises 4, 5 and 7, 1963.

Surface temperatures and salinities plotted for spring, summer, and fall by areas (Fig. 7) suggest that the Penobscot Bay region represents a transition zone between surface waters of lower salinity and higher temperature ranges located in the western sector and higher salinity, cooler waters of the eastern area. Whether these environmental differences are the result of local conditions or advection cannot presently be determined, but will be subject to future investigation. In addition to hydrographic differences, faunal changes east and west of Penobscot Bay occur for: 1) mean length at age of immature herring, 2) erythrocyte antigen frequencies of two-year-old herring, 3) myxosporidian parasite infestation of young herring, 4) differential herring spawning as evidenced by length frequencies of larvae. The high zooplankton volumes, greater numbers of groups, and copepod species found in the western Gulf, when considered with the surface temperature and salinity differences, suggest that the Penobscot Bay region represents a faunistic boundary between eastern and western coastal biota.

REFERENCES

BIGELOW, H.B. 1926. Plankton of the offshore waters of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, 40 (2): 1-509.

1927. Physical oceanography of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, 40 (2): 511-1027.

BUMPUS, D.F. 1960. Sources of water contributed to the Bay of Fundy by surface circulation. *J. Fish. Res. Bd. Canada*, 17 (2): 181-197.

COLTON, J.B., R.F. TEMPLE and K.A. HONEY. 1962. The occurrence of oceanic copepods in the Gulf of Maine-Georges Bank area. *Ecology* 43 (1): 166-171.

FISH, C.J. 1936*a*. The biology of *Calanus finmarchicus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull., Woods Hole*, 70 (1): 118-141.

1936*b*. The biology of *Pseudocalanus minutus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull., Woods Hole*, 70 (2): 193-216.

1936*c*. The biology of *Oithona similis* in the Gulf of Maine and Bay of Fundy. *Biol. Bull., Woods Hole*, 71 (1): 168-187.

1955. Observations on the biology of *Microstella norvegica*. *Deep-Sea Res. Suppl.* 3: 242-249.

FISH, C.J., and M.W. JOHNSON. 1937. The biology of the zooplankton population in the Bay of Fundy and Gulf of Maine with special reference to production and distribution. *J. Biol. Bd. Canada*, 3 (3): 189-322.

GEHRINGER, J.W. 1962. The Gulf III and other modern high-speed plankton samplers. *Contrib. Symposium on Zoopl. Prod., Rapp. Cons. Explor. Mer*, 153: 19-22.

REDFIELD, A.C. 1939. The history of a population of *Limacina retroversa* during its drift across the Gulf of Maine. *Biol. Bull., Woods Hole*, 86 (1): 26-47.

1941. The effect of the circulation of water on the distribution of the calanoid community in the Gulf of Maine. *Biol. Bull., Woods Hole*, 80 (1): 86-110.

REDFIELD, A.C., and A. BEALE. 1940. Factors determining the distribution of populations of chaetognaths in the Gulf of Maine. *Biol. Bull., Woods Hole*, 79 (3): 459-487.

SIEGEL, S. 1956. *Nonparametric Statistics*. New York. McGraw-Hill Co., 312 p.

SINDERMANN, C.J. 1961. Parasite tags for marine fish. *J. Wildlife Mgmt.*, 25 (1): 41-47.

1962. Serology of Atlantic clupeoid fishes. *Amer. Nat.* 96 (889): 225-231.

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ICNAF ENVIRONMENTAL SYMPOSIUM

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SECTION I.

INTRODUCTION

Dr C.E. Lucas

It was Dr Lionel A. Walford who, while Chairman of the Research and Statistics Committee, first suggested that ICNAF should hold a Symposium concerning the effects of the environment on the fisheries in its area, but it was not until March 1961 that a working party met at the Marine Laboratory in Aberdeen, with the specific task of advising the Commission on environmental matters.

In particular, the Commission requested advice on

(a) the effects of the environment on the survival of the eggs and larvae, growth, long-term abundance and distribution of cod in particular, but also of redfish and haddock;

(b) how studies of such matters might be directed so as not only to provide evidence of associations and correlations but also to lead to prediction;

(c) what fundamental studies requisite for such investigations and not already proceeding should be initiated;

(d) how plans could best be laid for holding an Environmental Symposium.

In order to prepare for their task, summaries of information already available to scientists working under the Commission were drawn up, and these at once revealed that, while there was an abundance of salinity and temperature data for the area, there was a relative scarcity of biological data and a greater scarcity of other physical and chemical data. Since that time, as the Symposium has shown, there has been some improvement, although this is still largely true, as is shown by the fact that, out of seventeen contributions concerning the effects of physical factors, fourteen were directed to evidence from temperatures.

It was in the light of such information that the Working Party recommended, and the Commission subsequently adopted, a general programme of environmental studies (ICNAF Redbook 1961: pp. 69-86), to include experimental and physiological investigations, and prepared a programme for a Symposium divided into eight sections, each concerning a specific aspect of fisheries environmental problems (p. 5). Of the former, it is possible to say now that several aspects of the environmental programme are in progress, in particular the first multi-ship survey of a considerable area of ICNAF waters has been completed under the leadership of Mr A.J. Lee, and reports on it are being prepared.

Only one significant change was made in the original programme for the Symposium, arising from the recently developed offshore fishery for herring in the southern part of the ICNAF area, as a result of which it was decided to provide an additional section, concerning the environmental aspects of the life of the herring in the North West Atlantic. A very important point, however, was the recognition that, while the Commission is responsible for a strictly prescribed area, neither the fish nor their environment are so restricted. Stocks of both cod and redfish, for example, extend almost continuously from the southern part of the area to the north, through Icelandic waters and across to the Barents Sea and Spitsbergen; other species also have wide distributions and the Commission resolved to request the assistance of scientists of the ICES area, in subscribing to a Symposium which in fact would be focussed on the principal groundfish of the North Atlantic area. Work done in the North Sea and other marginal seas was to be excluded, as also pelagic fish in general, but, although the objectives of the Symposium were to be limited in this way, it was also recognised that environmental aspects of research on other marine species might be very relevant, so that four special lecturers were invited to provide (a) an up to date account of the hydrography of the North Atlantic area and (b) reviews of environmental studies in relation to the Pacific tuna and sardine fisheries and the Atlantic herring fisheries. Moreover, although the special lectures were to be delivered in full during the Symposium, arrangements were made for all the other contributions to be written and circulated in advance, so that only brief accounts of them need be provided at the meeting, and the bulk of the time available could be given to discussion.

Reference should be made here to the arrangement to hold the Symposium in the FAO Building in Rome, for which ICNAF and the organisers are greatly indebted to the courtesy and hospitality of the Director General, Dr Sen, and his staff in Fisheries Division. This kind gesture not only solved an urgent problem, but provided a sense of occasion for the whole meeting. A sad feature was the inability at the last minute of the USSR representatives to attend the Symposium. The valuable contribution they would have made to the discussions was greatly missed. One consequence was that the organizers were greatly indebted to Mr B.B. Parrish for taking over Dr Ju Ju Marty's responsibilities at very short notice and for reporting on the proceedings of his Section G.

Most of the special lectures and contributions, in somewhat reduced form, are available for all to see in this volume, together with the reports of the Section Conveners. References are given to the few contributions which are being published elsewhere. It remains here to give some general impressions of what was undoubtedly a most interesting and valuable symposium, and to express my personal appreciation of the efforts not only of the special lecturers and contributors but of the Secretariat of ICNAF and all those who helped in various ways to prepare for and to organise the Symposium itself. Examples of the interest it attracted are the facts that some ninety contributions were received and that some seventy scientists attended from twelve countries, several from outside the North Atlantic area. An idea of the progress made in the last few years may be obtained by comparing this with a somewhat similar Symposium organized by ICES in 1951, which attracted only one "physiological" paper, whereas in 1964 it was possible to devote a whole session to experimental and physiological studies (although there was a general feeling that such work needed to be intensified considerably). It may also be fair to suggest that some of the lessons of that 1951 Symposium have still to be fully digested!

What then came out of the Symposium, apart from the special lectures and numerous contributions of which this volume is a permanent record - of facts and suggested correlations, hypotheses and ideas, and new growing points? Among other things, it attracted from the archives masses of data which might otherwise have taken long to see the light of day! It led to valuable discussions of present problems and future needs. If one has to select one most prominent problem, it concerns those correlations and associations suggested as illustrating relationships between different aspects of life in the sea, both in this Symposium and elsewhere. From one point of view, one of the chief objectives of the "environmentalists" has been to provide evidence for associations between two or more variables. In environmental studies, one is never concerned simply with any single factor, but always with its possible relationships to the fish and the fisheries themselves, and the usual approach is through the use of correlation analysis. But the elementary assumption that such a simple relationship exists in an inherently complex ecological system is all too often fraught with danger. It is a disturbing thought that we must immediately be dissatisfied with a "very good" correlation in such circumstances, if only because it is so unlikely that life in the sea is as simple as that, particularly when, as so often, the correlates may be separated by several ecological levels, as between the groundfish and the plankton, for example. Here and elsewhere there is the great danger of fallacious, or over-simplified, associations - and in several sections the dangers of this approach were apparent, particularly when trying to provide causal interpretations which might be used for prediction.

This is not to say that correlations should not be looked for and studied, but they require the greatest care in sampling and analytical techniques, and they require either the passage of time for their testing or the application of specific experiments to investigate the basis of the correlations. And even when the raw data are themselves sufficiently reliable, as, for example, series of temperature data with associated data concerning the abundance of organisms, say fish, there is always the snare that in fact the organism may not be responding in any direct manner to temperature, but that the association may in fact be with some other factor, itself associated with temperature. Also, simple temperature associations may themselves be modified by, say, food associations, or change markedly with season. Oceanographic parameters prescribe the containment of fish populations but nearly always we require much more basic knowledge of the ecology and dynamics of both the fish populations and the organisms with which they are associated. To just what factors are the organisms reacting? So often we know too little and there is the greatest need for more detail and more precise experiment and physiological study.

For all that, and particularly where reliable data can be obtained, we do need long series of records, such as temperature records, for associating with fishery data, either directly or through other variables in the ecological pyramid. Although no formal resolutions were passed in this Symposium (these were left for the Environmental Sub-Committee to consider)[1], it was widely recognised that one ultimate aim must still be to draw on past data so as to be able to predict future events, and that the effects of long-term climatic trends could be most important. Thus it was

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[1] See "Redbook" 1964, Part I: pp. 46-49.

particularly valuable to have comparisons of hydrographical events in the eastern Atlantic with those in the west, sometimes similar and sometimes otherwise. Such changes in environmental characteristics are far from simple, however, and they are best studied from long series of systematic data (such as some we have now which should be continued and indeed extended, perhaps particularly through the use of instrumented oceanographic buoys). But we urgently need to understand more of the motivation of these changes, the processes underlying them and perhaps particularly of their links with meteorological events, air-sea interface relationships, which themselves are of direct interest to fishermen, as some papers ably showed.

Turning now to experimental and physiological studies, despite the progress made during the last ten years, it was some of those who had helped to make this progress who were most conscious of the need for much more detailed knowledge than we have at present of fish physiology and behaviour, and particularly of the sensory channels and the hormone systems that regulate behaviour. How do fish and their larvae react to currents, for example, and how to changing light intensity? Data collection alone is inadequate for the understanding which is essential. Just as a knowledge of the processes determining vital changes in the oceans is essential, so we have to acquire more understanding of the organisms' reactions to such physical changes, and their rates of change, and of course to each other. While much of this work can and must be done in the laboratory, or on shore in relatively large tanks, much can only be usefully undertaken at sea, sometimes by the study of conditions and life within quite small areas: or within small populations where detailed observations can be made of the fish and the several aspects of their environment at the same time, such as has been suggested by the Herring Committee of ICES for the elucidation of key herring problems.

In fishery research one is, of course, concerned sooner or later with all levels of the ecological pyramid, and in the life of the fish itself there is always the question as to which stages in its life history are the most susceptible to environmental changes and on which to concentrate most productively. Apart from the obvious relevance of the adult stage, most attention so far has been devoted to egg and larval studies but, not for the first time, the question was raised in these meetings whether (a) the resources so far given have been adequate to provide significant results, and (b) in some instances at least, year-class strength and recruitment might not be determined more by mortalities at a rather later stage than those usually examined. In making these points, those concerned were seldom trying to suggest that the relationships existing between larval densities and fish stocks were irrelevant, but rather to ensure that henceforth investigations at this level should be intensive enough to support the conclusions that might be drawn from them, and also to ensure that too facile assumptions were not made that adult numbers depend, or do not depend, substantially on success during critical egg and larval phases. Many more, and more intensive, egg and larval surveys will undoubtedly be needed, but it is becoming evident that much more attention must be paid to the adolescent stages in the life of the fish which follow the first year of its life, and that mortalities should be followed through these as well as in the earliest stages.

Thus, in another context, the meeting was faced again with the need for intensive as well as extensive studies, and reference was naturally made to the ICNAF Environmental Survey, on which some communications were based, and Mr Lee briefly reported, during the final discussion. In many respects, despite unusual natural difficulties, it had been surprisingly successful - and had certainly shown how by international co-operation a large area can be covered several times in fair detail. Yet 1963 scarcely seemed to have been a "typical" year! Good egg production was followed by very sparse distribution of larvae, both of cod and redfish. Although the three surveys were made, the key to the critical point of larval failure may be missing. There was at once keen appreciation of the great efforts made and widely expressed views that at least one more set of surveys must be made (a) to examine conditions in another and possibly more "typical" year and (b) to do this, through international co-operation, in even greater detail.[2] For some purposes, of course, greater detail in certain parts only of the work may suffice.

It is scarcely necessary to add that once again the question was raised as to the information needed by the biologist from the hydrographer to solve his problem, and experience is showing more and more that the essential thing is for hydrographers and biologists - and members of other disciplines - to work together on these problems. This was stressed in the ICES Symposium on "Fisheries Hydrography" in 1951 by Professor Sverdrup, who said that hydrography "must take its place as an integral and indispensable part of the combined effort"! Paraphrasing Professor Sverdrup, the Chairman then said "It is the task of the biologist to demonstrate the reactions of the fish towards different types of environment. In the light of this knowledge the hydrographer should study the

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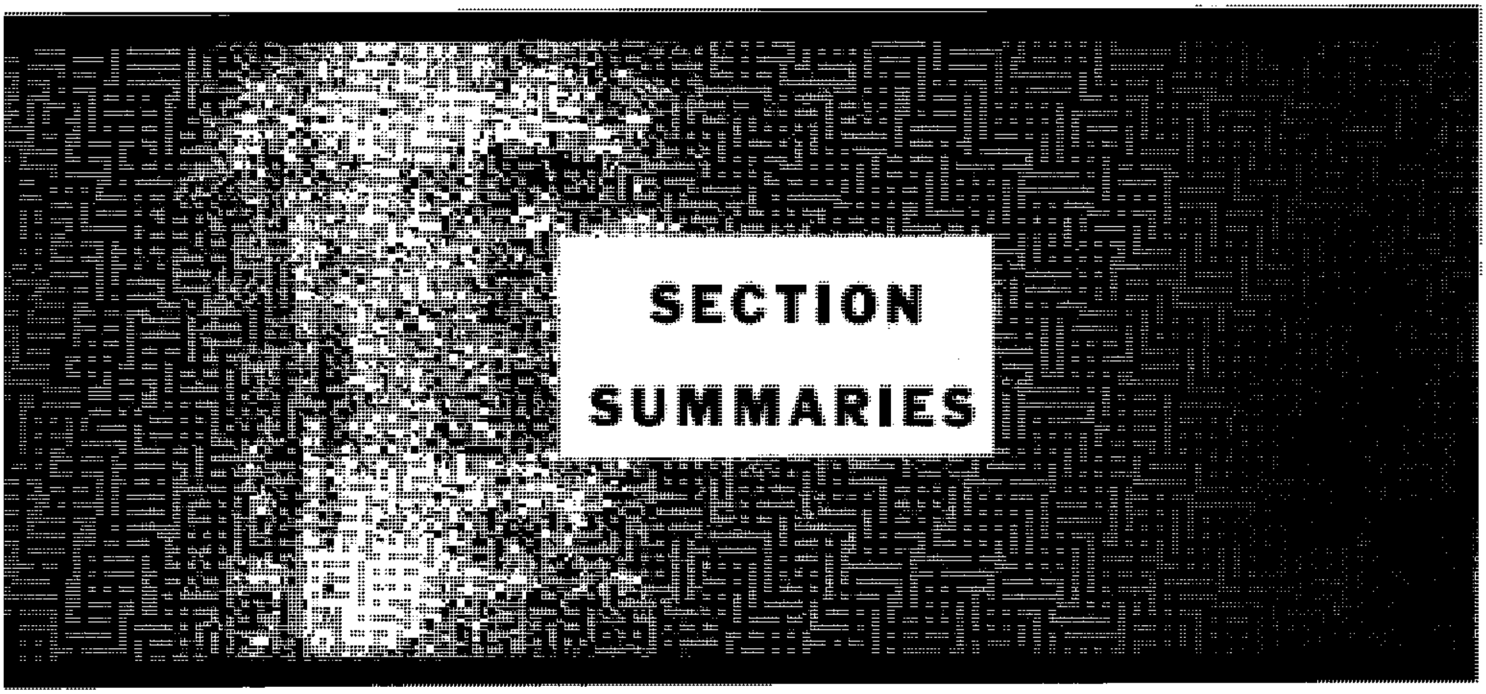
[2] See "Redbook" 1964, Part I: p. 49 and pp. 57-58.

processes by which the environment is changed, as well as its momentary condition, so as to be in a position to forecast hydrographic situations of fisheries significance". In particular he made a plea "for the hydrographer and the biologist to meet daily and to learn to write and speak so that each understands the other, as well as to disseminate their information speedily." This seems to apply as much today as it did then!

It also became clear that no longer can the "hydrographers" be content merely with measuring temperatures and salinities. In conjunction with their biological colleagues, they should also be measuring water movements, both large and small scale, and the nature and intensity of light at different times and places, and investigating their effects, along with more chemical aspects of the environment.

It might seem almost equally unnecessary to add that biologists and hydrographers, and others, must plan carefully so as to have a reasonable chance of securing the information that is seen to be needed. Yet not only are resources often inadequate enough for this, but often workers are almost too easily satisfied with what is available without the extra effort which alone can promise results. The sea is vast, and the fish roam widely in it. If our work is to be successful, then we have to plan for an ingenious and economical mixture of extensive investigations for certain purposes and intensive - indeed, intimate - investigations to provide the understanding of the processes, biological as well as physical, which govern events over the wider areas: and often the second of these must be tackled first! Indeed, as one of my colleagues expressed it, perhaps the greatest value of the Symposium was that it provided a valuable "confrontation" on several aspects of fisheries research. These and many other matters arising should give food for thought to environmental workers and fishery research generally for some time to come.



SECTION SUMMARIES

SECTION SUMMARIES

SECTION A

Effect of Physical Environmental Conditions on the Distribution of Adult Fish (*i.e.* Immediate and Seasonal Effects)

CONVENER: A.J. Lee RAPPORTEUR: J. Corlett

Contributions submitted to this Section were as follows (parentheses indicate original contribution number):

A-7 (A-1) "About Possible Fishing/Temperature of Water Relationship" by O. Cendrero

A-16 (A-2) "Interpretation of Fish Distribution in Respect to Currents in the Light of Available Laboratory and Field Observations" by T. Laevastu

A-10 (A-3) "Influence of Cold Water on Fish and Prawn Stocks" by Sv. Aa. Horsted and Erik Smidt

A-4 (A-4) "Cod and Low Temperature in St. Mary's Bay, Newfoundland" by W. Templeman and A.M. Fleming

A-5 (A-5) "Mass Mortalities of Marine Fishes in the Newfoundland Area Presumably Due to Low Temperature" by W. Templeman

A-8 (A-6) "Distribution of Haddock on the Grand Bank in Relation to Season, Depth and Temperature" by W. Templeman and V.M. Hodder

A-2 (A-7) "Seasonal Distribution of Cod (*Gadus morhua* L.) Along the Canadian Atlantic Coast in Relation to Water Temperature" by Yves Jean

A-3 (A-8) "Distribution of Haddock off the Eastern Canadian Mainland in Relation to Bottom Temperatures" by F.D. McCracken

A-11 (A-9) "Influence of the Temperature Regime Upon the Behaviour of Redfish off the West Greenland in Springs 1959-1961" by L.M. Pechenic and I.I. Svetlov

A-6 (A-10) "Research Vessel Catches of Cod in the Hamilton Inlet Bank Area in Relation to Depth and Temperature" by W. Templeman and A.W. May

A-15 (A-11) "Data on the Distribution of Tuna Fish Concentrations During the Feeding Period in Some Areas of the Atlantic Ocean" by V.L. Zharov

A-14 (A-12) "The Influence of Hydrographic and other Factors on the Distribution of Cod on the Spitsbergen Shelf" by R.J.H. Beverton and A.J. Lee

A-9 (A-13) "Distribution of Haddock on St. Pierre Bank (ICNAF Division 3Ps) by Season, Depth and Temperature" by W. Templeman and A.W. May

A-13 (A-14) "The Water Temperature as a Factor Guiding Fishes During their Migrations" by K.G. Konstantinov

A-18 (A-15) "Effects of Light upon Behaviour and Distribution of Demersal Fishes of the North Atlantic" by P.M.J. Woodhead

A-1 (A-16) "Relation of Temperature to Fish Abundance and Distribution in the Southern New England Area" by R.L. Edwards

SECTION B
Effect of the Environment on Pelagic and Early Demersal Stages of Groundfish

CONVENER: R.S. Glover RAPPORTEUR: J.M. Colebrook

Contributions submitted to this Section were as follows:

B-1 "The Relationship Between the Distribution of *Sebastes* Larvae, Zooplankton and Temperature in the Irminger Sea" by J. Magnusson and I. Hallgrimsson

B-2 "The Analysis of Variation in the Plankton, the Environment and the Fisheries" by J.M. Colebrook

B-3 "A Preliminary Study of *Sebastes* Larvae in Relation to the Planktonic Environment of the Irminger Sea" by V. Bainbridge

B-4 "Redfish Larvae in the North Atlantic" by G.T.D. Henderson

B-5 "The Distribution and Behaviour of Pelagic and Early Demersal Stages of Haddock in Relation to Sampling Techniques" by John B. Colton, Jr.

B-6 "Factors Controlling Dispersal of the Pelagic Stages of Fish and their Influence on Survival" by A. Saville

B-7 "Comparative Characteristic of Some Biological Indices of the Bottom Stages of 0-Group Cod Belonging to the 1956, 1958, 1959, 1960 and 1961 Year-Classes" by I. Ja. Ponomarenko

B-8 "Drift Migrations and their Significance to the Biology of Food Fishes of the North Atlantic" by Ju. Ju. Marty

B-9 "Survival of the Youngest Stages of Fish and its Relation to Year-Class Strength" by J.A. Gulland

B-10 " Winds, Currents, Plankton and the Year-Class Strength of Cod in the Western Barents Sea" by J. Corlett

B-11 "On the Life-Cycle Pattern of Labrador Cod" by A.I. Postolaky

B-12 "Changes in the Recruitment to the Stock With Reference to the Environment and Mathematical Modelling with Notes to Changes" by T.F. Dementjeva

B-13 "On Primary Food Supply - the Base of Productivity in the Northwest Atlantic" by M.V. Fedosov and I.A. Ermachenko

B-14 "The Effect of Temperature and Current on the Distribution and Survival of Cod Larvae at West Greenland" by F. Hermann, P.M. Hansen and Sv. Aa. Horsted

B-15 "Notes on the Condition of Formation of the Arcto-Norwegian Tribe of Cod of the 1959-1961 Year-Classes During the First Year of Life" by A.S. Baranenkova

B-16 "The Relation Between the Feeding of Cod Larvae and Pelagic Fry and the Distribution and Abundance of their Principal Food Organisms" by T.K. Syssoyeva and A.A. Degtereva

B-17 "Dependency of Redfish Breeding and Larval Redfish Distribution on Water Temperature" by A. Kotthaus

B-18 "Some Results of Soviet Research Work on Ichthyoplankton in the Northwest Atlantic" by V.P. Serebryakov

Fluctuations in the fisheries are the result partly of migration, disease, predation and changes in the availability of the stock to capture but the greatest source of uncertainty about the yield is the variability of year-class strengths. This point was emphasized throughout the papers and during the discussion and it was clear that variations in the strength of a year-class must have their origins at some time before the fish enter the commercial fishery.

Such variations could result from changes in the numbers or mortality of eggs, through predation, developmental, metabolic or density dependent effects. Most of the authors and participants, however, thought it more likely that fluctuations in the strength of a year-class may arise during the planktonic or later phases of the development of the fish as the result of mortality or emigration. Gulland, in contribution B-9, draws hypothetical curves showing the sequence of phases of mortality: at first massive (and probably unrelated to year-class strength), then density dependent, followed by the critical phase when the year-class strength is determined.

There is adequate evidence of the dependence of larval fish on various aspects of their external environment. For example, the distribution and abundance of redfish larvae seem to be related to water temperature and the supply of their planktonic food (contributions B-1, B-3, B-4, and B-17). Russian work on the herring and anchovy shows that the abundance of larvae is dependent on the abundance of their food (B-12). Haddock larvae are found in the thermocline off the New England coast (B-5). The numbers of cod larvae off West Greenland are positively correlated with temperature (B-14). Some of the participants in the symposium discussed the effect of water currents on the drift and survival of larvae. For example, fluctuations in the abundance of haddock larvae at Faroe are related to the strength and direction of wind, presumably through its effect on water movements (B-6). In the same contribution, Saville provides a detailed analysis of wind, water movement and larval drift in the herring stocks of the Clyde. Predation of 0-group cod by older fish of the same species may be dependent on the growth rate and nutritional condition of the young fish (B-7).

There is less evidence of the dependence of year-class strength on the numbers of larvae although Gulland (B-9) quotes work which suggests that the abundance of plaice larvae in their later planktonic stages may be related to year-class strength and he gives indirect evidence of similar relationships in Lofoten cod, North Sea haddock and sock-eye salmon. Saville (B-6) shows that the abundance of haddock near the end of their planktonic phase near the Faroes was related to the numbers of one year old haddock which are a satisfactory index of subsequent recruitment to the fishery.

The analysis of such relationships must depend on adequate estimates of the distribution and abundance of the young stages. This information is difficult to obtain and has seldom been available in the detail and accuracy required. For this reason, fishery biologists have been compelled to study correlations between the parameters for which estimates are available; for example wind, temperature or planktonic food on the one hand, and the year-class strengths on the other. Saville (B-6) concludes that there is no relation between wind during the larval phase and subsequent year-classes of haddock in the North Sea or herring in the Clyde. Gulland (B-9), in a number of references to his own and other work, finds no relationship (or rather dubious ones) between wind, temperature or plankton and subsequent year-classes of Arcto-Norwegian cod. However, Corlett (B-10) using a different estimate of year-class strength, shows correlations between wind, dry weight of plankton and year-class strength of cod in the Barents Sea. Hermann, Hansen and Horsted (B-14) claim that drift of larvae is a major feature of the early life of West Greenland cod, but are unable to detect any relation between wind and brood strength. But they do find statistically significant correlations between temperature during the larval phase and the subsequent catch of 6-10 yr old fish.

It is not surprising that the results should be confusing and contradictory. In a hypothetical case, let us exclude food supply, predation, competition and metabolism, and assume that the size of a year-class is related to the numbers of larvae at some unknown stage of their life history and that these, in turn, are dependent on some unknown function of water movement which, in its turn, is partly a product of the bottom topography and the earth's rotation and partly under the influence of winds. In this very simple model, fishery biologists would often be able to test only the beginning and end of the chain (wind and year-class). Even without the added difficulty of detecting the relevant wind parameter and of deciding how to estimate the strength of a year-class, it would be surprising if a simple linear correlation co-efficient would be sufficiently sensitive to test the hypothesis. In the contributions and discussions the danger of fortuitous correlations was emphasized and, since each year yields only one pair of observations, research of this kind is likely to extend over a long period of years.

Some of the contributions drew attention to the importance of treating each population as a separate unit since growth, mortality and migration may differ in different patches of larvae. It was recognized that the numbers and distribution of larvae are dependent on a complex interaction of many factors. None of the physical and biological parameters of nature operates in isolation and it is a dangerous over-simplification to try to study them in isolation. The possibility of using multivariate methods to analyse the natural system as a whole is illustrated in contribution B-2, dealing with sources of variation in the plankton.

Repeatedly, in the discussion, it was emphasized that we lack the basic ecological and physiological knowledge which is essential for an adequate understanding of events in the fish stocks. Few of the papers mentioned other organisms in the community, except as food for fish. As Dr Ahlstrom's special lecture shows (p. 53-74), competition may be very important in determining the abundance of a commercial stock. It is notable that only one of the contributions (B-7) deals with 0-group fish. Fairly detailed statistics are available for the adults in fished stocks and there are modest collections of the planktonic stages but there is a most serious dearth of data about all the stages of the fish life cycle between the early larval stage and the entry of adults into the fishery.

One of the most successful developments in recent years has been the method of studying the population dynamics of adult fish in which mortality and growth rates are ascribed to different causes and built up into quantitative models of events in a population. A similar method has been used in studying plankton production by constructing a model of the major terms (such as photosynthesis, respiration and grazing) and inserting into the model as many as possible of the factors impinging on each of these (such as light, temperature, turbulence and nutrients).

It seems highly desirable that an attempt should be made to bring together these two levels of model-making, based on an adequate understanding of the whole system of interacting variables of which fish form a part. Steele (C-4) has made a tentative start in this direction with a model of the energy chain from photosynthesis to commercial fisheries.

Objectives of this kind will only be achieved if much greater facilities are available than in the past both for collections at sea and experiments in the laboratory. Frequent and detailed surveys will be needed to detect the critical events which determine larval mortality and year-class strength. But if such surveys are to be successful, it will be necessary to develop improved methods for sampling the larvae and young stages (B-5).

We are still left in doubt about the precise critical phase; indeed Baranenkova (B-15) concludes that every year-class has its own period of maximum mortality. It would seem that a much greater effort must be directed towards an ecological study of the young stages. Knowledge of these pre-recruit stocks is essential in attempts to predict and control fisheries. The technical and intellectual problems are very testing and progress will be dependent on the integration of the skills of marine scientists of many kinds, and on co-operation between laboratories and nations.

SECTION C

Effect of the Biological Environment (including parasites) on the Distribution of Adult Fish

CONVENER: W. Templeman   RAPPORTEUR: A.W. May

Contributions submitted to this Section were as follows:

C-1 "Remarks on Effect of Food Animals on Cod Behaviour" by Sv. Aa. Horsted and Erik Smidt

C-2 "Food as a Factor or Indicator of Vertical Migrations of Cod in the Western Gulf of St. Lawrence" by Pierre Brunel

C-3 "Some Instances of Cod and Haddock Behaviour and Concentrations in the Newfoundland and Labrador Areas in Relation to Food" by W. Templeman

C-4 "Some Problems in the Study of Marine Resources" by J.H. Steele

C-5 "The Impact of the Environmental Factors on Survival of the Far Eastern Young Salmon During the Acclimatization of the Latter in the Northeast Part of the USSR" by E.L. Bakshtansky

C-6 "The Copepod Ectoparasite *Sphyrion lumpi* (Kroyer) in relation to Redfish (*Sebastes marinus* L.) in the Gulf of Maine" by G.F. Kelly and A.M. Barker

C-7 "Density-dependent Food Relationships with reference to New England Groundfish" by R.L. Wigley

Most of the papers of this section dealt with concentrations and behaviour of cod, haddock, and other groundfish due to food. It was apparent from these contributions (C-1, C-2, C-3, C-7) and from other contributions (A-6, A-10, A-11, A-12, E-2) that food can be a concentrating factor for commercial fish, allowing them to gather in large numbers within some part of a favourable temperature and depth range. These concentrations may be in different parts of the preferred temperature and depth range depending on the temperature and depth ranges of the food animals. It is evident that food can modify the temperature and depth preferences of fish and that such preferences can often be best explained in relation to food. The relationship of food to concentrations of commercial fishes should therefore be studied whenever catch and related temperature and depth data are being collected by research vessels.

In discussion Blaxter, with reference to cod becoming glutted with capelin and sinking to the bottom (C-3), wondered whether there was any connection between this behaviour and a report in the Underwater Naturalist of "sleeping" cod. Corlett raised the question of how long it takes cod to digest food. He noted that Brunel (C-2) quoted from Karpevitch and Bokoff that the time for digestion may vary from 5 to 6 days in the case of a fish meal and from 3 to 3 1/2 days for a *Gammarus* meal. Corlett's impression, from Barents sea cruises, was that digestion in cod was more rapid than this. Meyer, from personal observation, said that cod taken at mid-day in one of his cruises contained fresh capelin and those taken in the evening contained digested capelin. Templeman remarked that because of the fullness of cod stomachs in the Newfoundland area during the trap season digestion would take longer than this. Kohler said that cod kept in tanks digested a herring meal in 1 day but the cod were not glutted. Hempel said that plaice took 12-24 hr and saithe up to 3 days to clear the stomach, the time depending on stomach fullness and water temperature. Magnusson remarked that feeding of redfish in several areas occurred at well defined periods, thus the stomach would probably be cleared between these periods. Horsted noted that there were 2 daily periods of cod activity in Greenland in late summer and autumn. Food (plankton and capelin) taken in the morning period was all gone by evening. Edwards said that for 8 fish species investigated at Woods Hole there were clear-cut feeding periods, either once or twice a day. Indications from these, and from some observations at sea, were that the stomachs were cleared within 6 hr.

One paper (C-4) examined the energy dynamics of the related trophic levels from phytoplankton to commercial fish and concluded that a great deal of the information necessary to apply primary production and related plankton and benthos data to estimation of potential yield of commercial fish is lacking.

There was considerable discussion on the point raised by Beverton as to whether availability of food to adult fish is influenced by their own abundance. In comparing pre- and post-war plaice stocks in the North Sea (Steele) there was an increase in yield, but also an increase in growth rate after the war which is opposite to what is to be expected. It is necessary to distinguish between food as a controlling factor and food fluctuating independently of the fish (Beverton). The plaice food supply had evidently changed but this was not related to density of plaice. Plaice larvae and *Ammodytes* larvae compete for food and it is possible that *Ammodytes* may be "controlling" the plaice. The availability of food in relation to growth is likely to differ in different sizes of fish of the same species which use different sizes and kinds of food (Templeman). If large fish are greatly reduced in numbers the large food is not utilized. These kinds of food such as capelin, herring and launce may become more numerous and eat great numbers of the fry of the former predators such as the cod. If the smaller commercial fish are more numerous they are now competitors for food of a small size range and here density dependent effects may be more likely to occur. Flatfish in the Kattegat ate only 2% of the available bottom food and the large changes in stock size of Norwegian herring did not affect the growth rate (Hempel). These results indicate that other factors, rather than food supply are responsible for limitation of stock abundance.

Another contribution (C-6) described the distribution and abundance of *Sphyrion lumpi* in relation to redfish in the Gulf of Maine. In discussion it was noted that a well documented example of the effect of parasites on the distribution of adult fish is the great destruction and reduction in stock size of spring-spawning herring in the Gulf of St. Lawrence by at least 2 great epidemics caused by the fungus *Ichthyosporidium hoferi*. Lucas and Parrish mentioned that Kabata's work on haddock parasitized by *Lernaeocera* showed that condition factors, liver fat and red blood cell levels were lower in parasitized than in non-parasitized fish of the same length and age. Sundnes noted that the presence of *Lernaeocera* on Arcto-Norwegian cod has so far not been found to have any adverse effect on the parasitized individuals.

Yearly differences in success of survival of maturity of young Pacific pink and chum salmon, introduced into the Barents and White seas, were attributed (C-5), mainly to differences in predation by herring. These young salmon were also eaten by cod, saithe, sea trout and other fishes.

SECTION D
Effect of the Environment of the Growth, Survival and Age and Size at First Maturity

CONVENER: Paul Hansen RAPPORTEUR: A.C. Kohler

Contributions submitted to this Section were as follows:

D-1 "The Possible Effects of Temperature on the Fecundity of Grand Bank Haddock" by V.M. Hodder

D-2 "Relation of Periods of Successful Year-Classes of Haddock on the Grand Bank to Periods of Success of Year-Classes for Cod, Haddock and Herring in Areas to the North and East" by W. Templeman

D-3 " Changes in Growth, Feeding, and Density of Gulf of St. Lawrence Cod" by A.C. Kohler

D-4 "Temperature and Growth of Cod in Icelandic Waters" by J. Jonsson

D-5 "Some Problems of Zooplankton Production and the Problems of Fisheries" by W. Mankowski

D-6 "Cod Growth and Temperature in the Newfoundland Area" by A.W. May, A.T. Pinhorn, R. Wells and A.M. Fleming

D-7 "Possible Influence of Water Temperature on the Growth of West Greenland Cod" by F. Hermann and P.M. Hansen

D-8 "Relationship Between the Growth Rate and Density of Population of Haddock in the Barents Sea" by M.A. Sonina

D-9 "Changes in the Growth Rate of the Barents Sea Cod as Affected by the Environmental Factors" by T.F. Dementjeva and E.M. Mankevich

Of the eight contributions presented and discussed at the meeting, six dealt with growth (D-3, D-4, D-6, D-7, D-8 and D-9), one with the effect of the production of zooplankton on fatness of sprat and length of herring in the Baltic (D-5), and one with the relation of the occurrence of year-classes, in the stock of haddock on the Grand Bank, with year-classes of cod, haddock and herring in all regions in the North Atlantic (D-2).

The contributions concerning growth covered Newfoundland and the Gulf of St. Lawrence area, West Greenland, Iceland and the Barents Sea. In the contributions and in the discussion it was pointed out that many interrelated factors have influence on the growth, but that temperature is a primary one.

In one contribution (D-6) it was shown that in the Newfoundland-Labrador area water temperatures and growth of cod were very closely related. Laboratory experiments with cod from the Gulf of St. Lawrence area have shown a relation of growth to food consumption, and food consumption again was related to temperature (D-3).

Increases in growth rate could be related to special mortality of food organisms, as shown by Kohler, who described a case of epizootic in the herring stock in the area of St. Lawrence (D-3); this had the result that moribund herring became an easy prey for the cod.

It was shown in several contributions that abundance of food and higher temperatures produce good growth in different kinds of fish. In the Icelandic area it was shown that growth and water temperatures were positively correlated, so that in the warmer parts, the area west of Iceland, the growth was greater than in the colder areas north of Iceland, and in the still colder area east of Iceland where the growth was very slow (D-4).

Among other factors which have an influence on the growth of fish is the density of population. Some contributions suggested that it is the density of the combined stock of haddock in the Barents Sea (all age-groups), and not single rich year-classes, that cause changes in the growth (D-8). When a stock has been diminished, *e.g.* by strong fishing, the growth of the individuals increases.

It was shown in contribution D-5 that the production of zooplankton in the Baltic is strongly correlated with the growth of sprats and herring, and especially that the fat content increases strongly in years with good amounts of zooplankton.

In the discussion Corlett pointed out that fish having a fish diet rather than crustacean usually grew better: possibly because less energy is expended in gathering food and fish protein is more efficient than crustacean. Horsted also noted that, regarding differences in growth between species, slow-growing redfish eat mainly crustaceans while cod, which grow faster and larger, are fish eaters.

Contribution D-9 referred to Nikolsky's view that for each species there is an optimum temperature which is the most suitable for metabolism and provides the fastest growth; when the temperatures are above and below this optimum the growth decreases. In the discussion Beverton touched on this problem and referred to a contribution by Ursin incorporating temperature data in the Von Bertalanffy growth equation. Kohler added that recent laboratory experiments with cod growth at St. Andrews (N.B.) gave similar results.

Edwards noted the effects of water temperature on the growth of haddock in the Gulf of Maine which show an inverse relation to those being demonstrated for cod. This could be related either to distribution or to fact that haddock in this area may be living near the upper temperature limit mentioned by Beverton.

Temperature is selected for consideration as an environmental factor because it is very easy to measure, but it was pointed out that it was difficult to decide which temperature should be chosen as the relevant one. The ideal temperature would of course be the temperature of the water in which the fish live, but in most cases this will be impossible to measure. In the contributions surface temperatures have been used mainly.

In the discussion Blaxter questioned the use of the Van't Hoff relationship to compare lengths of fish at different temperatures (D-4), and also commented on the apparent anomalies regarding findings of improved growth of cod and L_∞ of the Bertalanffy equation at higher temperatures.

Colebrook commented on the possibility that techniques used for correlating temperature and growth might be invalid, but noted that, when a relationship appears in three widely separated areas, there is fairly strong evidence for its existence.

In referring to contribution D-6 Lee warned against assuming a simple relation between latitude and water temperature at fishing depths in the Northwest Atlantic. Isotherms often tend to run in a north-south rather than east-west direction, especially off Labrador.

SECTION E
Herring and the Environment in the ICNAF Area

CONVENER: B.E. Skud RAPPORTEUR: B.B. Parrish

Contributions submitted to this Section were as follows:

E-1 "Effect of Light on Movements of Herring in the Bay of Fundy" by S.N. Tibbo

E-2 "Distribution of Plankton and Summer Feeding of Herring in the Norwegian Sea and on Georges Bank" by E.A. Pavshtics

E-3 "Water Temperatures and the Herring Fishery of Magdalen Islands, Quebec" by L.M. Lauzier and S.N. Tibbo

E-4 "The Influence of Water Masses of the New England and Nova Scotia Shelf on the Formation of Commercial Concentrations of Herring" by V.A. Bryantsev

E-5 "Effects of Environment on Several Diseases of Herring from the Western North Atlantic" by Carl J. Sindermann

E-6 "Seasonal and Areal Distribution of Gulf of Maine Coastal Zooplankton, 1963" by Kenneth Sherman

E-7 "Ecology of Herring Larvae in the Coastal Waters of Maine" by Joseph J. Graham and Harold C. Boyar

E-8 "Distribution of Wintering Herring in the Southern Part of the Norwegian Sea According to Temperature Conditions" by L.R. Shmarina

The convener opened the section by outlining the planned schedule, which, following introductory remarks, was the presentation of contributed papers, a special discussion on Bay of Chaleur herring, and the general discussion.

The introductory remarks were directed toward a geographic orientation of herring distribution and fisheries in the Western North Atlantic. The major divisions within the known range from Greenland to Cape Hatteras were Newfoundland, Gulf of St. Lawrence, Nova Scotia, Gulf of Maine, Georges Bank, and the Middle Atlantic Bight. The major spawning areas and seasons were also discussed: spring spawning in Newfoundland, Gulf of St. Lawrence and Nova Scotia, and fall spawning in the Gulf of Maine and Nova Scotia.

The convener reviewed the types of fisheries practised in the ICNAF area and described the various gear utilized and the utilization of the landings. Total catch by country in the last two years was compared:

	1961	1962
Canada	80,000 metric tons	100,000 metric tons
USSR	70,000 " "	150,000 " "
USA	30,000 " "	85,000 " "
Total	180,000 " "	335,000 " "

The convener reviewed the past research efforts in the Western North Atlantic and outlined the results of the 1963 ICNAF meetings which concerned herring, and discussed the long-term needs of research on this species. The objectives of this section of the Symposium were then listed as follows:

1. To call attention to and discuss studies of the environment of herring in the ICNAF area.

2. Appraise recent environmental research on herring with the intent that areas of limited knowledge could be emphasized and that suggestions for programs to improve these deficiencies would be offered.

3. To stress specific problems of concern in the herring fisheries and to cite the relationship of the environment to these problems.

4. To compare the state of knowledge of herring biology in the ICNAF area with other herring fisheries of the world.

Following the presentation of Contributions E-1 to E-8, the convener called attention to those contributions in other sections of the Symposium which referred to herring. These were, according to subject:

HERRING AND THE PHYSICAL ENVIRONMENT
A-2 by T. Laevastu. "Interpretation of fish distribution in respect to currents in the light of available laboratory and field observations."
B-6 by A. Saville. "Factors controlling dispersal of the pelagic stages of fish and their influence on survival."
B-8 by Ju. Ju. Marty. "Drift migrations and their significance to the biology of food fishes of the North Atlantic."
B-9 by J. Gulland. "Survival of the youngest stages of fish, and its relation to year-class strength."
D-5 by W. Mankowski. "Some problems of zooplankton production and the problems of fisheries."
F-7 by T. Iles. "Factors determining or limiting the physiological reaction of herring to environmental changes."
H-3 by L. Lauzier. "Long-term temperature variations in the Scotian Shelf area."
H-8 by D. Bumpus and J. Chase. "Changes in the hydrography observed along the east coast of the United States."
H-9 by J. Tait and J. Martin. "Inferential biological effects of long-term hydrographical trends deduced from investigations in the Faroe-Shetland Channel."
I-1 by L. Lauzier. "Foreshadowing of surface temperatures at St. Andrews, N.B."
I-7 by J. Eggvin. "The possibility of forecasting oceanographic conditions in North-West European waters and their significance for fisheries."

PHYSIOLOGY AND BIOLOGY
F-1 by K. Kalle. "Oxygen dependence of vertical migration in shoaling fish."
F-2 by J. Blaxter. "Effect of change of light intensity on fish."
F-3 by F. Holliday. "The significance of environment/endocrine studies to the investigation and exploitation of fish stocks."
F-5 by G. Hempel. "Egg size and fecundity in relation to the environment."
F-8 by G. Sundnes. "Energy metabolism and migration of fish."
G-3 by H. Mohr. "Changes in the behaviour of fish due to environment and motivation and their influence on fishing."

INCIDENTAL REFERENCES TO HERRING
A-12 by R. Beverton and A. Lee. "The influence of hydrographic and other factors on the distribution of cod on the Spitsbergen Shelf."
C-5 by E. Bakshtansky. "The impact of the environmental factors on survival of the far eastern young salmon during the acclimatization of the latter in the north-east part of the USSR."
D-2 by W. Templeman. "Relation of periods of successful year-classes of haddock on the Grand Bank to periods of success of year-classes for cod, haddock and herring in areas to the north and east."
D-3 by A. Kohler. "Changes in growth, feeding, and density of Gulf of St. Lawrence cod."

The discussion period was then opened with a continuation of a topic first broached in Dr Hempel's section (F). The discussion concerned spring and fall spawning stocks in the Bay of Chaleur and was initiated by Dr Harden-Jones. Messrs. Skud, Parrish and Blaxter also participated and the validity of scale ratio and otolith nucleus as a method of indicating when a fish was spawned was discussed.

The general discussion of section contributions was then opened. (a) Blaxter drew attention to the differences in temperature preferences of herring in the Northwest and Northeast Atlantic as shown in contributions E-8 and E-3. In E-8, it is stated that spring spawning in the Norwegian Sea does not take place below about 3°C, but in E-3, spring spawning is quoted as taking place in the vicinity of Magdalen Islands at lower temperatures; good herring catches are even recorded there at -0.7°C. A somewhat parallel situation is observed with the cod, which appears to occur in colder water in the Northwest than in the Northeast Atlantic. Blaxter also asked whether there are any recorded instances of herring being found dead in cold water in the Northwest Atlantic. Templeman reported that some years ago, in May, herring had been observed floating, dead in Fortune Bay, but it could not, of course, be claimed that their death was necessarily due to the cold water. Herring are commonly found, in winter, in very cold water in bays, such as the Bay of Islands, off Newfoundland. These bays are completely covered with ice in winter, and the herring must spend a considerable part of this time in temperatures below 0°C.

Lauzier announced that the temperature of 2.1°C in the Magdalen Islands area should not be taken as a preferred temperature. In the middle of the season, the temperature is higher, at 5-6°C.

Holliday announced that herring larvae can live at super-cooled temperatures. (b) Parrish asked if large herring concentrations are ever found in the open sea to the south of Newfoundland (Grand Bank area) or in the area between Labrador and W. Greenland (Labrador Sea and Davis Strait).

Templeman replied that some trawl catches of up to several hundred herring have been taken on the southern Grand Bank. A few herring have also been caught by trawlers on St. Pierre Bank. However, no large catches have been reported from these Banks, and herring have not been recorded in cod stomachs in this area. Further, there are no records of herring from the Hamilton Inlet Banks area, either in catches or fish stomachs. Herring are found in the inshore, Labrador area and formerly a good fishery for large, fat herring took place off southern Labrador, mainly from late summer to autumn.

Hansen announced that herring also occur off W. Greenland, from the Southwest coast northwards to the Arctic Circle. The herring are usually very large fish, up to 45 cm in length. Some tagging experiments have been carried out on these herring, but the recaptures have been taken near to the tagging locality. Herring larvae have been caught in Southern Greenland waters, and fishermen report that there are herring in the open sea waters of the Davis Straits.

Lucas drew attention to the usefulness of predatory fish as samplers of prey species such as herring. Fish stomach analyses should be carried out in these areas.

Convener. There is no evidence of herring in Hudson Bay, but concentrations of *C. pallasii* occur around the north of Alaska.

Glover said that there were no records of herring larvae in the Hardy Plankton Recorder material from Ireland to Newfoundland.

(c) Bumpus questioned whether Labrador water was present in the Gulf of Maine to the extent indicated by Bryantsev in Contribution E-4. Insufficient Labrador water rounds Avalon Peninsula or the Tail of the Grand Bank for this to be possible. The water in the Gulf of Maine is a complex mixture of slope and coastal water, with minor contributions from the Scotian Shelf, with considerable Laurentian characteristics. The location of the herring concentrations concurs with the divergence of the cyclonic Gulf of Maine gyre and the anti-cyclonic Georges Bank eddy, and the retreat to the westward as the season progresses coincides with the breakdown and diffusion of these circulations.

Lauzier agreed with Bumpus' comments and pointed out that the Gulf of Maine water masses should be defined as a mixture of 5 water types and not 3, as Bryantsev has done. He further announced that while the relationship between herring catches and wind seems to be good during late winter and early spring, he would not expect it to be so in other seasons when thermal stratification is greater than in the winter.

(d) Dr Uda commented on the large long-term fluctuations in the Japanese herring and sardine fisheries in the Pacific. These appear to correspond with fluctuations and trends in warming and cooling of the waters in the area. In the cold regions, water transport is lower than in the warmer ones. The records indicate that with warming in the northern Pacific, the herring fishing grounds shift further to the north.

(e) Convener. Is there any evidence that herring change their spawning grounds? There is no evidence that the extensive spawning on Georges Bank was in existence 50 yr ago, whereas there was evidence of inshore spawning which is now very limited.

Templeman announced that in the Newfoundland area, spring herring spawn in late May-early June in shallow water (the milt patches can be easily seen) while autumn spawners spawn in considerably deeper water. It is possible that there is more continuity between spring and autumn spawning than we have observed. For example, Capelin on the east coast of Newfoundland begin spawning in very shallow water (on the beach); spawning then continues throughout July and August, extending gradually into deeper water as the inshore water warms up, until in August they may spawn down to 20-25 fathoms or deeper.

(f) Blaxter asked if, as a result of the southerly drift of larvae from Georges Bank, a substantial part of the larvae population is lost to the area? Edwards thought that they would not be lost in the Gulf Stream, but would be held in the Southwest drift, and so perhaps not lost to the Georges Bank stock.

Convener announced that Colton's observations on the drift of haddock spawning products from the Bank were very pertinent to this question; he also announced that investigations on the larvae of Pacific herring had concluded that larvae are probably lost to the population whenever they move outside the coastal zone.

The section was then closed and was briefly summarized later by the convener. He concluded that some of his objectives were optimistic, but that several areas of limited knowledge were emphasized and existed in European waters as well as in the ICNAF area. Of particular concern in the western North Atlantic was the problem of stock identification, including the separation of spring and autumn spawners. The importance of temperature, water movement and plankton distribution in relation to herring abundance was emphasized. These are in general agreement with the research interest of the ICNAF herring scientists and are areas which are actively being studied.

The convener also cited the excellent presentation of Mr Parrish as a guest speaker. His talk compared the herring fisheries of the western and eastern North Atlantic in terms of production and ecological boundaries which govern the distribution of herring stocks.

SECTION F
Physiological Reactions to Changes in the Environment

CONVENER: G. Hempel RAPPORTEUR: J.H.S. Blaxter

Contributions submitted to this Section were as follows:

F-1 "Oxygen Dependence of Vertical Migration in Shoaling Fish" by K. Kalle

F-2 "Effect of Change of Light Intensity on Fish" by J.H.S. Blaxter

F-3 "The Significance of Environment/Endocrine Studies to the Investigation and Exploitation of Fish Stocks" by F.G.T. Holliday

F-4 "Effect of Abiotic Factors in Young Stages of Marine Fish" by K. Lillelund

F-5 "Egg Size and Fecundity in Relation to the Environment" by G. Hempel

F-6a "Seasonal Changes in the Physiology of the Cod in Relation to its Environment - I. Seasonal Changes in the Physiological Reactions of the Barents Sea Cod, *Gadus morhua* L., Particularly Affecting Migration and Maturation" by A.D. Woodhead and P.M.J. Woodhead

F-6b "Seasonal Changes in the Physiology of the Cod in relation to its Environment - II. Physiological Reactions of Cod, *Gadus morhua* L., to Low Temperatures" by P.M.J. Woodhead and A.D. Woodhead

F-7 "Factors Determining or Limiting the Physiological Reaction of Herring to Environmental Changes" by T.D. Iles

F-8 "Energy Metabolism and Migration of Fish" by Gunnar Sundnes

F-9 "Supercooling and Osmoregulation in Teleosts of the Subarctic and Arctic Region" by J. Leivestad

The papers were divided into five main topics:

1. The internal environment (endocrine systems) - Holliday (F-3),Woodhead and Woodhead (F-6A).
2. Reproduction - Hempel (F-5), Hodder (D-1), Iles (F-7), with additional reference to Steele (C-4), Bakshtansky (C-5), Mankowski (D-5) and Martin and Kohler (H-7).
3. Importance of light - Blaxter (F-2), Woodhead (A-15), with additional reference to Colton (B-5), Mohr (G-3) and Tibbo (E-1). A film by Shaw was also shown.
4. Tolerance to the environment - Lillelund (F-4), Kalle (F-1), Leivestad (F-9), Woodhead and Woodhead (F-6B), with additional reference to Cendrero (A-1), Horsted and Smidt (A-3), Templeman and Fleming (A-4), Jean (A-7), Templeman and May (A-10), Beverton and Lee (A-12), Postolaky (B-11), Serebryakov (B-18).
5. The "artificial" environment - Sundnes.

The purpose of this last section was to provide some background information on immediate and delayed responses of fish to changes in the physical properties of the sea. The classical approach to this problem is the experiment in the aquarium where all factors but one are kept constant (or are assumed to be constant). The limitations of this method have been stressed. Fish live in the aquarium in an unnatural environment which offers only a selected range of stimuli, and where it is almost impossible to control some variables (*e.g.* atmospheric pressure). The variable supposedly under consideration is often changed over a wider range than that found in natural conditions.

Other variables (*e.g.* the effect of weather on fish movement) have not been studied in isolation at all. In spite of those limitations the potential value of the aquarium approach cannot be gainsaid. Nevertheless, a general improvement in experimental techniques is desirable in order to detect the interaction and influence of groups of environmental variables. For example, the reaction to light might change with different conditions of temperature or food supply. An increase of work done in fish pounds in sheltered areas of the sea is also desirable in an attempt to link aquarium results with investigations at sea.

Observations in the sea can provide valuable information on the importance of environmental factors if they are especially designed for an analysis of this kind, but a simultaneous measurement of the biological and hydrographical features of the habitat is essential. An analysis of data on commercial catches combined with information from meteorological records rarely reveals knowledge of the isolated effect of a single factor.

In general the physiological capabilities of fish, especially in the young stages, are wider than might be assumed from their distribution in the sea. Distribution may be partly imposed on young fish by the location of spawning grounds and the inability of the young stages to change their position substantially by active movements. However, the optimum for fish, or their preference for a certain range of conditions, are certainly narrower than the range of tolerance. One must differentiate between what a fish is capable of withstanding and what it "chooses" to do. Further, what may seem to be tolerance in a limited experiment may well prove to be deleterious over a longer term, or adverse conditions which fish can live in might later cause premature death or inability to reproduce. The dependence of a physiological process on an environmental factor is rarely a straight-line relationship. Curves with a maximum in the region of preference may be more common than detected so far. Tolerance, preference and the reaction of fish to an environmental factor may change seasonally or with different phases in the life history. The seasonal change in the temperature preference of Arcto-Norwegian cod and their survival near freezing point, and the drop in reactiveness of spawning herring, all described in this section, are good examples of this.

The question of preference is a central problem when considering the spatial distribution of fish and the establishment of physical and chemical boundaries in the otherwise continuous sea. These boundaries cannot always be defined by a single limiting factor, but rather as an accumulation of several conditions, which may be outside the preference of fish but within their range of tolerance. Under such stress the fish might become more sensitive to a single adverse influence. The changes in activity of fish at boundaries of this sort are of the highest importance as, indeed, are changes of activity of fish as a result of temperature, food supply, light or internally-controlled rhythms unconnected with boundaries.

The discussion on the effect of the environment on reproduction showed that we are very poorly informed on what controls spawning time, fecundity and egg size. Some knowledge of these aspects is essential in the furtherance of population dynamics and studies in early survival rates and recruitment. The need for combined studies in the laboratory and at sea has also been stressed. Besides direct influences on the reproduction of fish of a given size and age, indirect influences of the environment, such as food supply and temperature affecting growth rate and possibly maturation, have to be considered.

Most of our fisheries are carried out in the photic zone of the sea where light may have an important influence on the distribution and migration of fish, as well as being essential for feeding, shoaling and spawning in some species and affecting the hormonal cycles. The interrelationship between migratory behaviour and maturation as controlled by the endocrine glands has been discussed in this section in connection with new information on maturing herring and Arctic cod. Apart from light intensity, the effect of transparency on visibility underwater is of far-reaching importance. Comparative measurements of light intensity and visibility made at the same time as biological observations are highly desirable. The help of physical oceanographers would be appreciated in providing overall synoptic charts of light measurements on the sea bed. From these charts biologists could assess whether certain behaviour patterns, particularly visually-controlled net avoidance would, or would not, take place on the various fishing grounds at stated times.

Fish are not only influenced by the environment; they themselves affect their own environment and that of other fish. This is especially evident in a shoal. Reports on possible oxygen lack within a shoal and the reaction of fish to moving patterns of the background show this. The immediate effects of competition and predation on the activity states and growth rates of fish have not been discussed adequately, but the possible loss in terms of fish weight due to a highly active or over-stimulated existence has been mentioned. The value of further investigations in this field is evident.

The convener's thanks are due to his rapporteur, Mr J.H.S. Blaxter, who prepared the notes for this summary.

SECTION G

The Effect of the Environment on the Process of Fishing

CONVENER: B.B. Parrish RAPPORTEUR: J.G. Harvey

Contributions submitted to this Section were as follows:

G-1 "A First Look at Some Wave and Wind Data from Trawlers" by J.A. Ewing and N. Hogben

G-2 "Relationship Between Drift-Ice, Atmospheric Circulation and Fishing Possibilities off South-East Greenland During the First Halves of the Years 1959-1963" by A. Meyer

G-3 "Changes in the Behaviour of Fish Due to Environment and Motivation and Their Influence on Fish" by H. Mohr

G-4 "Bottom Contour and Nature of Grounds and their Significance for Trawl Fishery" by I.K. Avilov

Although only four contributions were presented to this section of the symposium, their subject matter provided abundant evidence and examples of the importance of various physical and biological factors in their effects on the process of fishing. The factors covered included climate and sea-state relationships, sea-bed topography and structure and biological features of the exploited stocks. The discussions on each are summarised below.

A. Climatic Factors (Contributions G-2 and G-1)

1. Meyer's data in contribution G-2 prompted a lively discussion on the importance of investigations of the relation between the occurrence and distribution of ice and meteorological conditions, especially atmospheric pressure and wind, and of the urgent need for the extension of sea-state forecasting in the northern fishing areas.

In reply to a comment from Lee that 1963 had been a bad ice-year in the area covered by the Norwestlant survey, Meyer said that reports from German trawler captains showed it to be an average year; this indicated that ice conditions in the Greenland area can change very rapidly. Laevastu referred to earlier statements of the importance of meteorological data in relation to ice-drift in the Greenland area, and pointed out that this area is the birthplace of sudden atmospheric depressions, which could be predicted somewhat in advance, using heat exchange computations. Harvey also referred to Bjerknes' comparisons between the changes in atmospheric circulation and Smed's surface temperature anomalies for this area.

Uda described the icing-up of trawlers in the North Pacific and asked if this was a frequent occurrence in the East Greenland area. Meyer said that this was not so, but mentioned the loss of two trawlers off Labrador, from icing, in February 1960. Similar losses of trawlers off West Greenland were mentioned by Hansen. Kotthaus also referred to the loss of a trawler in the Angmagssalik district through "black-frost" icing. Lee described the occurrence of this rare phenomenon on the *Ernest Holt* at Bear Island in 1953.

Meyer associated the increase in surface temperature anomaly in the East Greenland area since the war with the movement of haddock into these waters in recent years, catches of up to 30 baskets per hour has been caught. Hansen stated that no similar increase in haddock had been observed in the West Greenland area..

2. Ewing announced that in addition to the investigation described in his contribution G-1, other work was being carried out in conjunction with the British Meteorological Office, involving the analysis of data collected over the last 10 yr from observers on British merchant ships, covering the main shipping routes over the world.

There was considerable discussion of the interpretation and validity of the relationship between wind speed and mean wave height in Fig. 3 of Ewing and Hogben's paper. It was agreed that a number of factors could affect it, *e.g.* wind direction and the length of time it had been blowing, season, proximity to land-masses, etc. Ewing said that the wind speed and wave height data were skipper's estimates based on the appearance of the sea surface, but he announced that a comparison is being made between estimated wave heights and measured values taken by ship-borne wave-recorders.

Lee pointed out that, in Fig. 4, the accuracy of the estimates of wave-length appeared to improve as the wave-length increased above 200 ft. Ewing agreed that this was probably because at these lengths, the observers could use the lengths of the vessels as a yardstick. Uda suggested that currents would have an effect on wave height,but Ewing said that in the areas from which these data had been obtained, the currents were almost certainly too small to have any significant effect.

Laevastu concluded the discussion by drawing attention to the usefulness of comparative studies of this type of wind and wave data collected from trawlers in different areas, especially in providing information on sea-state condition for use in hydrographic forecasting and in fishing vessel design.

B. Sea-bed Topography (Contribution G-4)

Following his presentation of Avilov's contribution, Edwards described work done by Emery on bottom sediments, bottom topography and the associated benthic fauna in the sea areas off the Atlantic coasts of North America from the Gulf of Maine to Florida.

In reply to a question from the Chairman regarding the available information in other countries on bottom topography and structure of the fishing areas in the North-West Atlantic, Templeman stated that the grounds off Labrador were very badly charted. Cameron described the activities of the Canadian hydrographic service in this area, but emphasised that at present these are concerned principally with depth contouring, rather than determining the detailed nature of the sea-bed structure. Magnusson drew attention to the need for improved bottom charts for the East Greenland waters and of the Reykjanes Ridge. This was supported by Kotthaus who stated that the German charts of East Greenland were in error, most features appearing about 10 miles too far to the east. Meyer drew attention to tbe difficulty of charting in this area, which was out of range of the recognised navigation systems.

In conclusion, the Chairman pointed to the obvious advantages of international collaboration in the preparation of detailed fishermen's charts in large sea-areas like the North-West Atlantic, and suggested that a much larger scale version of Fig. 3 of Avilov's paper would provide valuable information for countries fishing in this region.

C. Biological Factors (Contribution G-3)

3. The importance of the effects of behavioural and distributional features on the accessibility and vulnerability of exploited fish stocks, as outlined in Mohr's paper was emphasised by the Chairman, who instanced the marked effects of diurnal variations in vertical distribution and the differences in behaviour of fish to fishing gear under visual and non-visual conditions as notable examples. Meyer explained that pelagic trawling for cod in Greenland waters was now being investigated in Germany and some good catches had been obtained. However, owing to unpredictable irregularities in vertical distribution, there was a need for trawl which could be fished either on the bottom or in mid-water, according to the observed distribution of fish.

D. Conclusions

In summing up, the Chairman highlighted the following items of major importance, arising from the discussions:

(a) the importance of more extensive information and forecast services, giving sea-state conditions, and especially of the ice-limits for the northern fishing areas;

(b) the need for international collaboration in the preparation of accurate, large-scale fishermen's sea-bed charts for the North-West Atlantic and East-Greenland fishing areas;

(c) the need for further intensive studies of distributional and behavioural factors influencing fish capture, and for close collaborations between biologists and gear design and improvement projects.

SECTION H
Effects of Long-Term Trends

CONVENER: L.M. Lauzier   RAPPORTEUR: T. Laevastu

Contributions submitted to this Section were as follows:

H-1 "Recent Changes in the Benthos of the West Spitsbergen Fishing Grounds" by R.W. Blacker

H-2 "Anomalies of Sea Temperature at Station 27 off Cape Spear and of Air Temperature at Torbay-St. John's" by W. Templeman

H-3 "Long-Term Temperature Variations in the Scotian Shelf Area" by L.M. Lauzier

H-4 "Effect of Long-Term Temperature Trends on Occurrence of Cod at West Greenland" by P.M. Hansen and F. Hermann

H-5 "Variation of the Temperature of the Surface Waters in Areas of the Northern North Atlantic" by J. Smed

H-6 "On Long-Term Variability of Oceanographic Conditions and Stocks of Cod Observed in the Areas of West Greenland, Labrador and Newfoundland" by A.A. Elizarov

H-7 "Variation in the Recruitment of Cod (*Gadus morhua* L.) in Southern ICNAF Waters as Related to Environmental Changes" by W.R. Martin and A.C. Kohler

H-8 "Changes in the Hydrography Observed Along the East Coast of the United States" by D.F. Bumpus and Joseph Chase

H-9 "Inferential Biological Effects of Long-Term Hydrographical Trends Deduced from Investigations in the Faroe-Shetland Channel" by J.B. Tait and J.H.A. Martin

This is the second time that long-term hydrographic changes and their effects have been discussed by ICNAF scientists. The first time was during the 1953 Annual Meeting. During both symposia, the main factor considered for bringing long-term changes in evidence was water temperature. Changes in water temperature have a direct effect on the biological processes, on the physiological functions and on the distribution of animals. However, changes in temperature may be the result of changes in the circulation or of advection. Temperature changes may indicate a change in the composition of water masses including its biological and chemical (nutrient) contents - a change in productivity. Temperature changes may be, in many cases, "coincidental" with biological changes within the same body of water, both being the effects of a common cause.

The papers and discussions at this session were concerned with the evidence for, and causes and effects of long-term trends. Related subjects were discussed but two aspects were emphasized: first, the possible causative mechanism of long-term trends and the variations of these trends from western to eastern sectors of the North Atlantic; second, the difficulties in measuring the changes in the fisheries that may be attributed to long-term trends. The possible effects of long-term trends on distribution of fishery resources were summarized by Dr A.V. Tåning in a contribution presented to the first symposium in 1953. These effects pertained mostly to the northern areas. At the time Dr Tåning considered these effects, most scientists had in mind the recent warming or amelioration of climate. There are now instances of reversal of trends in some areas. Will the possible effects of recent cooling trends be the reverse of those considered by Dr Tåning? It is difficult to give an answer at present; we probably will find that the physical factors have only a secondary effect. Can we wait for another 10 yr or so for an answer?

May I make for this section on the effects of long-term trends the following recommendation:

considering that changes have taken place in the distribution of fish and in the yield of fisheries in the North Atlantic and that these changes may be attributed to long-term trends or changes in the environment, it is recommended that the observations of environmental factors at coastal stations and offshore points, including weather ships, be continued and encouraged with a dual objective in mind: first, to monitor the climatic conditions; second, to find ways and means for prediction of long-term trends which might infer readjustment of some of the fisheries.

I would like to thank all the contributors for their contributions and Dr T. Laevastu for his assistance, as rapporteur, and his help in the preparation of this report.

SECTION I
Forecasting Environmental Conditions

CONVENER: D.F. Bumpus RAPPORTEUR: R.L. Edwards

Contributions submitted to this Section were as follows:

I-1 "Foreshadowing of Surface Temperatures at St. Andrews, N.B." by L.M. Lauzier

I-2 "Factors Affecting Water Temperature in the Seas North of Norway" by J.G. Harvey

I-3 "Is Oceanographic Forecasting (Hydrosis) Feasible for Fisheries?" by T. Laevastu

I-4 "Daily Heat Exchange in the North Pacific; its Effects on the Ocean and its Relations to Weather" by T. Laevastu

I-5 "Notes on the Problem of Predicting Near Surface Temperature Gradients in the Open Ocean" by C. O'D. Iselin

I-6 "Forecasting Environmental Conditions in the Faroe-Shetland Channel Region" by J.B. Tait

I-7 "The Possibility of Oceanographical Forecasts in North-western European Waters and Their Significance for Fisheries" by J. Eggvin

I-8 "Oceanographic Predictions" by J.J. Schule

The contributions presented in this section ranged in subject matter from a general discussion of the feasibility and problems of forecasting (I-7, I-6, I-8, I-3) to demonstrations of attempts to relate changes to various factors such as meteorological conditions (I-5, I-4, I-1, I-2).

Several contributions contained both suggestions and evidence that many changes occur weeks and even months in advance of local phenomena, so that some forecasting can already be done even today. In this regard, Eggvin (I-7) notes the significant negative air temperature anomalies of 1963, the relative lack of clouds and other related changes that lead Norwegian scientists to anticipate that the deep water of the Norwegian Channel would stay cold for many months longer than usual with significant effects on the fisheries. This condition persisted during the late months of 1963 and even into January 1964. Tait (I-6) makes comparable observations concerning variations in salinity in particular, which cycles over longer periods of time. He states that "the variation is gradual, which lends to this particular phenomenon the aspect of climatic change in the sea, and the fact that it is gradual anticipates the possibility of forecasting it, provided observations in the region are sufficiently regular and systematic".

Schule (I-8) presented a thorough review of the problem and scope of operations involved in oceanographic prediction. He discussed four approaches to the problem, namely: 1) a system that concerned itself primarily with factors characterized by continuity or persistence beyond normal day to day changes; 2) the point prediction method, based on, for example a bathythermograph record, modified for a period of time by other predictable or observable factors such as wind, air temperature and cloudiness; 3) the dynamic approach, based on extensive model studies that could ultimately allow for minimum, although admittedly critical imput, to predict change over a wide area. High speed computer capability is mandatory, plus a considerably better general understanding of the hydrographic regions than presently exists for most areas; 4) the statistical approach, or *post hoc* approach based on what are today relevant and seemingly causal factors.

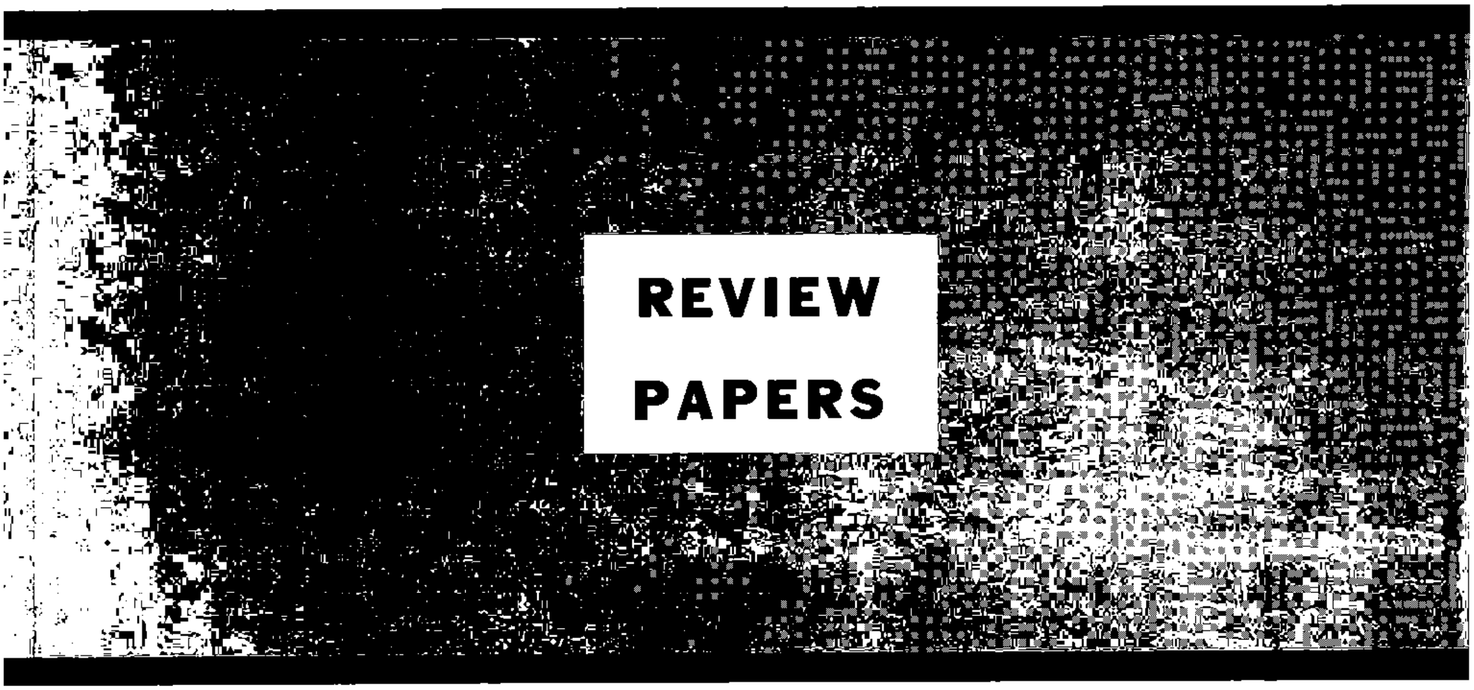
With regard to the fourth approach discussed by Schule, two contributions are of direct interest, namely I-1, Lauzier and I-2, Harvey. Lauzier examined surface temperature records for

St. Andrews and other North American localities in detail to determine the degree of predictability that might be achieved without recourse to other data. He showed, for example, that one can predict annual means with a fair level of significance given previous means and the minimum temperature for the year under consideration. Harvey concerned himself more with factors having an apparent or relevant causal connection, such as wind velocity, cloudiness and air temperatures. Highly significant correlations were obtained even though horizontal advection appeared to be the dominant influence in change.

Professor Laevastu pointed out that many events are predictable on the basis of meteorological conditions.

In the discussion that followed, two aspects of prediction were touched upon - the pragmatic aspect of keeping the fishermen informed and that bearing on academic or research problems. In both the presentations and discussions it was apparent that considerable promise lies in the understanding of the relation between atmospheric and oceanographic phenomena.

In addition to regular systematic temperature and salinity measurements throughout the water column in strategic places, an improved field of current measurements and a monitoring of the changes in the location of oceanographic fronts would contribute toward predictive capabilities. Support in the way of communicative, analysis and forecast procedures need to be considered to make efficient use of the data collection. The Canadian and U.S. Navies already have a data collecting net, analysis sections, and radio facsimile broadcasts of certain aspects of the ocean environment. Cooperation between the fisheries oceanographic programs and the naval predictive services would enhance the interests of both groups.



REVIEW PAPERS

REVIEW PAPERS

NEW HYDROGRAPHICAL ASPECTS OF THE NORTHWEST ATLANTIC

By

Günter Dietrich[1]

INTRODUCTION

The ICNAF Committee, preparing the meeting in Rome, January 1964, asked me to give a general review of the hydrographic features of the Northwest Atlantic. I was eager to accept this request, but I must confess that I am in a poor position. On the one hand, I can refer to two excellent and comprehensive recent reviews by research workers who have had much more contact with this region than I have had. These are the reviews by Dunbar (1951) on eastern Arctic waters and by Hachey *et al.* (1954) on the waters of the ICNAF Convention Area. On the other hand, during 1963, the Northwest Atlantic was the subject of a great systematic international co-operation in the so-called NORWESTLANT Program, when a fleet of research ships made three surveys of the area. The results are still being prepared by our colleagues who participated in these cruises. This means that all basic knowledge to 1953 is at hand in the two publications mentioned and that all the new observations of the joint cruises in 1963 are not yet available. Thus my reason for saying I am in a poor position.

Because I do not want to bore you with known facts, I will refer to the ten years between 1953 and 1962. In 1958, in the middle of this period, the International Geophysical Year (IGY) sponsored a special oceanographic program called The Polar Front Survey in the North Atlantic. This program is outstanding in various ways:

1. It covered the whole North Atlantic from the line Newfoundland - Azores - Gibraltar in the south to the ice edge off Greenland and the Polar Sea in the north.
2. It covered the area twice, first in the winter and second in the summer of 1958, thus giving an insight into the annual variations in the water.
3. A total of 25 research ships of 11 nations participated in the work in a quasi-synoptic way in order to avoid non-stationary conditions as far as possible.

The map of oceanographic stations (Fig. 1) shows the area investigated in the summer of 1958. The same cruise lines were followed six months earlier in the winter of 1958. In all, about 2,500 hydrographic stations were made. Some results, based on the physical, chemical and biological observations of the single ships have already been published in about 100 papers. (Partly as special volumes in Deutsche Hydrographische Zeitschrift, edited by Bohnecke and Buckmann, 1959 and Rapports et Procès-Verbaux of the ICES, Vol. 149, 1961.) All hydrographical material is being worked up by an ICES working group of Mr A. Lee, Dr J. Eggvin, Mr M.V. Fedosov and myself. In the following I shall refer mainly to the first results of this investigation.

BOTTOM TOPOGRAPHY

The Northwest Atlantic Ocean is like a great bight of the Atlantic Ocean proper, with a relatively simple arrangement of the main forms of the ocean bottom. This is best shown in a new physiographic map by Ulrich (1963) (Fig. 2) which is an extension of a map published by Heezen *et al.* (1959) for the northern North Atlantic Ocean. The terminology is the same as used by Heezen.

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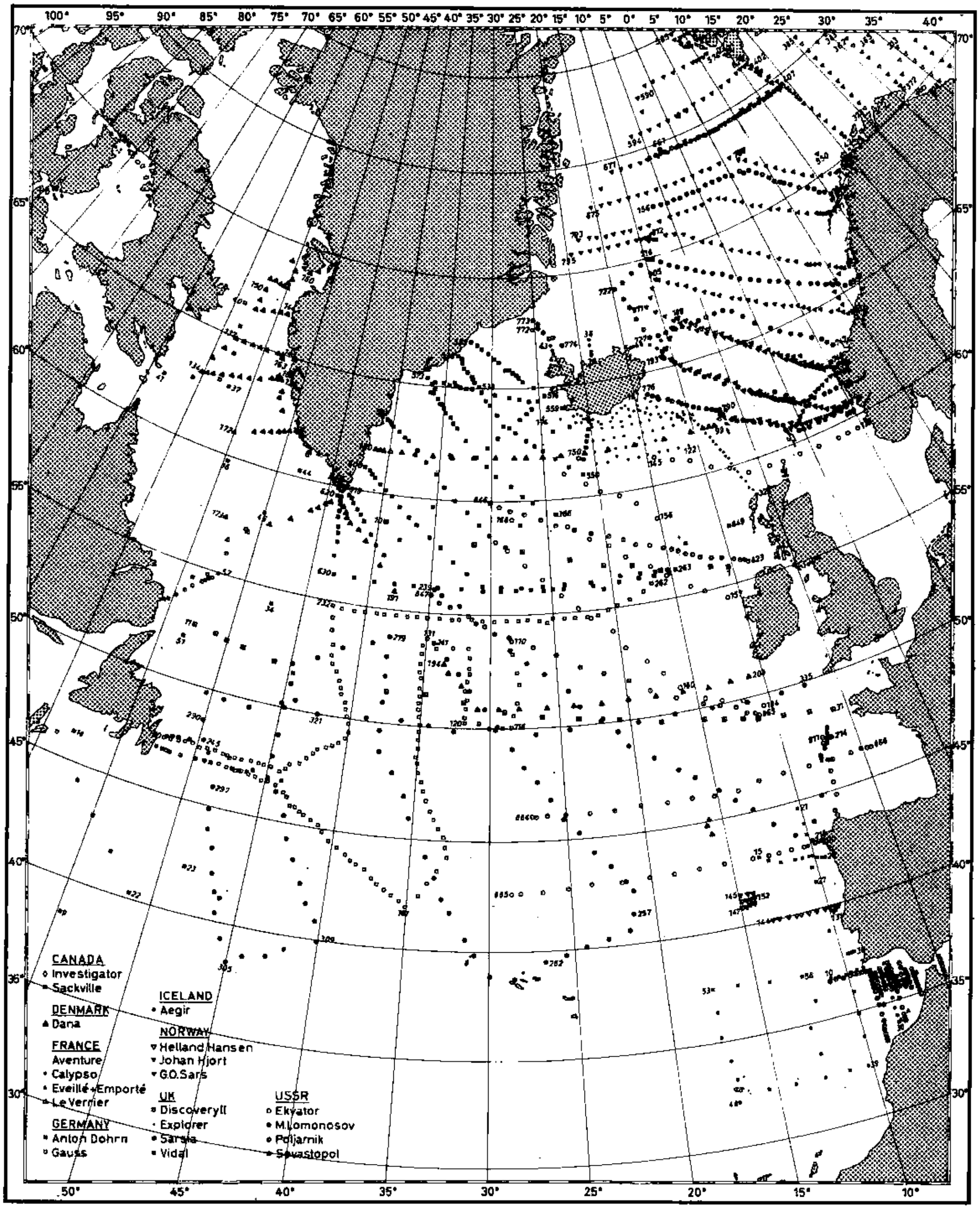

Fig. 1. Oceanic Polar Front Survey in the IGY 1958. Oceanographic stations in the northern North Atlantic (outside adjacent seas); July-December 1958, mainly late summer. Repetition of the cruises made in this program in late winter 1958.

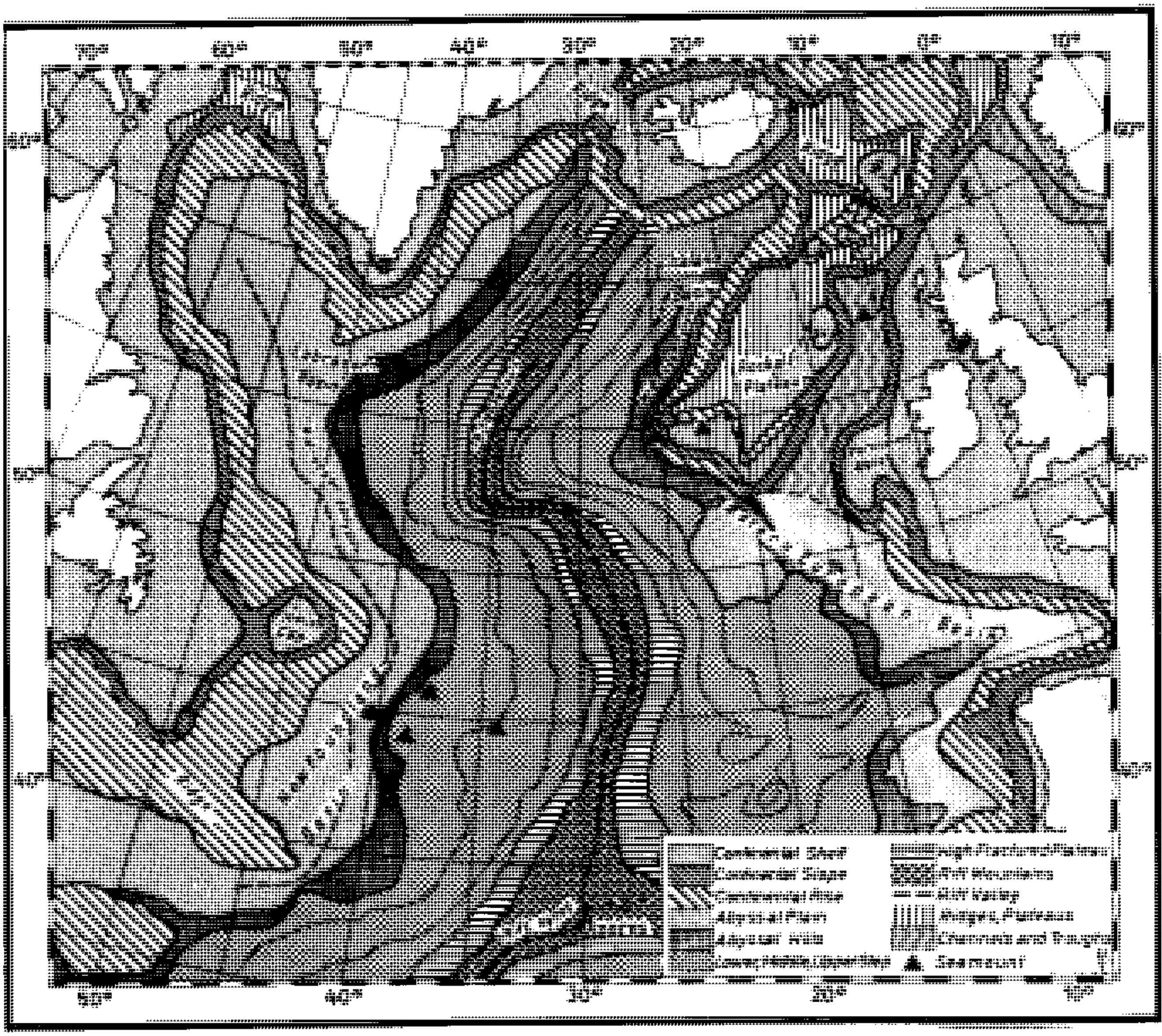

Fig. 2. Bottom morphology of the northern North Atlantic (After Ulrich, 1963).

The Mid-Atlantic Ridge partly separates the deep Northwest Atlantic Ocean from the deep Northeast Atlantic Ocean. It is distinguished by the deep rift valley which begins in 57°N and turns with the ridge to the east in about 52°N and to the south in about 30°W. These bottom features are of great importance for the water circulation, especially for the main branches of the Gulf Stream, as will be demonstrated later. The Mid-Oceanic Ridge is flanked by a high fractured plateau, further by the upper, middle and lower step of this fractured plateau. It follows the abyssal hills and the flat abyssal plains which cover the central part of the Labrador and Irminger Seas. These plains are distinguished by a mid-ocean canyon in the Labrador Sea, but not in the Irminger Sea as maintained by Heezen. The abyssal plains pass over to the continental rises, indicated by the wide hatched areas. These are surrounded by the steep continental slope and finally follow the continental shelf, differing greatly in their width. The shelf is narrow around southern Greenland, but broadens along the coasts of Labrador and Newfoundland. Without entering into details I wish to illustrate the nature of the morphological provinces with some examples. Figure 3 shows the echo sounding profiles made from *Anton Dohrn* during the IGY 1958. The area of sections I to III has no rift valley in the Mid-Atlantic Ridge. It follows the different steps of the fractured zone, the abyssal hills, the abyssal plains, the continental rise and the continental slope.

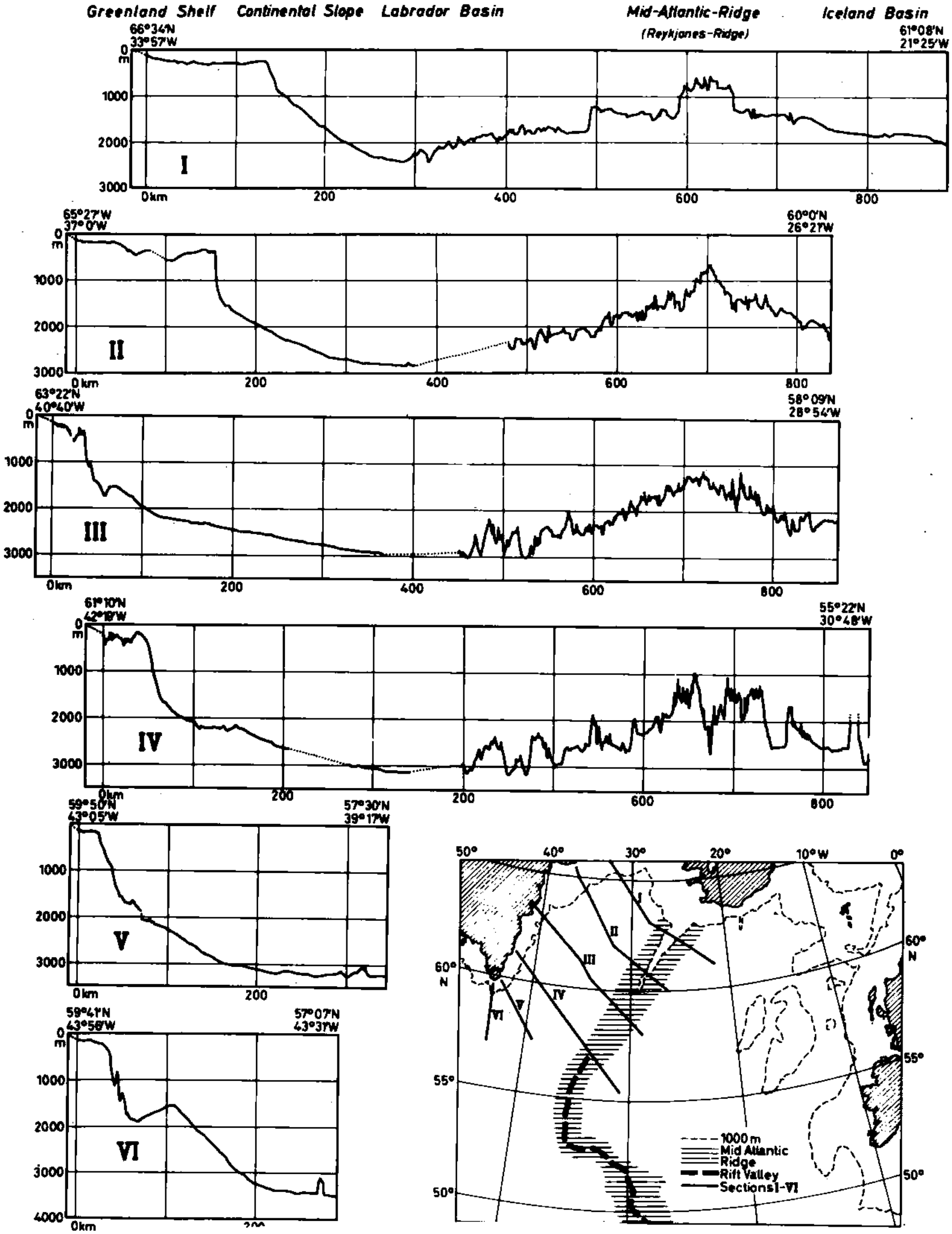

Fig. 3. Six bottom profiles normal to the East Greenlandic slope made by *Anton Dohrn* late summer 1958 (After Ulrich, 1962) (x 50).

The main point of discussion at this symposium will be the environment of the commercial fish. The main interest, therefore, is directed not to the deep sea, but to the shelf areas. These shelves are distinguished by special features which have become of great interest for the fisheries in the Northwest Atlantic Ocean during past years. In the well-known profile of the shelf in the world ocean, the water becomes deeper and deeper as we move away from the continental coast. Suddenly,

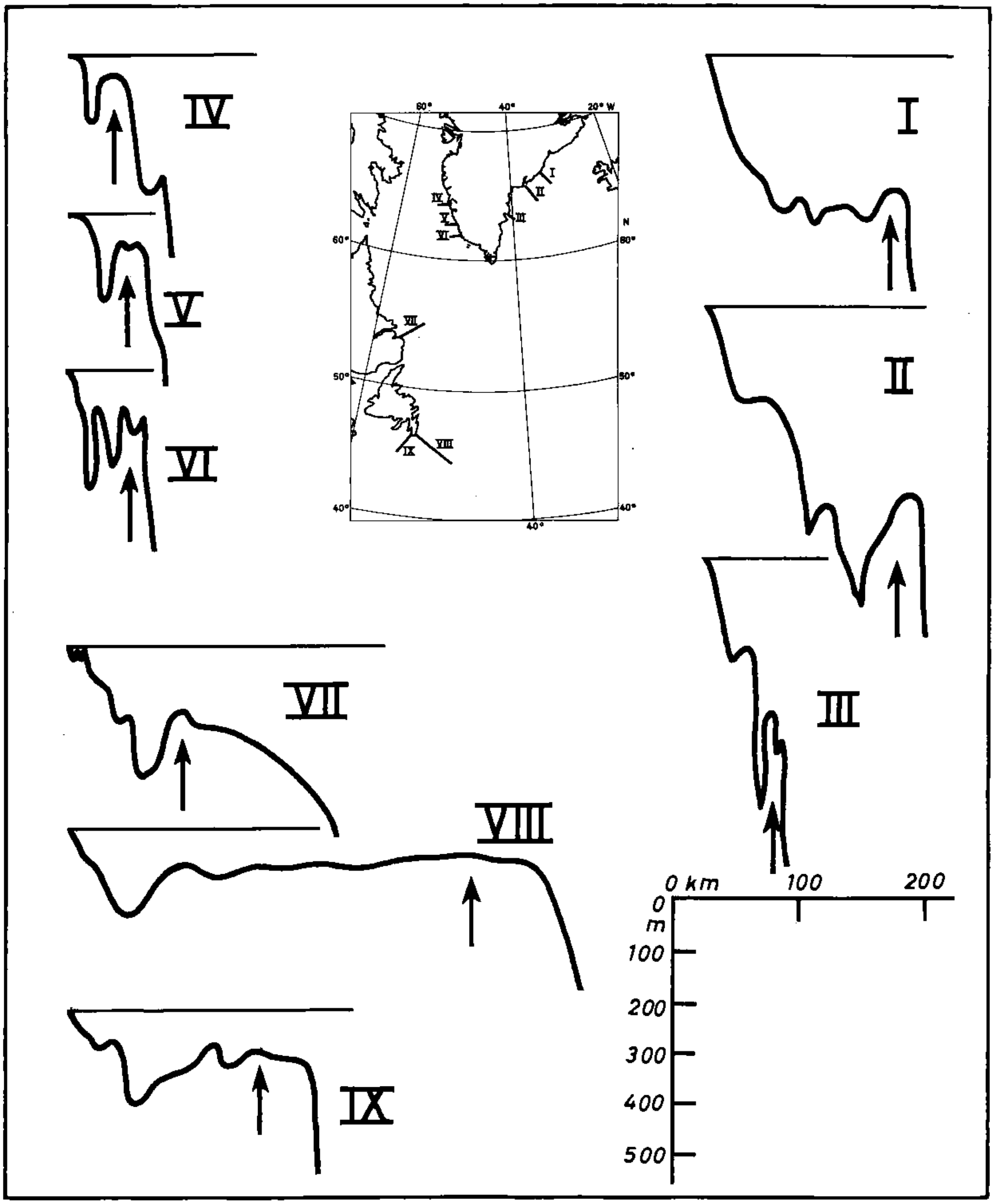

Fig. 4. Examples of bottom profiles across the Northwest Atlantic shelf. (Arrow indicates the sill of the shelf (magnification of profiles 400 times).

on the shelf edge in about 200 m depth, the steep continental slope goes down to the deep sea. This is the rule in the oceans, but not so in the Northwest Atlantic. Here one finds a small rise close to the shelf edge. This rise is well-marked even in the small scale profiles. It becomes more distinct when a larger scale is used and also when examples are taken from other parts of the Northwest Atlantic shelf. This special feature is illustrated in Fig. 4. It is an exception if one of the bottom profiles is without such a shelf rise. A topographic map may show this shelf rise more convincingly than the single profiles. Two examples of well-surveyed areas are the East Greenland shelf (Dietrich, 1957*a*) and the East Labrador shelf (Litvin and Rvachev, 1962). In the first example (Fig. 5) the waters over the shelf rise are 50 to 100 m shallower than the neighbouring waters nearer to the coast. The crest of the shelf rise is indicated by the broken line. Even the prolongations of the East Greenland fjords, crossing the shelf are closed by a rise against the deep sea.

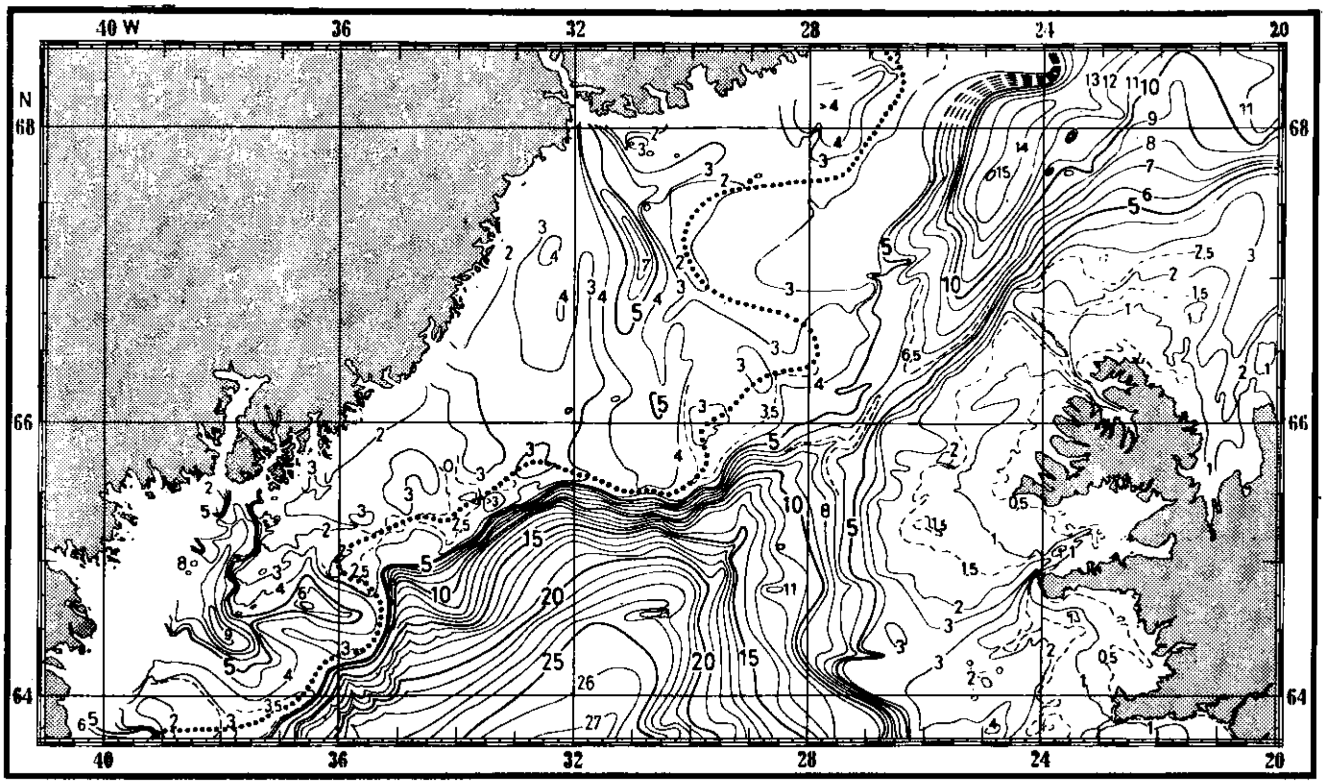

Fig. 5. Topographic map off East Greenland (depths in hectometer) and the crest of the shelf rise (dotted line) (After Dietrich, 1957*a*).

The second example (Fig. 6) off East Labrador shows principally the same features, namely a sill running along the shelf edge and closing also the deep channels crossing the shelf against the deep sea.

The surprising fact, that the shelf has a distinct rise just near the edge and is shallower there than nearer to the coast, must have a special cause. These rises are obviously terminal moraines of the pleistocene glaciers of Greenland and Labrador. Having established the shelf sill as a fact in many parts of the Northwest Atlantic, it is not difficult to imagine its importance for the near bottom water on the shelf coastwards of the sill. Before considering these facts, let us review, generally, the hydrographic conditions based on the IGY work in 1958.

LAYERING AND CURRENTS

The IGY work was known as the Polar Front Survey. How is this Polar Front defined in North

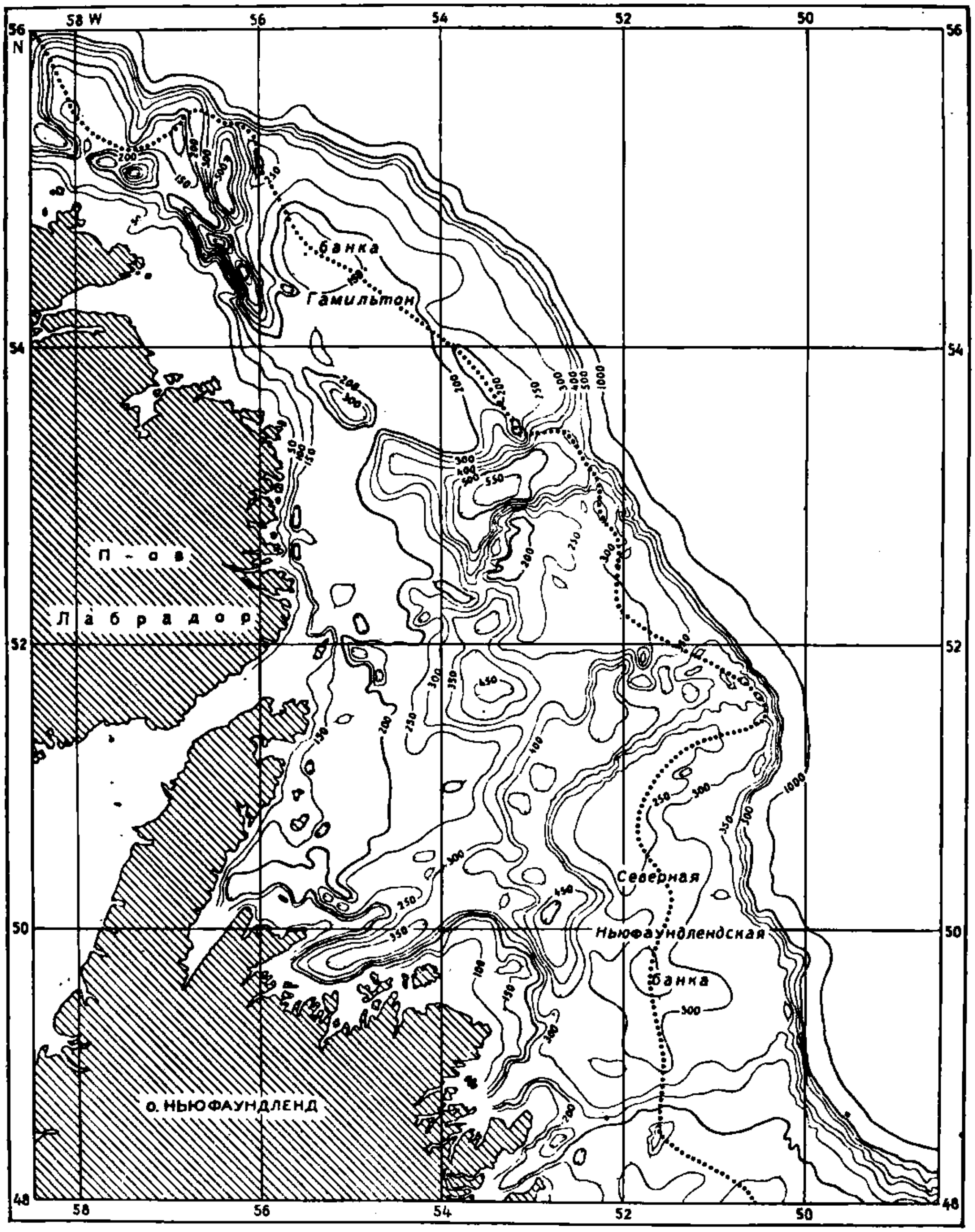

Fig. 6. Topographic map off East Labrador and the crest of the shelf rise (dotted line) (After Litvin and Rvachev, 1962).

Atlantic waters? No long explanation is needed when one looks on the maps showing the distribution of the two most important hydrographic factors - temperature and salinity. These maps are part of the ICES Atlas which is in preparation and which shows the distribution of temperature, salinity, oxygen and density at several levels during the winter and summer of 1958.

Let us consider, for example, the temperature distribution at 200 m depth (Fig. 7). No personal interpretation of the distribution is necessary because the stations are in a close net (Fig.1). Figure 7 shows that the cold and warm water lie side by side. The thermal front from Cape Hatteras to the Grand Banks is well known as the Gulf Stream. It extends to the north along the Flemish Cap and to the east to a point in 30°W and 52°N. This is the point shown on the physiographic map (Fig.2) where the Mid-Oceanic Ridge changes direction. This area is known for its very complicated topography, with deep depressions and high peaks. One can recognize a second thermal front in the Norwegian Sea, along East Greenland, Baffin Island and Labrador. Comparing this map with Fig. 8 which shows the summer distribution of salinity at 200 m depth, the thermal front appears as a haline front which also weakens remarkably over the Mid-Atlantic Ridge. The definition of the Oceanic Polar Front is now obvious. It is the boundary between cold, low haline, subpolar water and warm, high haline, subtropical water. As the Polar Front also separates waters with different oxygen and nutrient content, it is one of the most important and singular oceanographic features in the North Atlantic.

As mentioned previously, two surveys of the northern North Atlantic were made during the IGY. Thus one can compare the situations in the winter and the summer of 1958. Figure 9 shows the temperature distribution at 200 m depth in the winter of 1958. The thermic front is apparent with the 10° isotherm as its centre. Comparing the geographic positions of the fronts in IGY surveys in both winter and summer of 1958 (Fig. 10), the displacement of the front is evident. One can distinguish between the main front in the open Atlantic Ocean and the secondary fronts in the Norwegian and Greenland seas. The fronts in winter and summer show great horizontal meanders, but in different positions. In some places the winter and summer fronts cross each other. It is difficult to decide whether these crossings happen accidentally or regularly. However, it seems that there are two places which are distinguishable by bottom features; one being east of Flemish Cap and the other in 52°N, 30°W on the Mid-Atlantic Ridge. The front, meaning the main branch of the Gulf Stream, looks like a ribbon hanging from these two fixed points and swinging between with great horizontal displacement. The strong current splits east of the Mid-Atlantic Ridge where the weak and broad water movements in the Portugal Current, in the Northeast Atlantic Current and in the Irminger Current are found.

The horizontal displacement of the front between Flemish Cap and the Mid-Atlantic Ridge must have a great influence on the circulation system in the Northwest Atlantic. The water in the bay must react when the water in tbe mouth shows great displacements. However nothing is known about these relationships. Only the very first step has been taken to show the nature of the strong current system in the open Northwest Atlantic. It will be a task for the future to improve these statements and to investigate this current system which must have great influence on ocean and atmosphere not only in this area, but also in the Northeast Atlantic Ocean. I should be very happy if the audience picks up these new facts about the Northwest Atlantic Ocean and if the institutes find a way of coordinating further international investigations of this part of the ocean.

Since this symposium concerns the environment for life in the sea, we will have only a short look in the deep sea. I have chosen the distribution of salinity at 1,000 m depth as observed in the IGY 1958 (Fig. 11). Three facts may be pointed out:

1. There were no remarkable differences in the salinity winter and summer of 1958 at 1,000 m. Therefore, all observations from the IGY cruises were used in preparing Fig. 11.

2. The distinct salinity and temperature fronts have vanished at a depth of 1,000 m.

3. The influence of high haline water from the Mediterranean is evident and can be followed on four main courses, one leading to the Azores, another to the west-north-west, a third to north-west and a fourth along the European continental slope moving around the northern North Atlantic, crossing the Mid-Atlantic Ridge and entering the Labrador Sea. A central low salinity patch characterizes the Northwest Atlantic Ocean. It has the lowest salinity in the whole open northern Atlantic at this level.

The current velocity at 1,000 m is not known and can only be estimated. It should, however, be small compared with that in the near-surface layers. Therefore, the dynamic topography of the sea

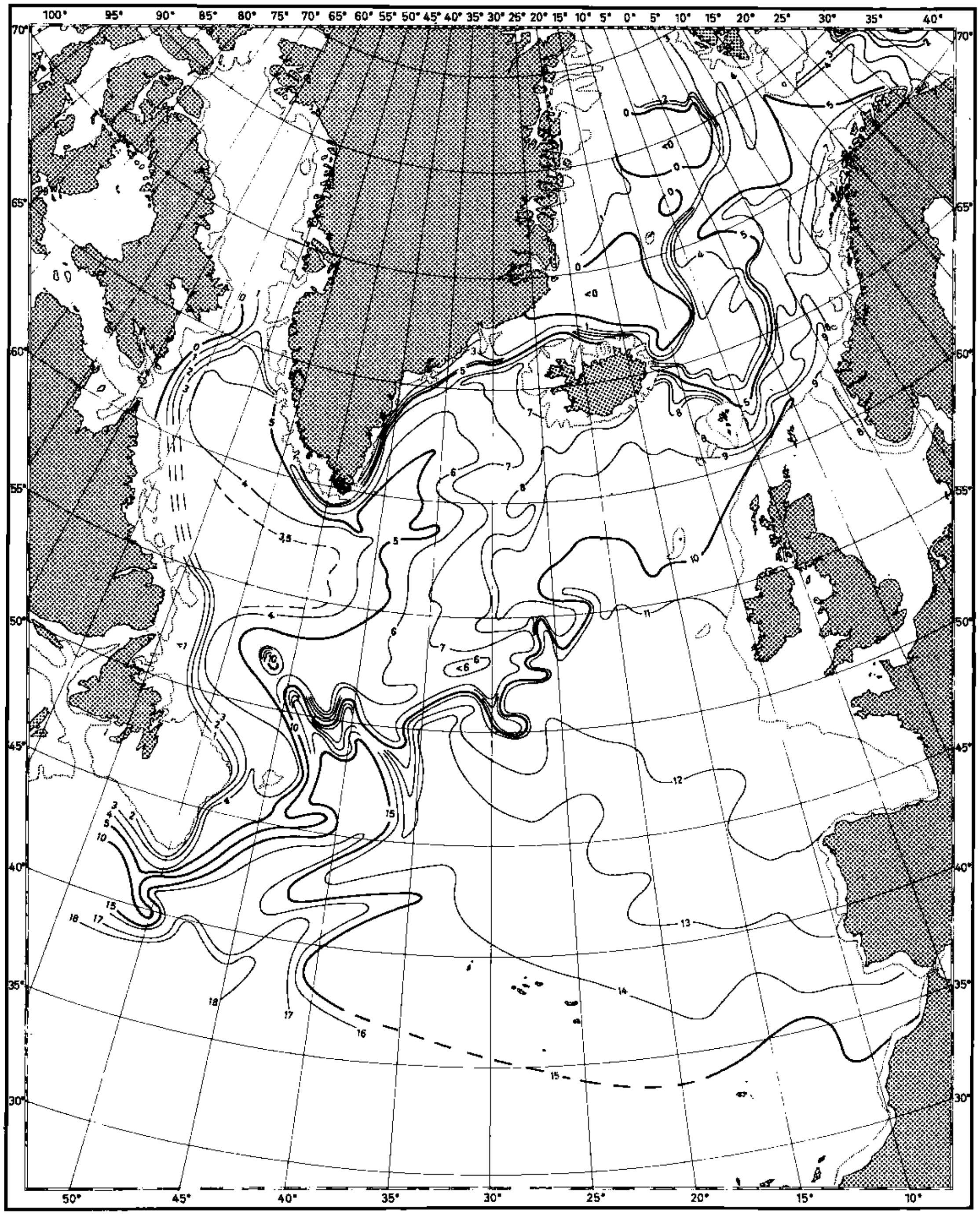

Fig. 7. Temperature in the northern North Atlantic in 200 m depth in late summer 1958 (Oceanic Polar Front Survey in the IGY).

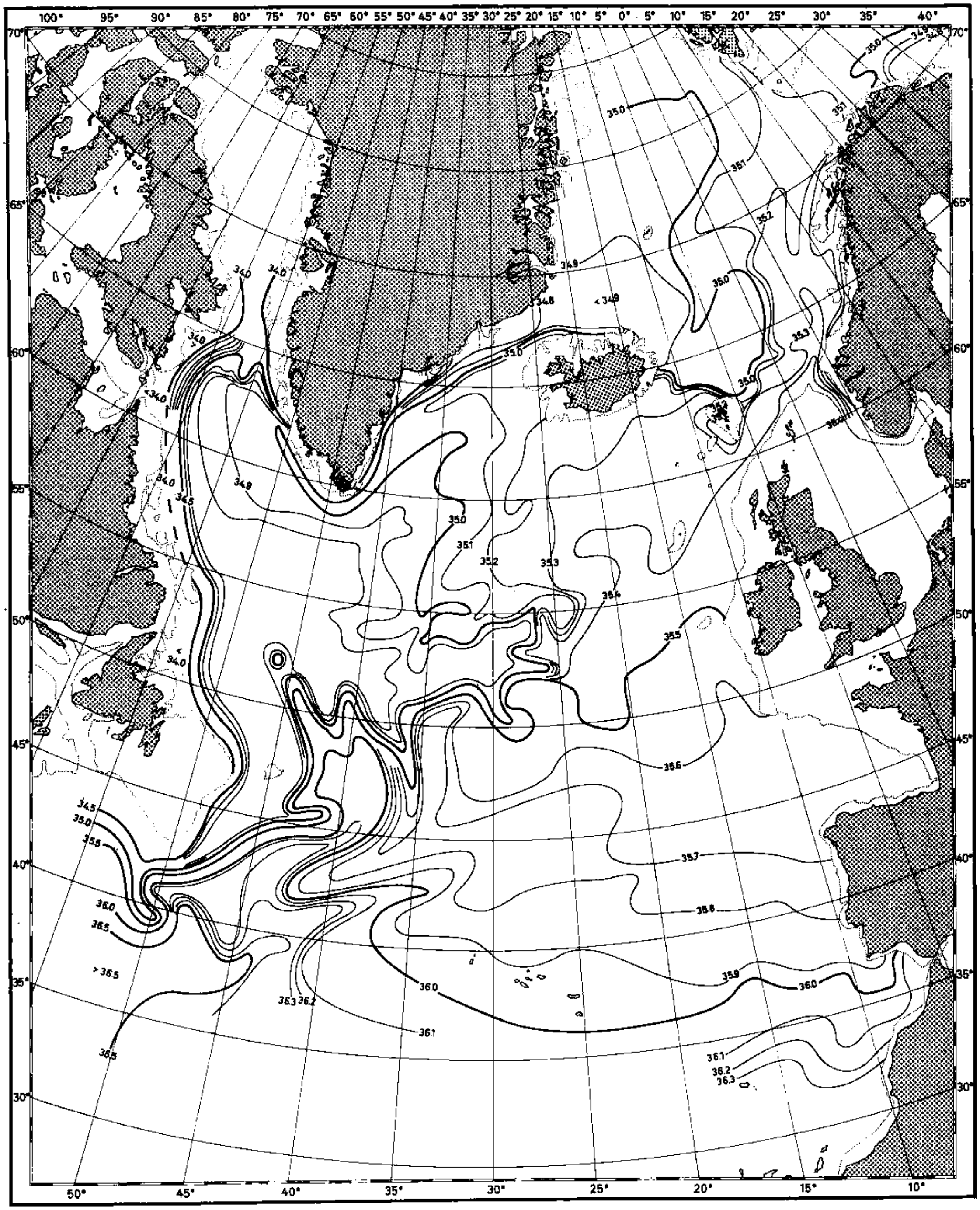

Fig. 8. Salinity in the northern North Atlantic at 200 m depth in late summer 1958 (Oceanic Polar Front Survey in the IGY).

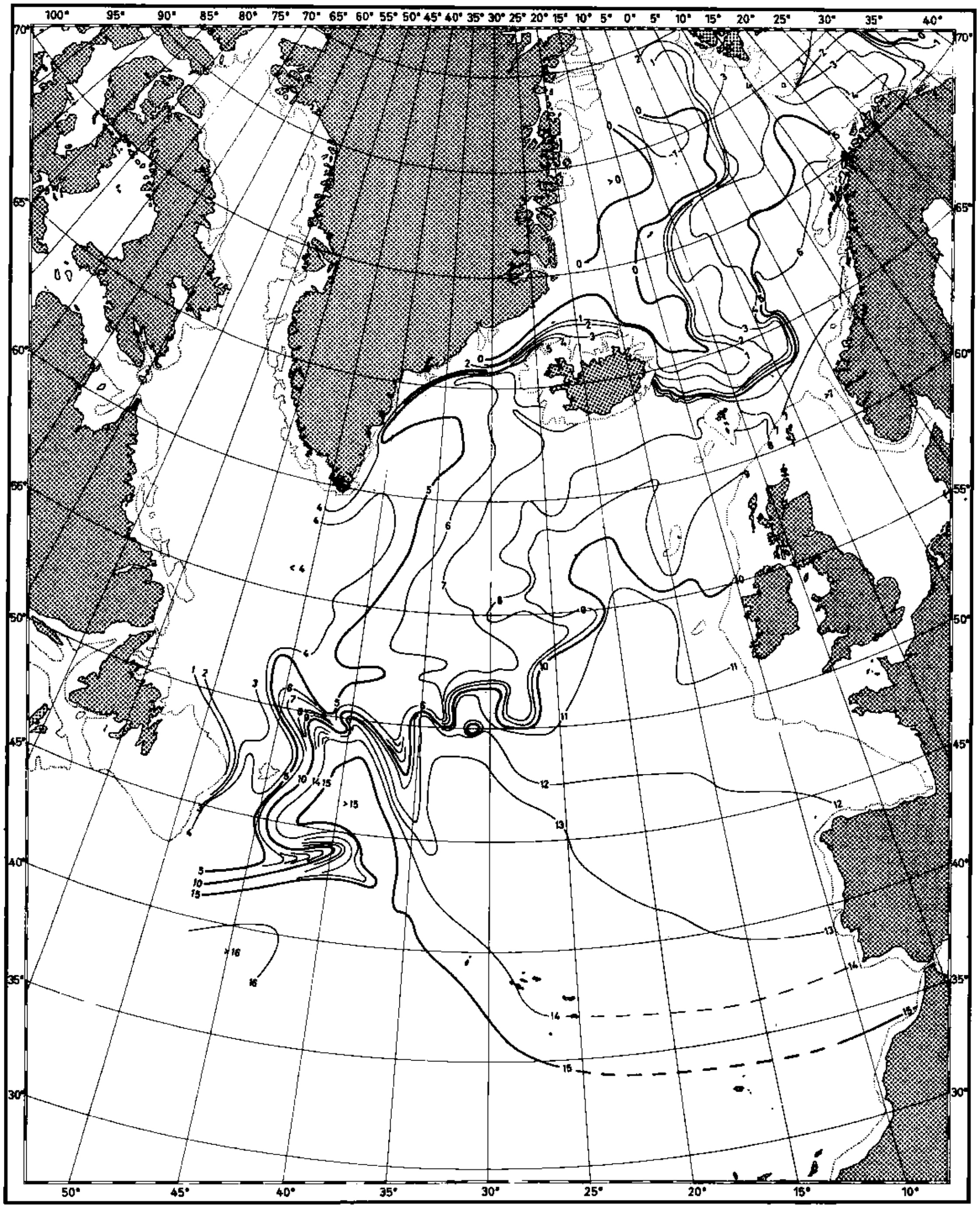

Fig. 9. Temperature in the northern North Atlantic at 200 m depth in late winter 1958 (Oceanic Polar Front Survey in the IGY).

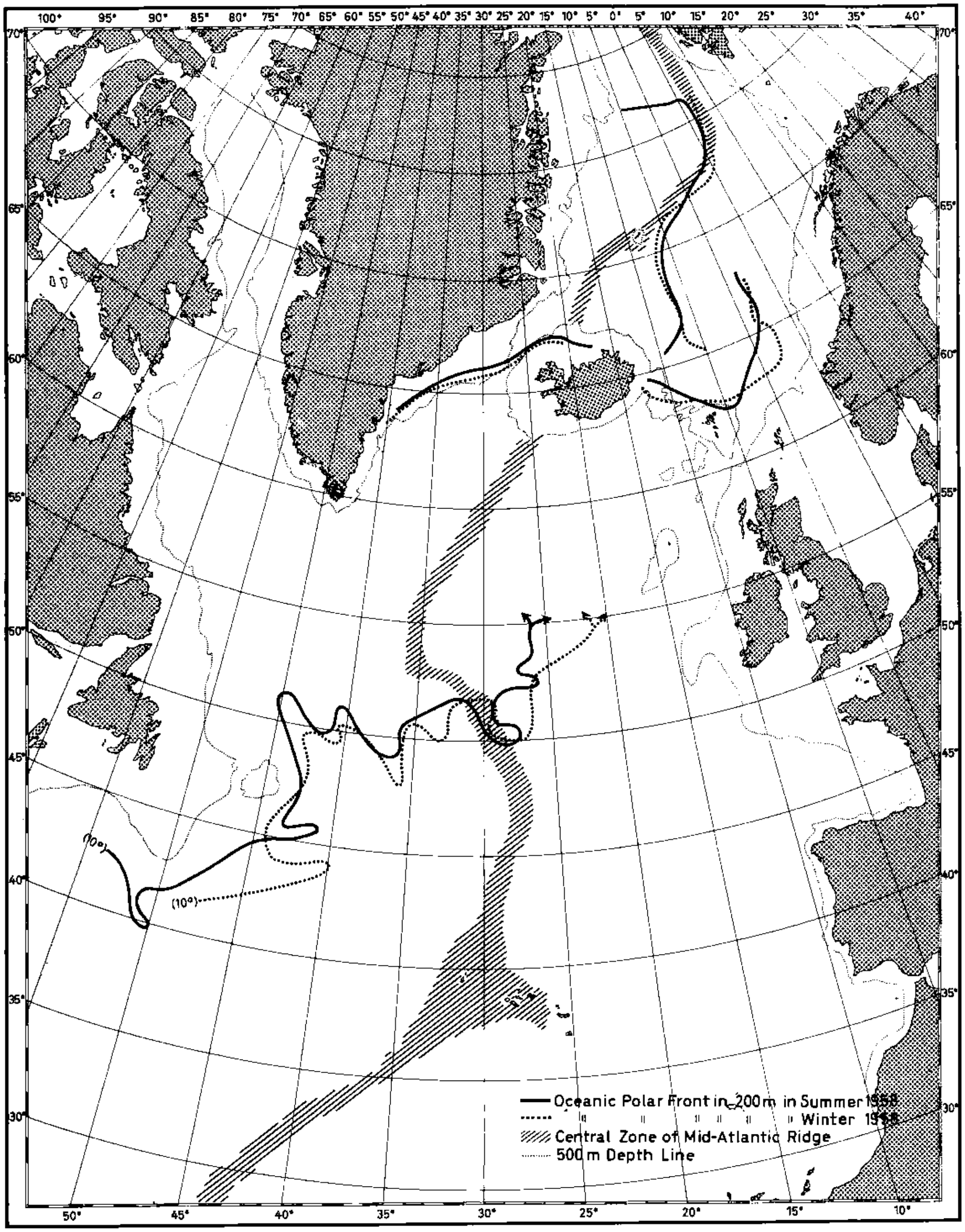

Fig. 10. The Oceanic Polar Front in the northern North Atlantic at 200 m depth in late winter and late summer 1958.

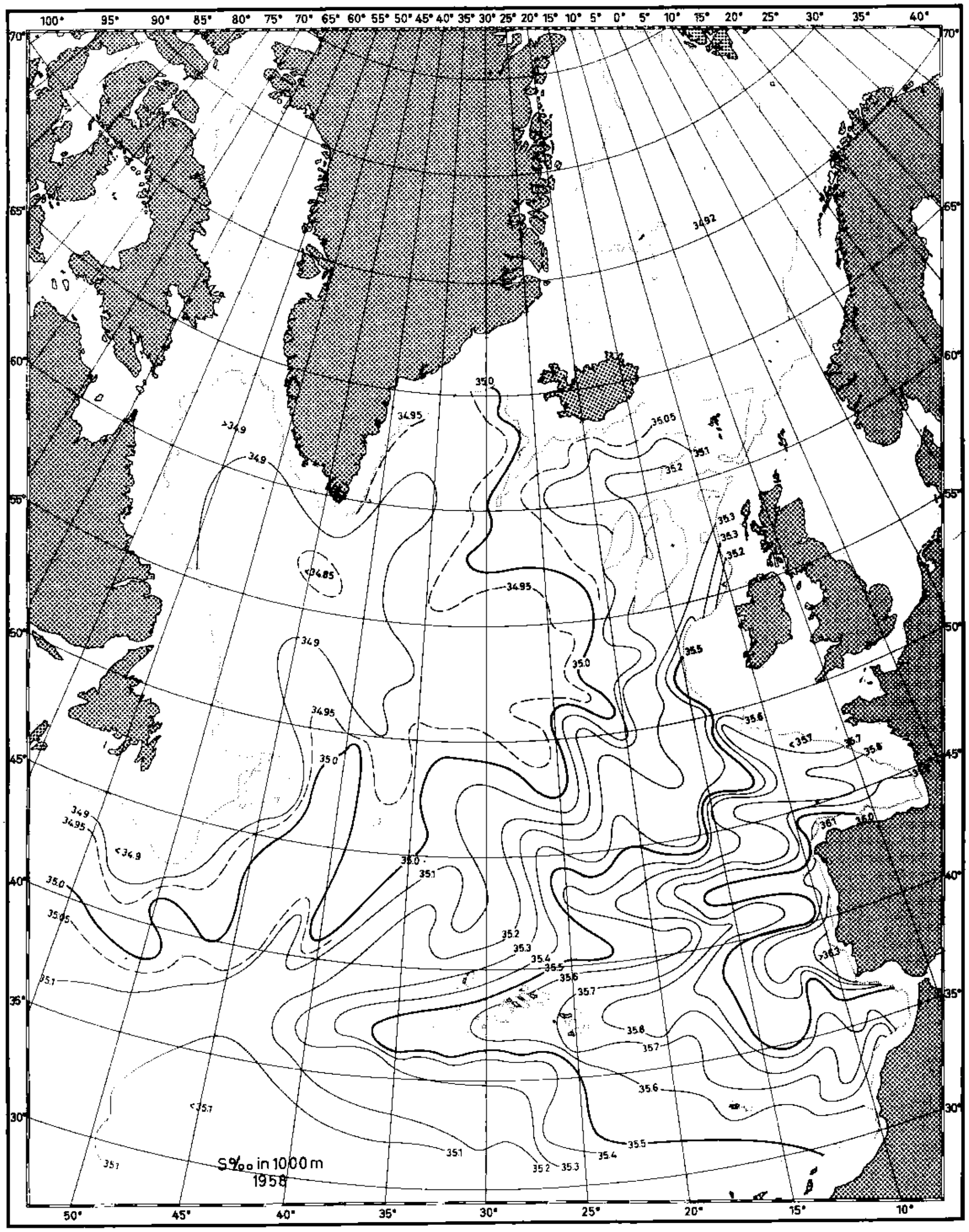

Fig. 11. Salinity distribution (in o/oo) in the northern North Atlantic at 1,000 m depth based on all IGY observations 1958.

surface over the 1,000 decibar surface gives an approximate review of the system of the geostrophic currents on the surface, in this case, for the summer of 1958. In Fig. 12 the Oceanic Polar Front appears again, this time as a jetstream, a very narrow ribbon, but with high velocities. It parts into a broad and a weak current system at about 52°N, 30°W, the distinguished point on the Mid-Atlantic Ridge that we know from the bottom topography and the Polar Front. Summarizing the different facts, one sees that the Gulf Stream system crosses the Northwest Atlantic Ocean as a meandering jetstream and separates the subtropic anticyclonic movement from the subpolar cyclonic movement. These two big cells determine the oceanic conditions of the northern North Atlantic Ocean.

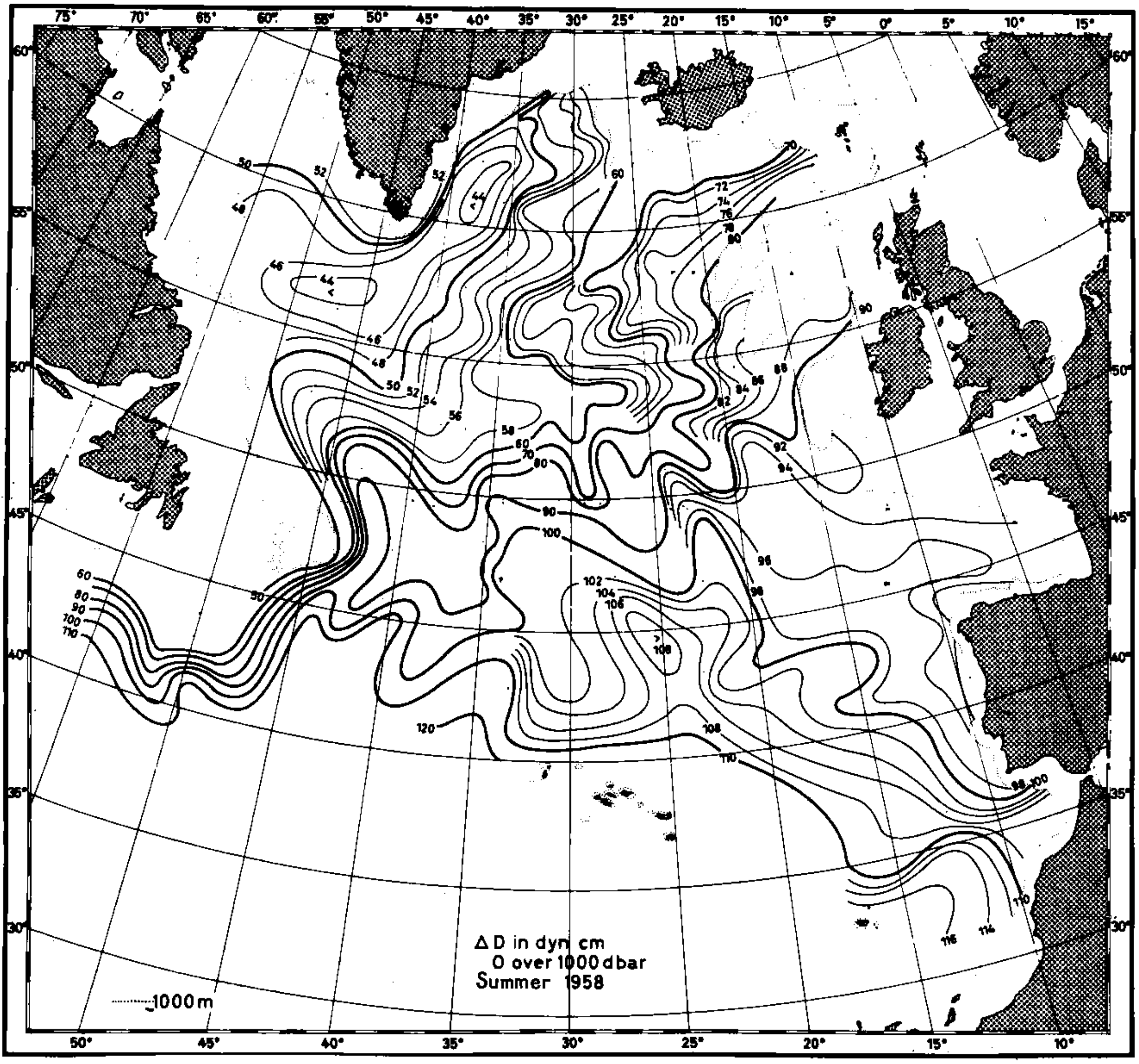

Fig. 12. Dynamical topography of the sea surface (0 over 1,000 decibar) in the northern North Atlantic in late summer 1958.

The general consequences of the vertical component of the water movement are known. Cyclonic movements in the ocean and atmosphere on the rotating earth are combined with upwelling in the centre of the cyclone, while anticyclonic movements are combined with downwelling in the centre of the anticyclone. This means that, in a cyclonic movement, cold, deep water, rich in nutrients is brought up near the surface. This can be seen in Fig. 13 which shows a section from Greenland to the Azores and represents the temperature and the oxygen distribution in the early spring of 1958. Note that the vertical scale is reduced four times at depths below 1,000 m. When in the

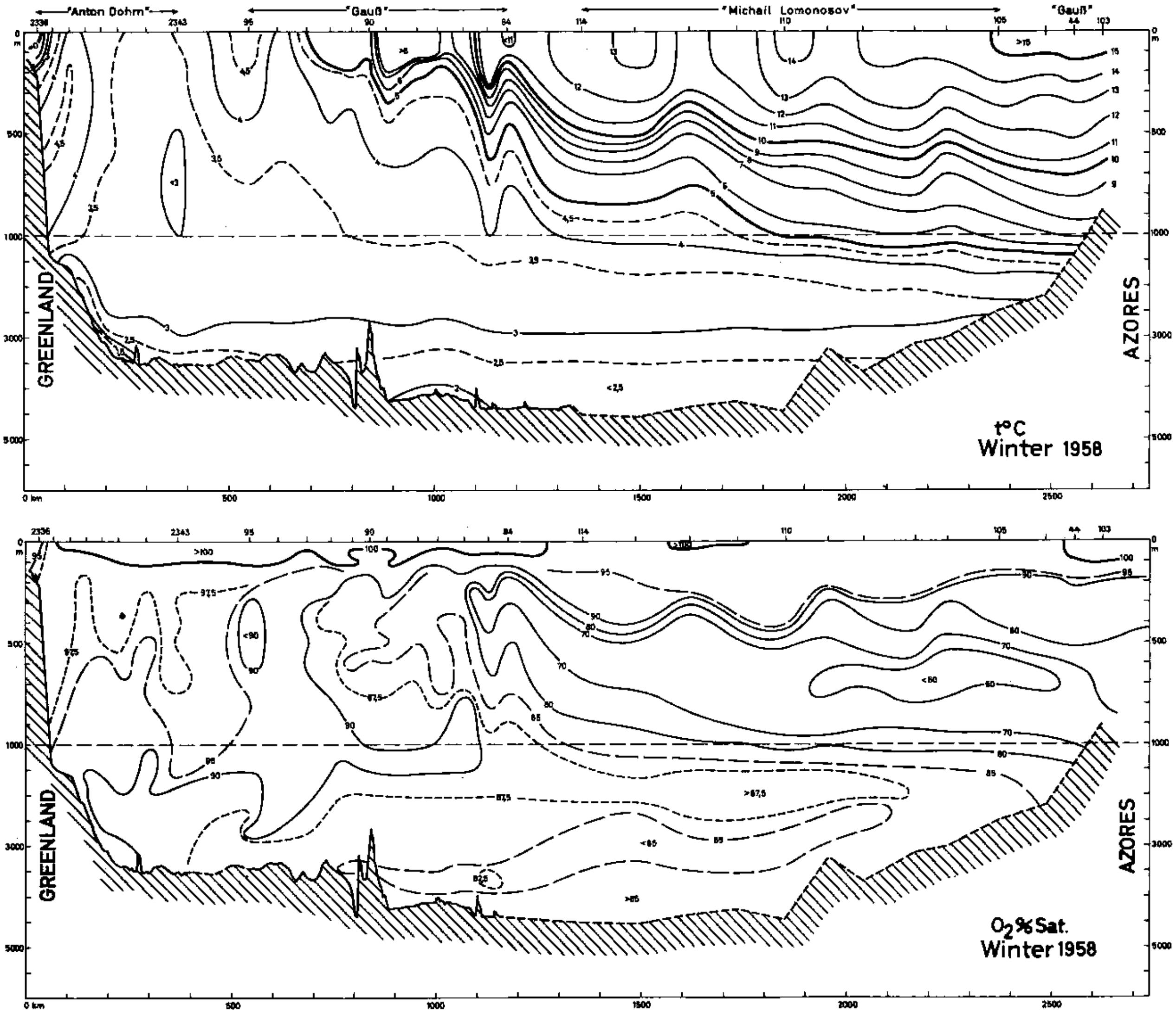

Fig. 13. Temperature and oxygen (in % of saturation) distribution on a section, South Greenland (Cape Farewell) to Azores, in late winter 1958.

centre of the cyclone, *i.e.* in the central Labrador Sea, the surface water cools in winter and a deep-reaching vertical convection starts. The water is nearly homothermal and the oxygen-rich surface water reaches the deep layers. The vertical renewal goes down to 3,000 m making the Labrador Sea one of the best aerated areas in the world oceans and the most effective source for the deep water circulation of the whole Atlantic Ocean. These cold water masses with high oxygen content can be traced through the whole Atlantic southward to the Antarctic waters. The Atlantic deep water breathes like a pair of lungs, but the frequency of breathing is small. It happens only once each year in winter, when the thermocline has vanished. In the North Atlantic Ocean proper this happens only in the Labrador Sea. It is mouth and air tube for oxygen for the deep Atlantic Ocean. Thus, the Northwest Atlantic, this rough, unpopular, part of the Ocean, holds a key position in the deep water circulation.

The convection processes in the Labrador Sea which are of great importance for the renewal of the surface layer and, therefore, for the environment of the eggs, larvae and fish, have already been mentioned. When this vertical convection was first studied 30 years ago by Hermann Wattenberg and myself on the old *Meteor* in the winter of 1935 between Farewell and Newfoundland, I thought the water column was homogeneous. The same conclusions were made in the winter of 1958 during the IGY cruises. Looking critically at the single observations they often seem to be an oversimplification of the processes. I was happy, therefore, to send some of my co-workers on the *Anton Dohrn* in 1963 to the NORWESTLANT Program in the same area. This was in April and it was expected that isothermal and isohaline water would be found. A new "in situ salinometer", developed in Kiel, recorded the temperature and electrical conductivity and, with its help, the salinity from the surface down to 1,400 m was computed. This new recording instrument, the bathysonde, was used at all stations.

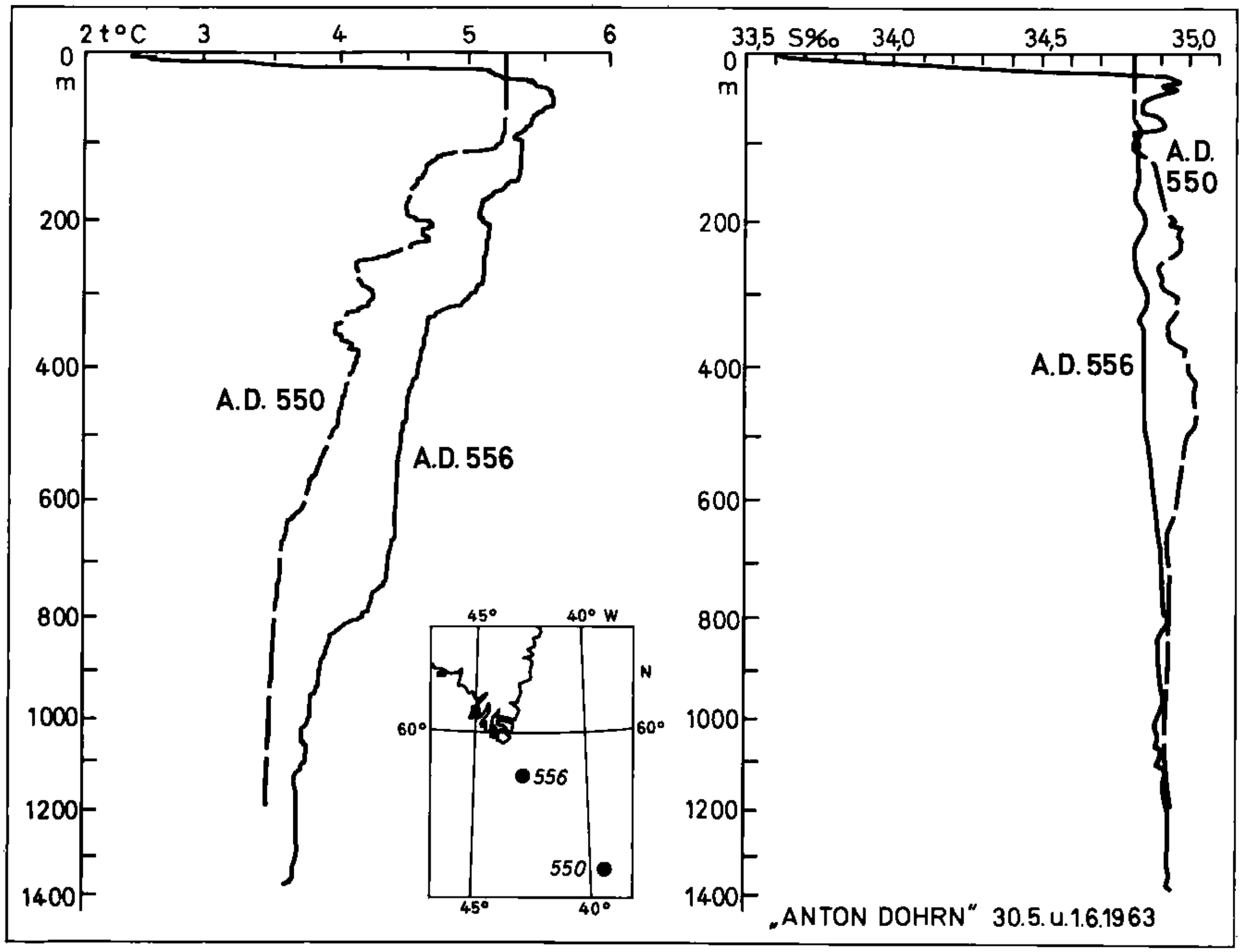

Fig. 14. Recording of temperature and salinity (based on recordings of electrical conductivity) with the bathysonde on two *Anton Dohrn* stations in the Labrador Sea 1963 (After Holzkamm, Krause and Siedler, 1964).

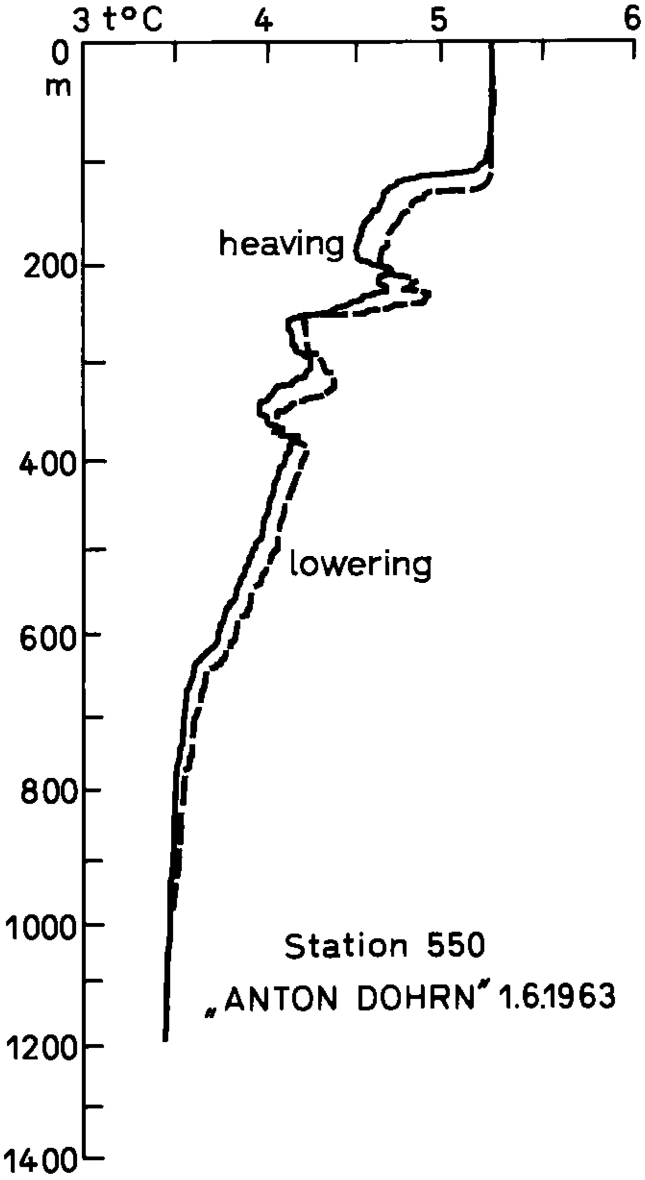

Fig. 15. Recording of temperature at the *Anton Dohrn* station 550 during lowering and raising of the bathysonde (After Holzkamm, Krause and Siedler 1964).

Figure 14 shows the typical results from two stations. The temperature, accurate to 0.01°C, shows a fine structure of layering. The differences are not great, some 0.1 to 0.3°C, but the vertical gradients are remarkable. The new recording instruments demonstrate in the cases of temperature, salinity, oxygen or transparency, that the ocean water is much more inhomogeneous than is suggested from the water sampling and the temperature measurements with reversing thermometers. From our observations, it seems that there is no vertical convection, but rather an inclined convection along density surfaces. Attempts to find characteristic layers in the recordings from neighbouring stations (the distance between our stations in the Labrador Sea was 20 nautical miles) were made without any definitive relations. A relatively small inclination of the layers is enough to prevent finding it again in a station 20 miles away. The situation appears even more difficult when examined in some detail. The temperature curves recorded at *Anton Dohrn* station No. 550, during the lowering and raising of the instrument, (Fig. 15) shows that in the isothermal surface layer the curves are identical, although the time between lowering and raising is about 30 min. But below the surface layer, the curves show that temperature differences are great. Most of the differences can be explained by internal waves. The water layers rose between the time of lowering and raising about 20 m, but there are also differences which cannot be explained by vertical changes, *i.e.* by internal waves, but which might be explained by horizontal differences in the layers. This is the local inhomogeneity with which the oceanographer is confronted, even in the open ocean. The consequences are far-reaching. On the one hand, it is stimulating for the scientist; on the other hand, it is discouraging to see how complicated the sea is. Reference stations for comparing the methods are useless in such a situation.

To this point, we have considered the bottom topography of the Northwest Atlantic, beginning in the open ocean and finishing on the shelf, as well as some new aspects of the ocean water starting in the open ocean. The last step is to consider the shelf waters. These waters are most important for the commercial fish. Our general knowledge of them is relatively good and is based on many expeditions. The current system includes the East Greenland Current, the West Greenland Current, the Baffin Current and the Labrador Current, all distinguished by their cold, low haline water. Some points of our knowledge can be summarized from a series of selected sections extending over the shelf from Denmark Strait to the Grand Banks. The general features of the shelf are found in many publications (Smith, *et al.* 1937; Dietrich, 1957*b*, 1960; Krauss, 1958; Hermann, 1961; Adrov, 1962). Two facts concerning the temperature features (Fig. 16, 17) should be mentioned.

1. The four currents are not one system, but two, namely the East and West Greenland Current system with its origin north of Denmark Strait and the Baffin and Labrador Current system with its origin north of Baffin Strait picking up only a weak branch of the West Greenland Current.

2. Each of the four currents is in some regions divided into two parallel currents, while in other regions the two branches are joined, depending on the width of the shelf and on the shelf rise, which I have mentioned as the characteristic feature of the Northwest Atlantic shelf.

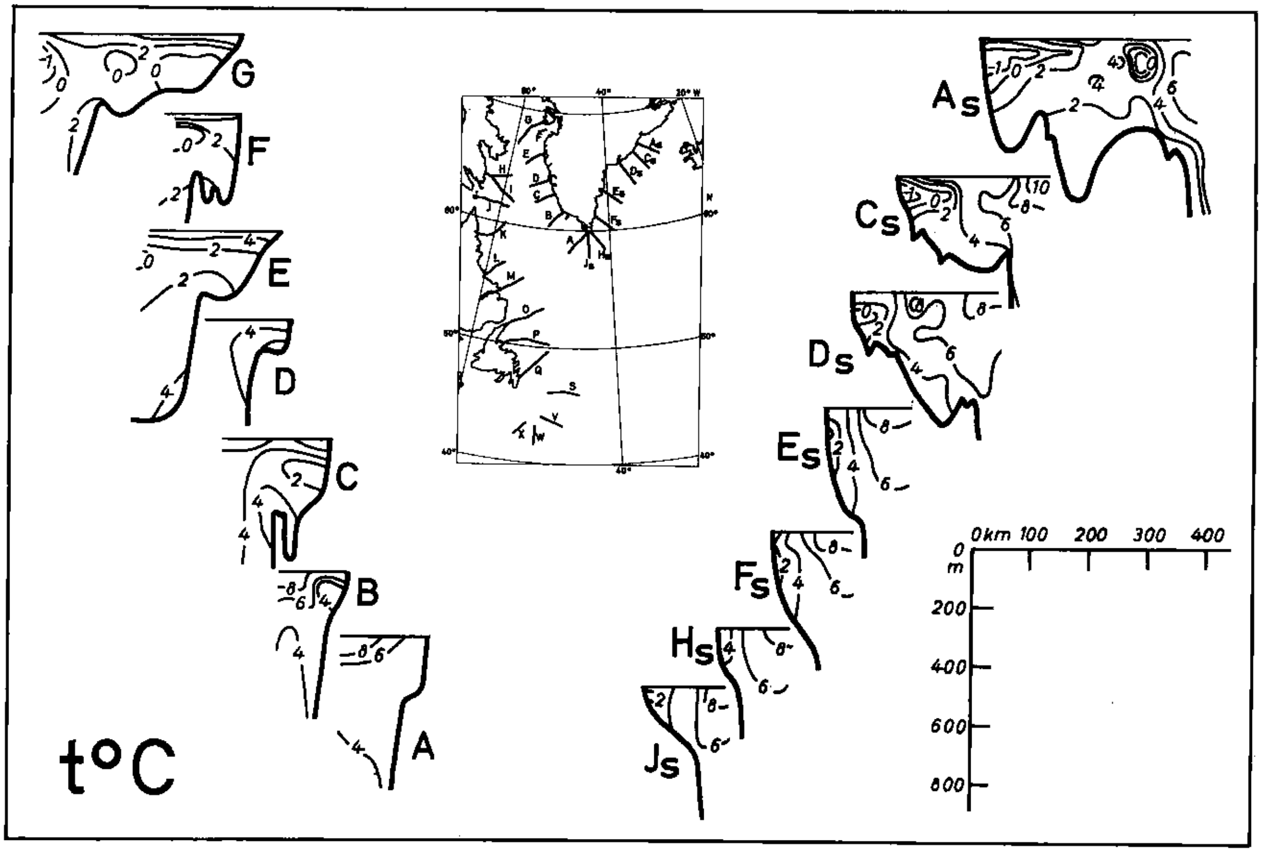

Fig. 16. Series of selected temperature sections over the Northwest Atlantic shelf (After Smith, Soule, Mosby, 1937 and Dietrich, 1960).

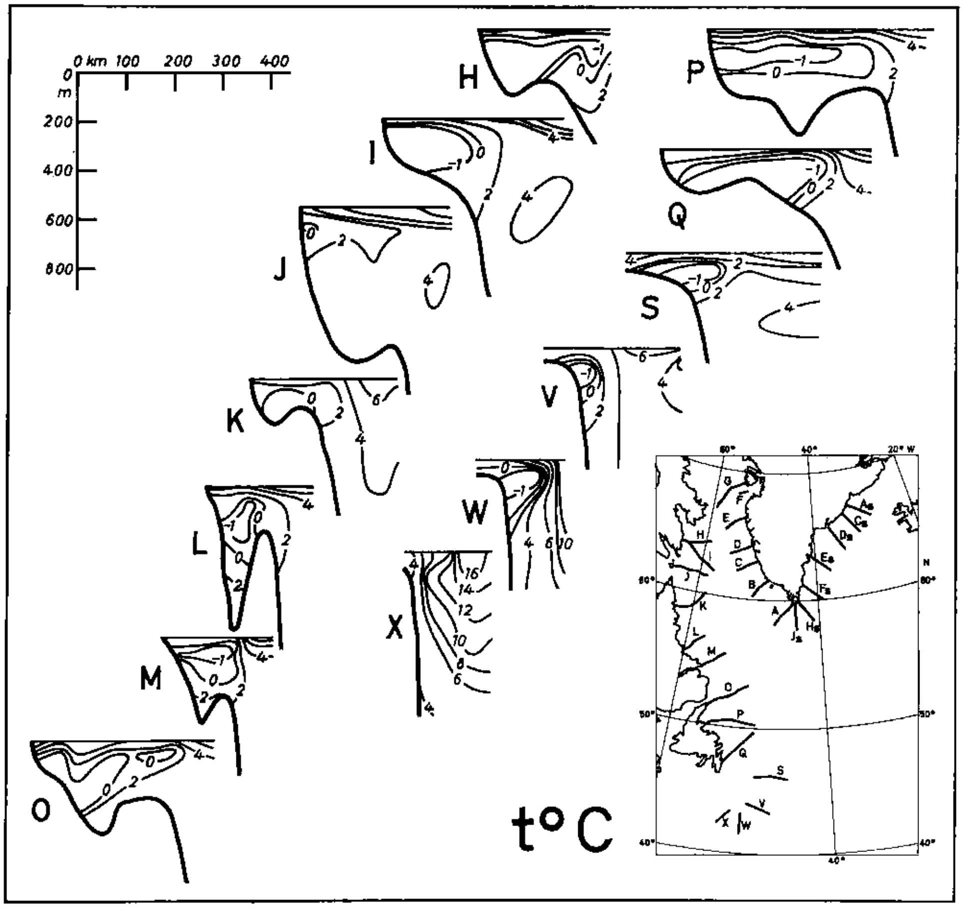

Fig. 17. Series of selected temperature sections over the Northwest Atlantic shelf (After Smith, Soule, Mosby, 1937 and Dietrich, 1960).

It may be added that the cold water cores do not represent the currents but are their borders. The density gradients are highly influenced by the salinity. Therefore, let us look at the same series of salinity sections in Fig. 18, 19. If we consider the sections carefully, we confirm the statements, namely two currents in some regions, on the whole decreasing along Southern Greenland and renewed in the Baffin Strait.

Many investigations have shown that the velocity of the currents is high (up to 1 m/sec and more) that the velocity and hence water transport changes in time and also that the axis of each current shows horizontal displacement. The changes of the currents in place and time make it evident that great changes in the natural environment, which the biologists want to know about, are taking place in temperature, salinity, oxygen and nutrients. The hydrographers therefore are in a very difficult position, because just the rises on the edge of the shelf, which belong to the main fishing places, are under the influences of great changes in the characteristics of the water masses. Satisfactory forecasting is nearly impossible unless we undertake systematic investigations of the dynamics of these strong ocean currents. Such work cannot be neglected. The hydrographic sections cannot be abandoned, but new research methods which are adequate to the problem must be used.

The following review of the natural situation may help to explain my proposed new method of research. In August 1956 we made a topographic survey of the new fishing grounds found by the *Anton Dohrn* and *Gauss* in 1955 in East Greenland waters and observed the surface temperature along the narrow echosounding sections. Figure 20 shows the quasi-synoptic map of surface temperatures obtained.

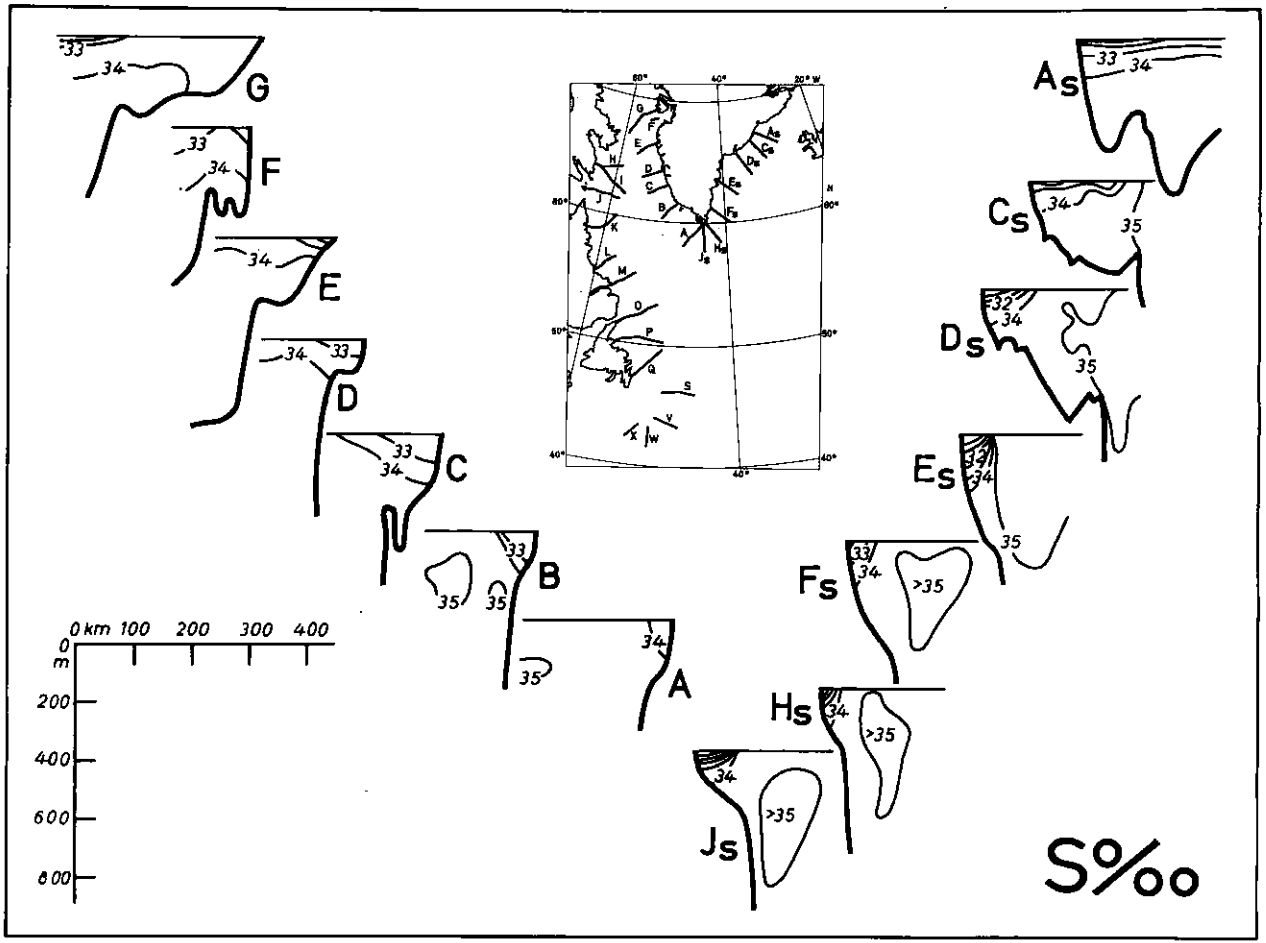

Fig. 18. Series of selected salinity sections over the Northwest Atlantic shelf (After Smith, Soule, Mosby, 1937 and Dietrich, 1960).

The East Greenland current is the thermal front where the temperature changes abruptly about 6 to 8°C. This front meanders and, although observations do not show it, the meanders are likely drifting in the main direction of the current. The front follows the shelf edge but with the horizontal displacements of the current axis also influencing the deeper water of the shelf. One method of following the displacement of this front is not with a ship, but with the use of an aircraft to measure the infra-red radiation from the sea surface. I made this proposal to the US Weather Bureau in 1957 but I have seen no results. Today, a new method is available and again I have a proposal for our American colleagues. We know that in springtime this thermal front is also the edge of the pack ice.

This edge of the pack ice can be distinguished in the pictures taken by the weather satellites. Photographs of the ice distribution in the Gulf of St. Lawrence taken from the first weather satellite "*Tiros I*" are very encouraging (Wask, and Popham, 1960). My guess is that the pack ice border in the Labrador Sea in springtime will also follow the thermal front. Perhaps our American and Canadian colleagues can find a way to use these outstanding technical devices to study the fishes' environment from outer space. It should be possible to take pictures of the ice edge repeatedly in order to evaluate changes in its position with time and to establish its general

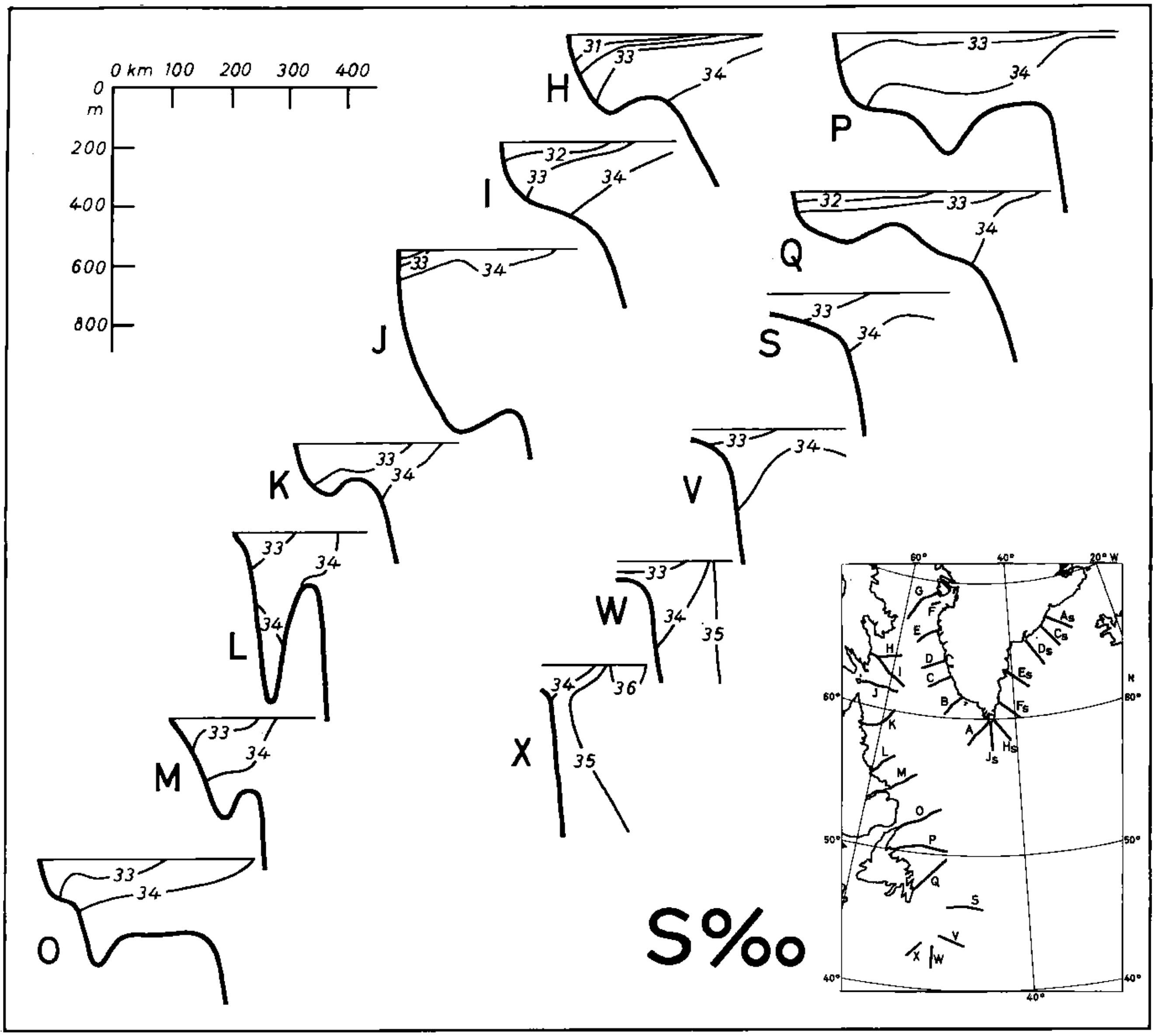

Fig. 19. Series of selected salinity sections over the Northwest Atlantic shelf (After Smith, Soule, Mosby, 1937 and Dietrich, 1960).

relationship with the meandering of the current.

The other method of investigation is to anchor recording instruments in the most interesting areas. This cannot be done by using surface buoys because of the pack ice and the icebergs. But it can be done by using instruments anchored near the bottom. The instruments can be released from the anchor by a signal and floated to the surface. This method of investigation has many difficulties, but these have to be overcome, because without continuous recordings for weeks and months, we cannot understand the dynamics of water movements and cannot make a decisive step forward in providing the marine biologist with the information he is asking for about the environment.

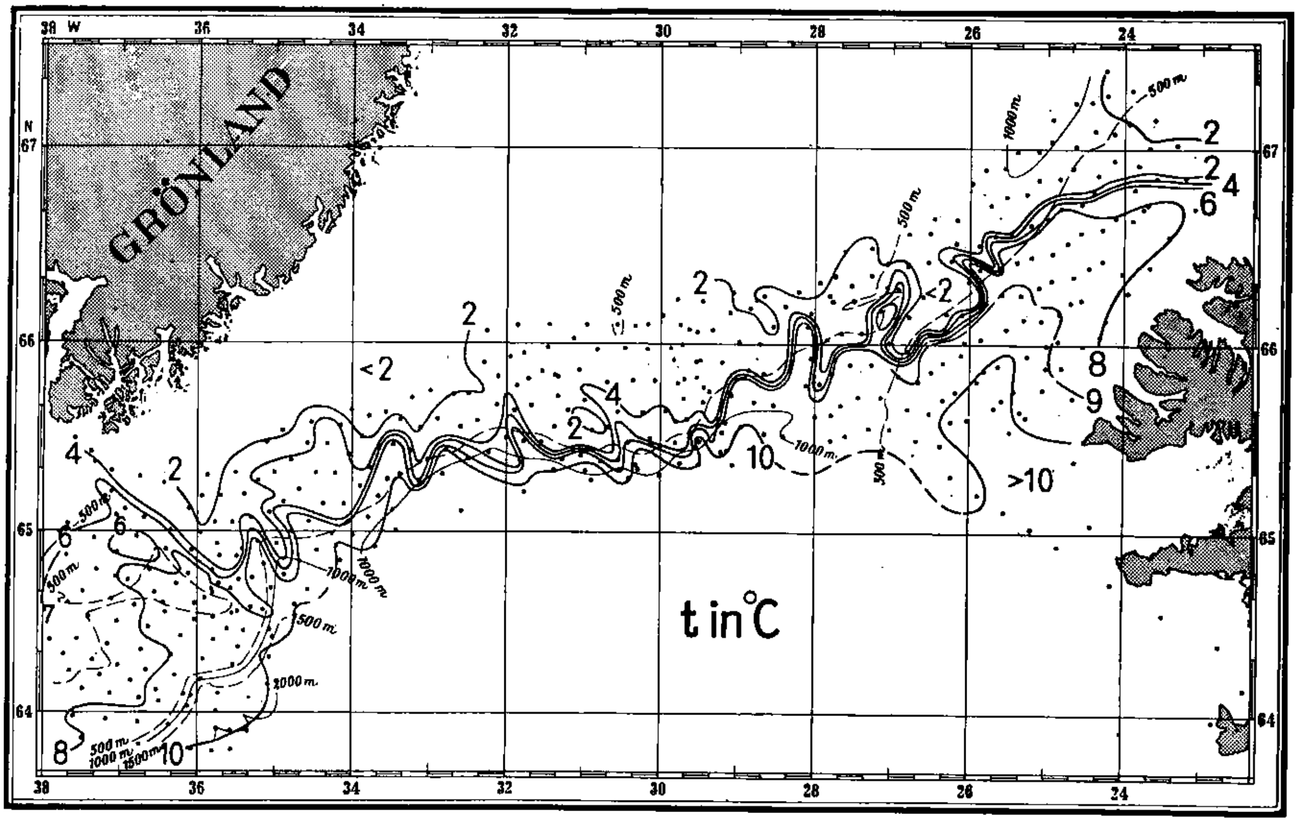

Fig. 20. The thermal front of the East Greenland Current in August 1956 (After Dietrich,1957*b*).

REFERENCES

ADROV, M.M. 1962. Hydrologic investigations off West Greenland. *Soviet Fish. Invest. in North-Western Atlantic.* Moscow. VNIRO and PINRO.

BÖHNECKE, G. and A. BÜCKMANN. 1959. Edit: Die Expeditionen von F.F.S. *Anton Dohrn* and V.F.S. *Gauss* im Internationalen Geophysikalischen Jahr 1957/1958. Erg. Heft Nr. 3, *Dtsch. hydrogr. Z.*

DIETRICH, G. 1957*a* Ozeanographische Probleme der deutschen Forschungsfahrten im Internationalen Geophysikalischen Jahr 1957/1958. *Dtsch. hydrogr. Z.*, 10: 39-61

1957*b*. Schichtung und Zirkulation der Irminger-See im Juni 1955. *Ber. dtsch. Komm. Meeresforsch*, 14: 255-312.

1960. Temperatur-, Salzgehalts- und Sauerstoffverteilung auf den Schnitten von F.F.S. *Anton Dohrn* und V.F.S. *Gauss* im Internationalen Geophysikalischen Jahr 1957/1958. Erg. Heft Nr. 4, *Dtsch. hydrogr. Z.*

1964. Oceanic Polar Front Survey in the North Atlantic in the IGY. US Nat. Acad. Sc., Spec. Vol. for IGY. (in press).

DUNBAR, M.J. 1951. Eastern Arctic Waters. *Bull. Fish. Res. Bd. Canada*, 88, 1-131, Ottawa.

HACHEY, H.B., F. HERMANN and W.B. BAILEY. 1954. The Waters of the ICNAF Convention Area. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 4: 67-102.

HEEZEN, B.C., M. THARP and M. EWING. 1959. The floors of the oceans. I. The North Atlantic. Geol. Soc. Amer. Spec. Paper 65.

HERMANN, F. 1961. Danish hydrographic observations under the Polar Front Programme. *Rapp. et Proc. Verb.*, 149: 118, Copenhagen.

HOLZKAMM, F., G. KRAUSE and G. SIEDLER. 1964. Observations of the vertical fine structure of water layers in the Irminger Sea. (In press).

INTERNATIONAL COUNCIL FOR EXPLORATION OF THE SEA. 1961. Contributions to special IGY Meeting 1959. *Rapp. et Proc. Verb.* 149, Copenhagen.

KRAUSS, W. 1958. Die hydrographischen Untersuchungen mit *Anton Dohrn* auf dem ost- und westgrönländischen Schelf im September-Oktober 1955. *Ber. dtsch. Komm. Meeresforsch,* 15: 77-104.

LITVIN, V.M. and V.D. RVACHEV. 1962. A study of bottom relief and types of ground in the fishing areas of Labrador and Newfoundland. *Soviet Fish. Invest. in North-Western Atlantic.* Moscow. VNIRO and PINRO. P. 9-111.

SMITH, E.H., F.M. SOULE and O. MOSBY. 1937. The Marion and General Green expedition to Davis Strait and Labrador Sea. *Bull. U.S. Cst. Guard,* 19.

ULRICH, J. 1962. Echolotprofile der Forschungsfahrten von F.F.S. *Anton Dohrn* und V.F.S. *Gauss* im Internationalen Geophysikalischen Jahr 1957/1958. Erg. Heft Nr. 6, *Dtsch. hydrogr. Z.*

1963. Zur Gestalt des Meeresbodens im Nordatlantischen Ozean. *Erdkunde* 17, 190-205.

WASK, D.Q., and R.W. POPHAM. 1960. *Tiros I* observations of ice in the Gulf of St. Lawrence. *Month. Weath. Rev.* 88, 182-186.

A REVIEW OF THE EFFECTS OF THE ENVIRONMENT OF THE PACIFIC SARDINE

By

E. H. Ahlstrom[1]

Four and a half years ago a sardine symposium was held here in Rome. The chief theme of that symposium was the marked fluctuations that occur in abundance of clupeid stocks. It, also, was basically an environmental symposium. My contribution to that symposium, a background paper on "Fluctuations and Fishing" has only an oblique relevance to our present symposium. Two sections of the sardine symposium dealt more directly with environmental factors; these were titled: "Fluctuations in abundance and availability caused by biotic factors" by Ramon Margalef, and "Fluctuations in abundance and availability of sardine populations caused by abiotic factors" by Zinziro Nakai.

Some points raised in the sardine symposium will reappear in my presentation, but the bulk of the material I wish to present is of more recent vintage.

When considering what I should include in my talk, I decided that primary emphasis should be placed on our recruitment studies. Our sea surveys combine oceanographic and biological observations, and thus permit us to relate environmental variables to the distribution and abundance of the younger stages of sardines and other pelagic fishes.

We are also concerned with the effect of physical environmental conditions on the distribution of the adult sardine population. A variable portion of the sardine population has been available to the U.S. fishery; this varying availability has constituted one of our major problems.

Our laboratory has spent a major part of its research effort on the problem of year-class strength in the Pacific sardine. Much of our research has been done in cooperation with the Scripps Institution of Oceanography. It covers the years 1939 to 1941, and 1948 to the present. Since 1949 the investigations have formed part of the California Cooperative Oceanic Fisheries Investigations, which we abbreviate into CalCOFI.

Systematic hydrographic-biological surveys have been made since the inception of CalCOFI. Surveys between 1949 and 1960 were made at approximately monthly intervals; since 1961 surveys have been spaced at quarterly intervals. The region being surveyed has as its dominant feature the southward flowing California Current, which is the eastern limb of the clockwise circulation in the North Pacific. Stations in the survey pattern are arranged in lines which are normal to the general trend of the coastline, hence cut across the California Current. The pattern that is routinely surveyed at present on the quarterly survey cruises extends from San Francisco, California, to Pt. San Juanico, Baja California, a north-south extent of 920 miles. Station lines are spaced 40 miles apart, stations on lines are spaced at 20 or 40 miles intervals, except near shore where the spacing is closer. Most of the 24 lines of stations in the pattern surveyed routinely extend 200 to 250 miles seaward, but two of the cardinal lines of stations off California extend over 600 miles to sea in order to completely delimit the offshore extent of the California Current.

Some cruises made during the 1950's had more extensive coverage than that just described, extending from Cape Mendocino, off northern California, to below Cape San Lucas, Baja California—a north-south extent of 1,320 miles. Our surveys have had the advantage of co-ordinated hydrographic and biological observations.

We have put more effort into investigating the distribution and abundance of the young stages of fishes than any other research group, so it becomes pertinent to ask, has it been worth the time and money expended?

If I were to single out one aspect of egg and larval surveys as of prime importance, it would be their use in fish resource evaluation. This is especially true off California, where our fish resources are but partially exploited. It is a most fortunate circumstance that most of our marine

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fishes spawn in the open sea, and their egg and larval stages may be quantitatively sampled by plankton gear. It was through our surveys that we found out how widely distributed the jack mackerel resource is at time of spawning, how consistently abundant and widespread are hake eggs and larvae, rockfish larvae, etc. But of more consequence to our research has been the information gathered on the northern anchovy. Without this body of information it would not be possible to document the marked increase in abundance of this resource that has occurred since 1950. The anchovy appears to have filled most of the ecological niche formerly occupied by the sardine.

I discussed various aspects of the use of larval surveys for resource evaluation in the talk I gave at the larval fish symposium we held as part of our CalCOFI Conference at Lake Arrowhead, California, in October of 1963.

A number of European biologists participated in the larval fish symposium including Gotthilf Hempel, Jim Shelbourne, John Blaxter, Fred Holliday and Wilhelm Einsele. The contributions to the symposium will be published in Vol. X of our CalCOFI Reports, so I will not enlarge further on the use of larval surveys in resource evaluation, except as they apply to the competition between sardine and anchovy.

We have also demonstrated that it is possible to delimit the spawning range of a widely distributed pelagic species and to follow the year by year variations in the time and place of its spawning.

Too much emphasis and concern has been placed on the precision with which the amounts of spawning can be determined. We estimate that the 95% fiducial limits of our yearly estimates of egg abundance are approximately half or double. The consistency of our results are compatible with this judgement. Furthermore, if surveys were limited to sampling of eggs alone, it would be possible to devise sampling techniques that would greatly increase the reliability of our estimates. In a paper on a high speed sampler, designed by John Isaacs, and co-authored by Ahlstrom, Isaacs, Thrailkill and Kidd, 1958, we demonstrated that horizontal strip sampling along cruise tracks using a series of high speed samplers is an excellent way of integrating the patchy distribution of sardine eggs over area. This technique was not used routinely because our high speed samplers did not collect sufficient larvae—the volume of water strained was just too little to get an adequate size representation of larvae. Hence, to avoid using two kinds of sampling gear, one for eggs, one for larvae, we have continued to sample with obliquely-hauled plankton nets.

We have found that estimates of larval abundance are more consistent than estimates of egg abundance. This is an interesting point, as it is often assumed that the reverse is true (*e.g.* in Saville's (1964) contribution to the 1963 ICES Symposium on the Measurement of Abundance of Fish Stocks). When I present our estimates of larval abundance of the anchovy in a later section, this point will become quite clear.

There are two contrasting approaches that can be followed in investigating the effect of environmental conditions on year-class strength. One approach considers that the environmental effect is a widespread, primary effect such as a marked warming or cooling of ocean temperatures throughout the spawning range, changes in the intensity or flow of major current systems, changes in productivity, and the like. The other approach is to consider that good survival is related to local, more transient effects—that we are, in point of fact, dealing with patchiness in survival—the coincidence in certain areas of high availability of food organisms at times that larvae begin to feed, or of low predation on the developing larvae, and so forth.

Most of the workers dealing with the effect of environmental conditons on year-class strength assume that the former is the correct approach to follow—that even if survival is patchy, there will be more areas of good survival under certain widespread environmental conditions such as high productivity or favourable transport.

There is good rationale behind this approach. In order to correlate environmental factors with year-class strength, the factors have to have certain consistency in their effects from year to year, and they have to be of the kind that can be quantitated.

For example, if there is a relation between temperature and survival, we carry out the correlation by having a single value for survival rate and for temperature for each year in a series. The same would apply to a correlation involving basic productivity, or the intensity of upwelling, or the amount of water carried by currents, etc. It is necessary to express some values in relative rather than absolute terms. With quantitative data, multiple correlations can be carried out as well as simple correlations.

On the other hand, if we should be investigating the more transient conditions that favour good survival, our problem becomes a more difficult one, perhaps by orders of magnitude. For one thing, it is difficult to locate and recognize transient phenomena. Their effective study would require more resources for sea surveys than are available to us. A more important consideration is that it is difficult to quantitate transient phenomena.

A good example of a successful application of this approach on a small scale is Shelbourne's (1957) paper dealing with,"The feeding and condition of plaice larvae in good and bad plankton patches".

I read Gulland's contribution to the symposium on "Survival of the youngest stages of fish and its relation to year-class strength" (B-9) with great interest. He points up the weaknesses in the correlation approach and he adds this pungent sentence, "Though many correlations between year-class strength and environmental factors have been suggested, few, if any, have stood the test of time."

Perhaps there have been several difficulties in the approaches followed to date. Fishery biologists, along with other scientists, like to simplify their problems. They know that the environment is complex, but they are nevertheless hopeful that some factors are of over-riding importance, and that it may be possible to find a straightforward relation between environmental variables such as wind, temperature or productivity and year-class strength.

Simplification is an essential technique in science, but it so easily leads to over-simplification. We begin to investigate a species as if it were living in vacuo, entirely separate from other species. Further, the environmental conditions looked at are often those that come easiest to hand, data collected over a series of years for other purposes, such as meteorological data, light ship data, or sea surface temperatures. These over-simplified approaches have not stood the test of time, and they lead inevitably to the conclusion that year-class strength is not mediated by any one factor alone.

One of the early correlations relating year-class strength to an environmental variable was Walford's (1946) correlation between year-class strength in the Pacific sardine and salinity. Walford used year-class strength as determined from the fishery and the summer salinity at Scripps Pier. The relation was interpreted as one between productivity and survival--high salinity was the resultant of more intensive upwelling with attendant transport of inorganic nutrients, which increased the phytoplankton production and which in turn was reflected in the other parts of the productivity chain. It has been pointed out by various investigators (*e.g.* Marr, 1960) that the correlation did not hold for subsequent years.

One of the difficulties with Walford's simplified analysis is that high salinity can result from causes other than upwelling. There are better indices of upwelling than salinity alone, indices that take temperature, oxygen and nutrient content of the water into account as well as salinity.

There is an implication in a correlation between general productivity and year-class strength that most fishery scientists have overlooked, mainly because they have been looking at a single species rather than the complex of species in an ecological assemblage. If the relation is a simple cause and effect relation between productivity and survival, then we would expect the effect to be reflected in all species in a trophic level. We should have good survival of anchovies in the same years when we have good survival of sardines, for example, along with good survival of jack mackerel and Pacific mackerel, etc.

It is very easy to demonstrate that this is just not so. There is no consistent relation between good year classes of sardines and good year classes of anchovies. In fact, as I will point out later, the reverse appears to be true. Neither is there a coincidence between good year classes of sardines and Pacific mackerel.

Furthermore, we have found that there is no consistent relation between one measure of productivity, the standing crop of zooplankton, and year-class strength of sardines. Here again, some of the poorest survival years have been years of high productivity.

I am fully cognizant of the fact that more sophisticated measures of productivity are needed than measures of general productivity. It has been pointed out by various scientists that what is needed is information on the kinds of food organisms important in the diet of fish larvae, determined in the areas where larvae occur over the time period of their development.

Arthur (1956) studied the sizes and kinds of food particles eaten by sardine, anchovy, and j mackerel larvae. He found that body shape and particularly head and mouth size determined the size of particles that could be engulfed. Sardine and anchovy larvae are, of course, elongated, threadlike larvae with small heads. Newly feeding larvae can engulf only very small food particles—up to about 80µ in length. These are the sizes of organisms that have to be sampled by water bottle rather than by nets. As the larvae of both species increase in length, they consume increasingly larger food particles, hence have a wider spectrum of choice. Even so, copepods in various stages of development formed the bulk of the diet of both species. Jack mackerel larvae have a much larger head and gape in relation to length, and as a consequence, have a greater choice of food items. The studies, as we will see later, show that sardine larvae are very directly competitive for food with anchovy larvae, much less so with jack mackerel larvae.

The CalCOFI surveys have sampled microplankton only intermittently, so we do not have the body of information needed for correlating larval survival with abundance of larval food. However, because the food requirements of sardine and anchovy larvae are so similar, and the larvae of the two species tend to co-occur, as I will show later, the two species should in general respond similarly, if abundance of larval food is a controlling mechanism in year-class strength. As I have noted earlier, there is no such correspondence.

Environmental conditions are often thought of in terms of primary physical parameters, such as temperature or drift. The only biological factor usually considered is food. This is too restricted a view. The thesis I wish to develop is that the primary environmental condition can in some situations be other fish—especially species occupying the same trophic level. I am not going to ignore other environmental factors, although I must confess that some of them have lost their glamour.

In developing my point, I will go into our sampling procedures and problems in enough depth to establish that we can sample eggs and larvae of sardines and anchovies with some precision. This is a necessary requirement if one is to deal with the effects of competition within a trophic level. As a prelude, may I say that we early established the depth distributions of sardine and anchovy eggs and larvae, to insure that our sampling at all stations more than covered this parameter.

First, I would like to discuss some of our observations on the distribution and abundance of sardine eggs during the decade of the 1950's. During these years sardine spawning occurred mainly between Pt. Conception, California and Pt. San Juanico, Baja California. Even within this area, the distribution of eggs was quite different from year to year. In 1952 and 1953, for example, very little spawning occurred off southern California and northern Baja California while heavy spawning took place off central Baja California. In 1954 there was an explosive spread northward to waters off northern Baja California and southern California. The 1954 distribution of both sardine eggs and larvae constituted the most widespread distribution encountered during the decade. I am including a figure (Fig. 1) to contrast the distribution of sardine eggs in 1953 and 1954.

There were no marked changes in oceanographic conditions between 1953 and 1954 that would account for the dispersion of sardines that occurred. A moderate increase in temperature is the only obvious difference. A plausible explanation is that sardines spread out in response to an increase in population abundance, resulting from the recruitment of the fairly successful 1952 year class. During 1954 approximately 38.5 % of sardine eggs were obtained off northern Baja California and southern California in contrast to the 1% obtained in these areas during 1953.

Sardines that came to California waters to spawn in the spring of 1954 remained in the area during the commercial season. The catch jumped from 4,000 tons in the 1953-54 season to 68,000 tons in the 1954-55 season. The change in spawning distribution preceded the change in catch,hence demonstrated that egg surveys could furnish advance information on availability, that is, on the portion of the sardine population likely to be accessible to the U.S. fishery. Distributions of sardine spawning in the immediately succeeding years, 1955, and 1956, were similar to 1954, although less widespread.

While the change in distribution that occurred between 1953 and 1954 has no obvious relation to oceanographic conditions, changes that occurred in the time and place of sardine spawning in 1958 were obviously influenced by the warmer regime then prevailing. During the years between 1950 and 1956, ocean temperatures off California were below the long term average. Professor John

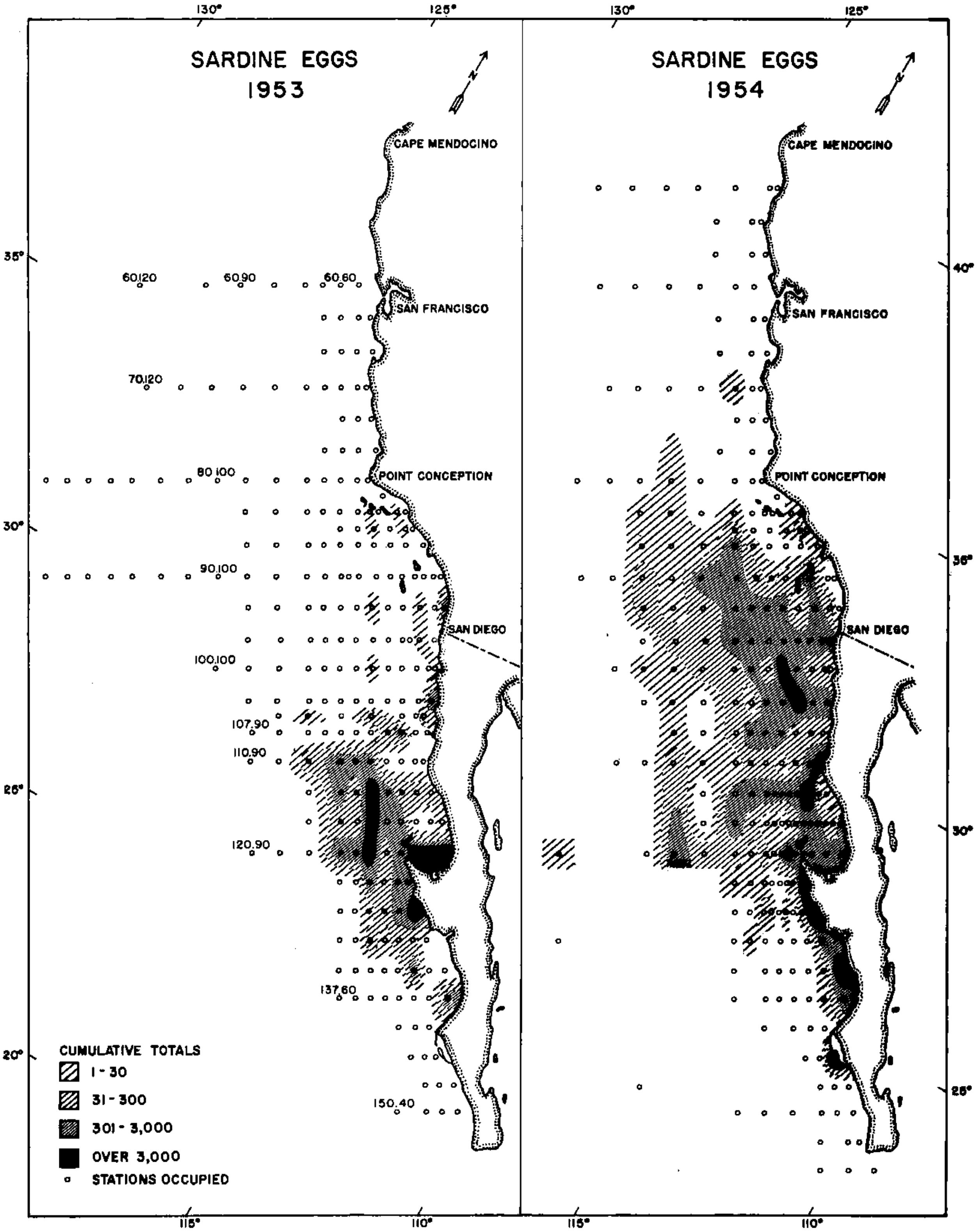

Fig. 1. Distribution and relative abundance of sardine eggs in 1953 and 1954. Selected station numbers of the CalCOFI survey grid are given on the chart for 1953.

Isaacs (MS) of Scripps refers to these years as the "soggy years". Warming in the region of the California Current began in 1957 and reached its height in 1958. There was a marked warming of several degrees centigrade in many parts of the California Current region. As a result, sardine spawning off southern California which had been mostly confined to the months of May and June during 1950-56 was both markedly earlier and more prolonged in 1958 (Table 1).

TABLE 1. PERCENT OF SARDINE EGGS COLLECTED IN EACH MONTH OFF SOUTHERN CALIFORNIA

	1951-1956	1958
January	0.01	51.33
February	0.03	1.61
March	1.93	17.16
April	5.59	5.06
May	44.59	16.06
June	35.89	1.59
July	11.96	7.12
August-December	0.08	0.08

John MacGregor (1957) of our laboratory has followed the maturation and fecundity of sardines over a number of years. He has found that sardines off southern California in most years reached an advanced stage of maturity by late February. Spawning, however, occurred mostly in May and June. Apparently, the fish held back the final phase of maturation until favourable conditions prevailed in the environment.

We have investigated the distribution of sardine eggs in relation to water temperatures. The lower temperature limit for sardine spawning is about 13°C. This appears to be a critical temperature for sardine eggs. Our physiologist, Dr Reuben Lasker (1964), has found from controlled laboratory experiments that sardine eggs do not develop normally at temperatures below 13°C.

There were extensive areas off southern California with temperatures below 13°C during the first four calendar months of 1951-56, especially during March and April. When spawning took place, largely in May and June of these years, it occurred at temperatures between 13°C-18°C, averaging 14.7°C. The earlier spawning of 1958 took place within the same temperature range, and averaged 15.3°C. Temperature appears to influence both the time of spawning and the length of the spawning season.

The sardine potentially can mature several batches of eggs during a season (MacGregor, 1957). The developing ovaries contain several size modes of yolked eggs. This type of ovarian development is found in many pelagic fishes. It seems logical to assume that more batches are matured during an extended spawning season, such as that of 1958, than during a shorter season, such as prevailed off southern California during much of the 1950's. We do not have definite evidence to prove or disprove this assumption. MacGregor did find that smaller fish, including a portion of the one-year olds, were maturing in 1958; these fish were precocious by about one year. One of the major needs in fecundity studies is an adequate method of determining the number of batches of eggs that are spawned per female and the relation of frequency of spawning to size and age of fish and to environmental conditions.

In considering conditions that might favourably influence the survival of a year class, I have theorized (Ahlstrom 1959*b*, p.203) that the extent of the area over which spawning was spread was probably one of the more important ones: the larger the area, the greater the chance of good survival. The 1954 distribution was the most widespread of any we have encountered in our surveys. As such it affords a test, of sorts, of this hypothesis.

I have given in Table 2 the estimated relative areal extent of sardine eggs for 1952 through 1959. The value for each year is the summation of the areal distributions of eggs on monthly cruises. Similar values for sardine larvae are also included.

The areal extent of sardine eggs in 1954 was nearly 1.5 times as great as in the next best year, 1955, and nearly 5.5 times as great as in 1957. The best survival years in the series are 1952, 1956, and 1957. Areal extent in 1954 was 2.4 times as great as in 1952 and 2.1 times more than in 1956. There does not appear to be any obvious relation between extent of spawning and rate of survival.

TABLE 2. RELATIVE AREAL EXTENT (ΣMONTHLY DISTRIBUTIONS) OF SARDINE EGGS AND LARVAE, IN SQ MILES, 1952 TO 1959

	Northern center (Sta. lines 107 and above)		Southern center (Sta. lines 110-157)		All areas	
	eggs	larvae	eggs	larvae	eggs	larvae
1952	27,800	41,600	89,900	174,900	117,700	216,500
1953	14,600	11,900	98,500	165,400	113,100	177,300
1954	149,900	135,400	137,700	187,900	287,600	323,300
1955	120,900	98,800	76,200	151,200	197,100	250,000
1956	80,400	57,200	55,100	98,600	135,500	155,800
1957	24,600	44,900	28,200	100,400	52,800	145,300
1958	57,500	68,300	21,500	73,600	79,000	141,900
1959	63,300	59,500	26,800	55,700	90,100	115,200

Sardine larvae in all years had a greater areal extent than the eggs. This is not at all surprising, for a larval sample potentially can contain an accumulation of sizes that span approximately 45 days, while a sardine egg sample, on the average, represents an accumulation of only 3 days' spawning.

In our publications we have subdivided the spawning distribution of the sardine in various ways, depending upon what feature we wished to emphasize. Our broadest grouping is a division into northern and southern spawning centers. The northern center comprises all of California and northern Baja California from the international border to Pt. San Quintin. The southern spawning center comprises central and southern Baja California. The areal extents of sardine eggs and larvae in the two centers are shown in Fig. 2. The marked change in distribution of sardine eggs and larvae that occurred in the northern center between 1953 and 1954 is nicely illustrated by this figure. Another reason for its inclusion is to call attention to differences in the distribution of eggs and larvae in the two centers. In the northern center the areal extent of sardine eggs is as great, on the average, as the areal extent of larvae. In the southern center, however, sardine larvae always have a greater areal distribution than eggs, and the difference is most marked below Pt. San Eugenio. The California Current carries developing larvae southward of the area where they were spawned. This happens in all seasons. We have not been able to discern any consistent relation between the strength of the California Current and the extent of larval transport on the one hand, and the rate of larval survival on the other.

Sette (1960) has proposed a rather complex model to explain successful year classes of sardines, especially in the area of the California fishery. To discuss his model in any detail would require more time than I have available. He hypothesized that with weaker winds in winter, the waters on the southern California spawning grounds more often warm earlier in the spring, permitting a longer period of spawning. As a further consideration weaker summer winds were conductive to the better development of the inshore counter-current, permitting the larvae hatched from the eggs to be retained in the southern California area, and to be carried to inshore feeding grounds. Thus successful year classes were likely to be produced during periods of weaker than average winds and warmer than average temperatures. These also would be years with weaker than average flow of the California Current and with reduced amounts of coastal upwelling. This is an attractive model in which the strength of the winds influence both water temperature and the transport of larvae. This pattern did not prevail, however, in 1939, when our most successful year class of sardines was produced. Winter and spring winds were stronger than usual in 1939, but winds were weak during the summer period. Perhaps the essential part of the model is the mechanism that assures the inshore transport of larvae to the feeding grounds.

The population of the Pacific sardine has been shown by Sprague and Vrooman (1962) and Vrooman (In press) to be made up of at least three genetically distinct stocks, two occurring in the Pacific off California and Baja California, the other in the Gulf of California. The stocks in the Pacific are referred to as "northern" and "southern" stocks. Not enough sardines have been tested serologically during the spawning season to definitely establish the spawning distributions of the two Pacific stocks. Enough "fall" spawning sardines have been tested to show that this group is

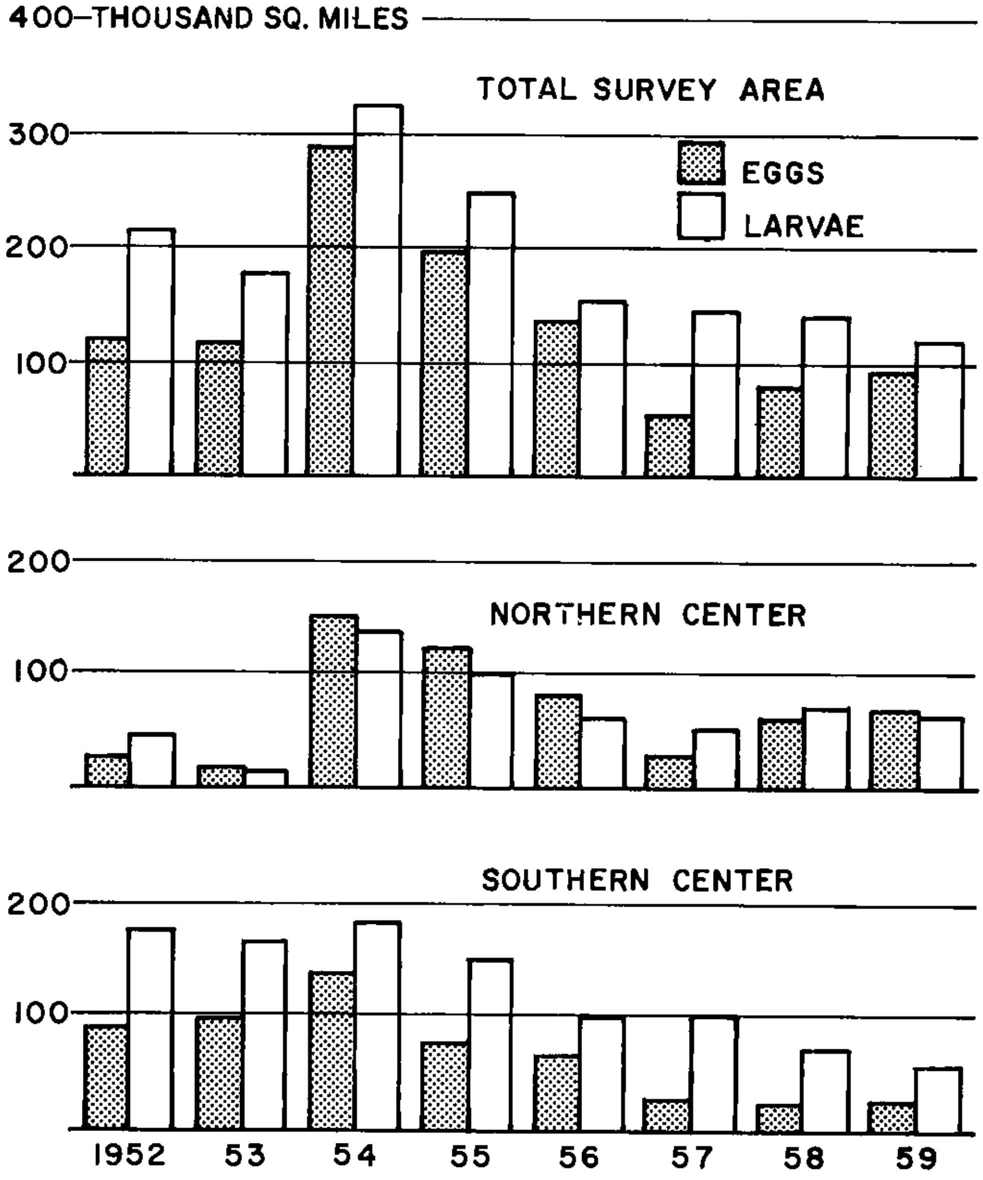

Fig. 2. Areal extent of sardine eggs and larvae, 1952 to 1959. Upper graph, total survey area; middle graph, northern center (station lines 107 and above); lower graph, southern center (station lines 110 - 157).

"southern" fish. Whether all the sardines spawning during the main spawning period belong to the other stock has not been clarified. Since the offseason spawning occurs at temperatures which average 2 to 3°C higher than the spring spawning, we would like to believe that the "southern" stock is a physiologically distinct group of fish.

We obtain an abundance estimate for sardine eggs, which is an estimate of the total number of sardine eggs spawned during a year, exclusive of the Gulf of California. We can determine rather precisely the number of days' spawning represented in each egg collection, either actually or potentially, hence can put each sample of eggs on a spawned per day basis (Ahlstrom, 1943). By integrating these values over time and area, we derive our estimates (Ahlstrom 1954, 1959*b*). Various studies have been made of the reliability of our egg estimates (Silliman, 1946; Sette and Ahlstrom, 1948; Taft, 1960). The fiducial limits of a season's estimate appear to be approximately half or double.

In a paper dealing with the 1950 and 1951 seasons, I also derived abundance estimates for sardine larvae by size (Ahlstrom, 1954). This was, in part, an exercise to demonstrate that such estimates could be derived. The principal weakness was an inexact knowledge of the growth rate of larvae.

Information about the time required to grow through any given unit of larval length is a requisite to meaningful integration of larval data over time. Average values for growth are probably not too meaningful. The rate of larval growth may be as much influenced by temperature as is the rate of embryonic development.

For the present I have given up the attempt to derive abundance estimates of larvae, and am content with a lesser estimate that I call a "census" estimate. The larval data for each collection, by size category, are integrated over area, but not over time. The yearly estimate is simply a summation of the monthly "census" estimates.

We have programs in progress to try to remedy this lack of information about larval growth and how it is affected by environmental variables. These include physiological studies of the nutritional needs of larvae, behaviour studies of sardine and anchovy larvae, and a concerted team attack on the problem of rearing larvae of pelagic marine fishes.

Because of the inadequacies of our growth data, there is little point in taking other than a rough and dirty look at larval survival. A simple way of looking at differences in survival during the larval period from year to year is to relate the number of larger larvae obtained to total eggs or total larvae (Table 3). A year class with good survival should have a larger proportion of larger larvae than a year class with poor survival.

TABLE 3. RELATIVE PROPORTION OF LARGER SARDINE LARVAE (15.26 mm AND LARGER) TO EGGS AND TO TOTAL SARDINE LARVAE COLLECTED DURING THE YEARS 1951-58.

	Estimated abundance eggs ($\times 10^{11}$)	Census estimates larvae ($\times 10^{9}$)	Census estimates larger larvae ($\times 10^{9}$)	Relative proportion larger larvae to eggs	Percentage larger larvae is of total larvae
1951	6108	5773	172.5	2.82	2.99
1952	1360	5465	108.6	7.99	1.99
1953	4402	4020	89.7	2.04	2.23
1954	3554	7298	97.8	2.75	1.34
1955	1626	4341	76.6	4.71	1.76
1956	2560	3897	134.5	5.25	3.45
1957	1108	2431	63.7	5.75	2.62
1958	896	2832	30.4	3.36	1.07

In relating larger larvae to eggs, we are attempting to look at differences in survival between the time of spawning and the late larval period.

I have explained earlier that the egg and larval estimates are not exactly comparable. The egg estimates are abundance estimates. They are an estimate, albeit a minimal one, of the number of eggs spawned during a season. The larval estimate takes only area into account, not time, hence is a partial estimate. In comparing eggs and larvae, therefore, we are concerned only with the proportion of larger larvae to eggs. It is a relative estimate, but a comparable one from year to year.

The values have a range of about four times. In this comparison the 1952 class has the best survival, the 1957 ranks next, and the 1956 class is third. The same three year classes were the most successful of any during the 1950's, based on their contribution to the commercial catch, but with a different ranking—1956, 1952, and 1957 classes in that order. The fact that there is a close correspondence between the rate of survival between the egg and late larval stages as determined from survey data, and year-class strength as determined from the fishery is encouraging. The range in survival to the late larval stage is only 4 times during the eight years being considered, however, and this value has an error of estimate which may be as great as half or double, hence it would be difficult to establish statistical significance.

In relating larger larvae to total larvae, we are attempting to look at differences in survival during the larval period itself. I am considering as larger sardine larvae, all larvae that are over 15.25 mm in length. During the 8-year period, 1951-1958, these sizes of larvae made up from 1.07% to 3.45% of the sardine larvae collected. This is a range of a little over three times.

In a word, the values from year to year are too similar. The bright spot is that the highest percentage of larger larvae occurred in 1956, and this year class was the best in this series, based on commercial landings. The next best, the 1952-class, does not show up as such in this analysis, but the third best, the 1957-class does. There is an error of estimate associated with these values, which we cannot be precise about, but which may have a noise level about as wide as the range of values shown.

Our anchovy larval data are so much more extensive than the sardine, that we like to check on observations, such as the above, by looking at the same features in the anchovy data. For this purpose I have used standard haul totals of anchovies, and in the category of larger larvae I have included all anchovy larvae larger than 14.26 mm (Table 4). The results are even more consistent than for sardine larvae. Seven of the eight years have almost identical percentages of larger larvae, 0.94% to 1.07%. Only one value is divergent, and this only moderately.

TABLE 4. RELATION OF LARGER ANCHOVY LARVAE (>14.26mm) TO TOTAL ANCHOVY LARVAE, 1951-1958.

	Total anchovy larvae (standard haul totals)	Number 14.26 mm larvae	Percentages that larger larvae are of total larvae
1951	29,076	280	0.96
1952	59,528	894	1.50
1953	99,020	928	0.94
1954	161,056	1,556	0.97
1955	140,019	1,476	1.05
1956	134,913	1,394	1.03
1957	146,551	1,494	1.02
1958	205,376	2,200	1.07

This consistency poses a real problem. It is generally assumed that survival during the larval period is quite variable, and that this period may be the determinant one as regards year-class strength. Our data do not support this. Despite the heavy mortality that occurs during the larval period, about the same percentage of larvae attained the late larval stage year after year. During the 1950's the sardine population was decreasing in abundance, the anchovy population markedly increasing. At the moment I am concerned with the increase in anchovy abundance as it related to rate of survival. The standard haul totals for anchovy larvae, given in Table 4, show a greater difference between 1951 and 1958 than do our census estimates, (Table 5) but even the latter show a tripling in the abundance of anchovy larvae between 1951 and 1958. We interpret the increase in larval abundance to reflect a similar increase in abundance of the adult population. Despite this marked increase in population abundance, the rate of larval survival remained remarkably constant, hence appeared to be independent of the density of larvae.

Obviously this consistency pulls the rug out from under any attempts to relate variation in larval survival to environmental conditions. It would be an understatement to say that we never anticipated this result.

I have considered the possibility that this seeming consistency is an artifact of sampling. There are two obvious problem areas in the quantitative sampling of clupeid larvae. One of these is the marked undersampling of larger larvae that occurs during daylight hours, a phenomenon that has been well documented in the literature (Russell, 1926; Bridger 1956; Ahlstrom, 1959, etc.).

TABLE 5. CENSUS ESTIMATES OF SARDINE AND ANCHOVY LARVAE, 1951-59.

	Census Estimates (x 10^9)		
	Sardine larvae	Anchovy larvae	Ratio: sardine to anchovy larvae
1951	5,773	15,104	1 to 2.6
1952	5,465	17,072	3.1
1953	4,020	23,680	5.9
1954	7,298	38,416	5.3
1955	4,341	37,660	8.7
1956	3,897	38,508	9.8
1957	2,431	40,441	16.6
1958	2,832	56,928	23.6
1959	1,158	54,167	46.8

The other problem is more directly related to the mesh size we employ in our CalCOFI nets. We construct our nets of No. 30 xxx grit gauze, which has openings of about 0.7 mm before use, and about 0.55 mm after the initial shrinkage. Some of the very small sizes of larvae escape through these mesh openings. We do not consider net selectivity a serious sampling problem except in one respect; anchovy eggs also are not completely retained, hence we cannot make a critical egg-larva comparison for anchovies.

I presented a day escapement graph for sardine larvae in a paper published in 1954. In deriving the graph, I utilized day and night catches for 1940 and 1941, and 1950 and 1951. We now have a much larger mass of data, and it appears that there are some differences between the 1940-41 data, collected by coarser-meshed nets, and the more recent data obtained with the CalCOFI net. Hence, the following discussion is based on the latter data only, covering the years 1950 through 1958.

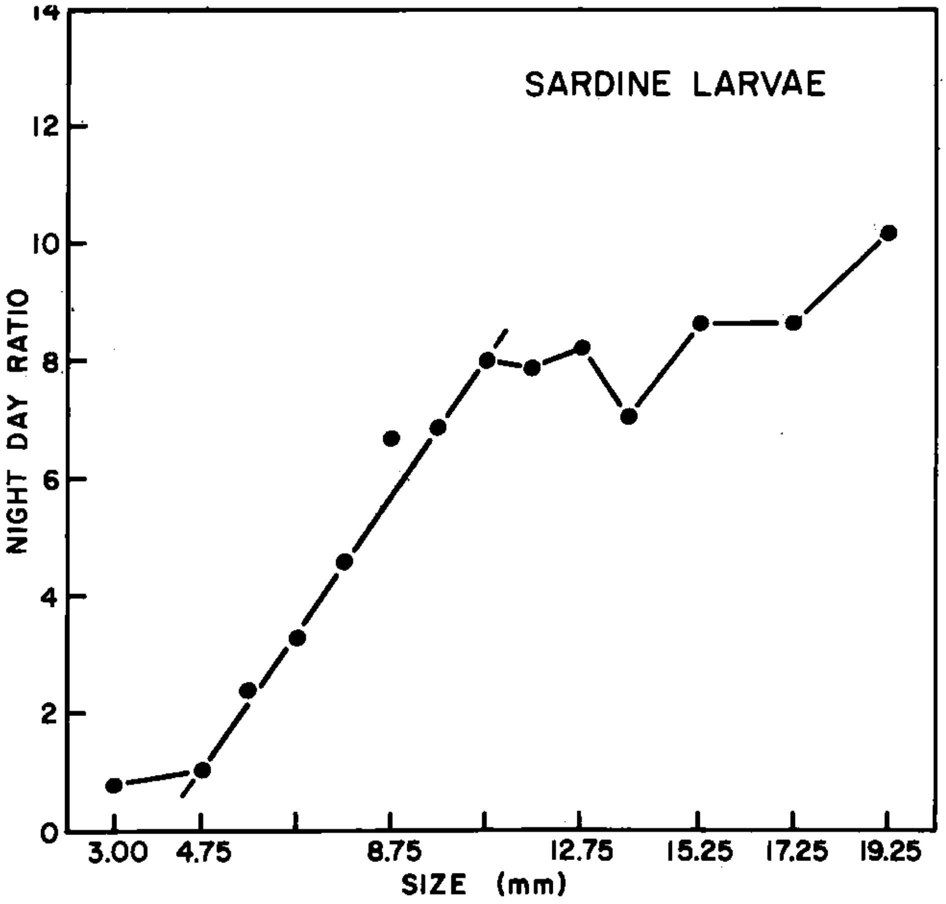

Fig. 3. Extent of undersampling of sardine larvae in day hauls as compared to night hauls, as a function of larval size, based on collections made 1950 to 1958. (All samples containing sardine larvae were used in this comparison, except those collected within one-half hour of sunrise or sunset.)

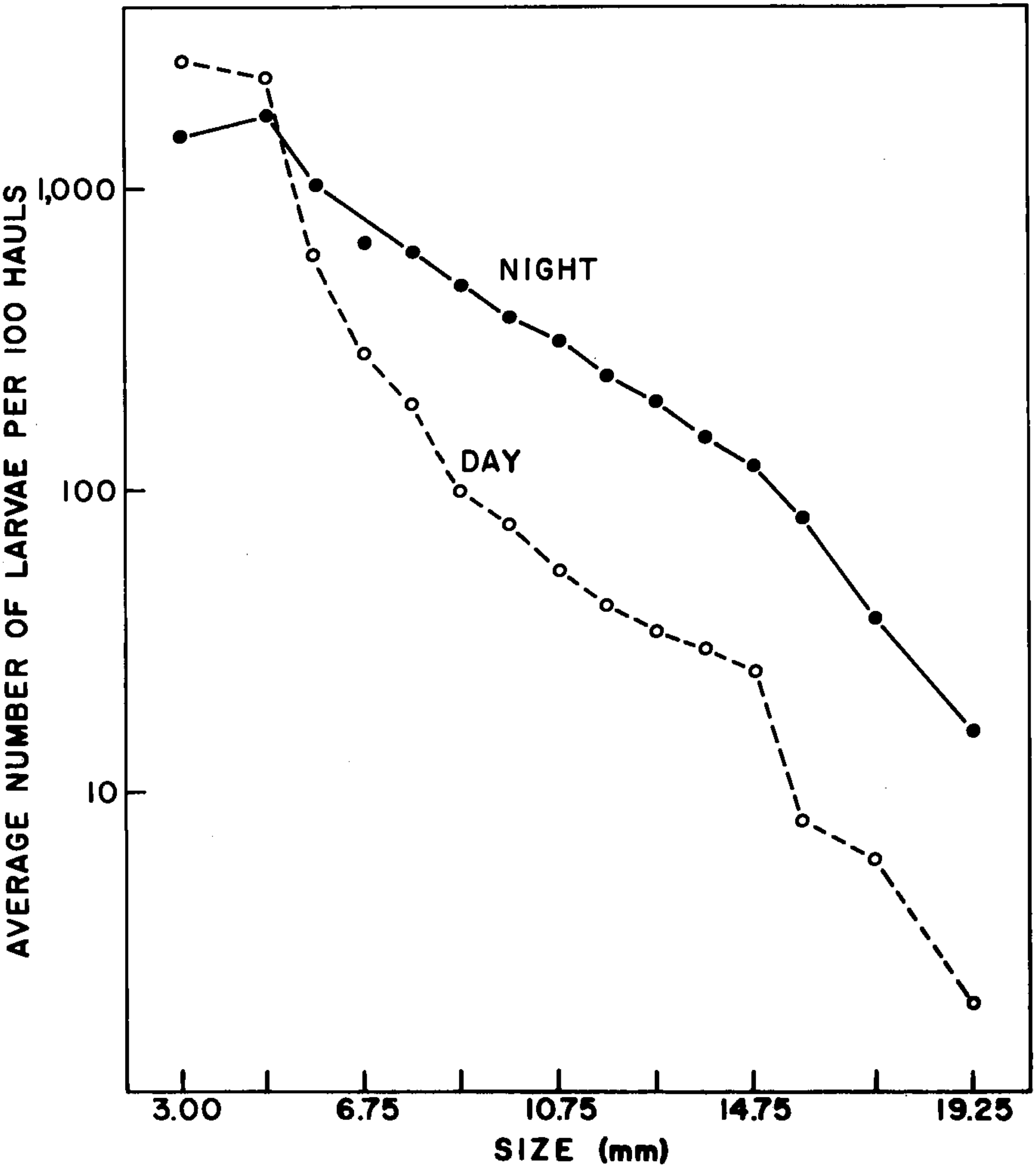

Fig. 4. Relative abundance of day-caught and night-caught sardine larvae, by size, based on the average number of larvae per 100 positive hauls during 1950 to 1958.

TABLE 6. AVERAGE NUMBER PER HAUL (X 10^2) OF NIGHT-CAUGHT AND DAY-CAUGHT SARDINE LARVAE, AND THE DIMINUTION IN NUMBERS OF NIGHT-CAUGHT LARVAE, 1950-58.

Size category	Night-caught larvae	Difference	Diminution in numbers of night-caught larvae	Day-caught larvae
5.75	1,050			602
		380		
6.75	670		208	282
		35		
7.75	635		92	192
		150		
8.75	485		125	99
		100		
9.75	385		85	77
		70		
10.75	315		72	54
		74		
11.75	241		57	42
		40		
12.75	201		44	34
		48		
13.75	153		40	30
		31		
14.75	122		36	25
		40		
15.75	82		42	8
		44		
17.25	38			

I am illustrating undersampling of sardine larvae in daylight hauls in two different figures. In the first, (Fig. 3) the ratios of night-caught larvae to day-caught larvae are shown as a function of larval size. The ratio is close to 1 to 1 at a larval length of 4.75 mm; rapidly increases to about 8 to 1 at 10.75 mm; and then more or less levels off.

The second figure (Fig. 4) is a semi-log plot. The average numbers (x 10^2) of larvae in day and in night hauls are given as a function of size. The difference between day and night hauls is also well shown by this type of plot. The decrease in numbers of larvae with size in the night hauls has a linear relation over the size range from 5.75 to 14.75 mm. This is not a mortality curve: growth rate is not taken into account. Sette (1943) analyzed available information on growth of fishes during the larval period and concluded that a simple logarithmic curve fitted the growth data for the few species about which he had information. The net effect of correcting the 10 size categories involved for logarithmic growth would be to change the slope of the straight-line relation. Obviously these are the sizes of sardine larvae that we sample most adequately. A similar plot is shown for anchovy larvae (Fig. 5).

John Isaacs of Scripps Institution of Oceanography has been intrigued by our sardine and anchovy larval data. He presented a paper on this subject at the Larval Fish Symposium held at Lake Arrowhead last October (Isaacs, MS). One of his novel suggestions is that day-caught sardine larvae are in some way a measure of the mortality of larvae. He concluded from an inspection of day and night records that day-caught larvae in each of the size categories between 5.75 and 15.75 mm are numerically almost equal to the diminution of the numbers of night-caught larvae over the same intervals.

I have plotted the average numbers of sardine larvae (x 10^2) in the day catches and the diminution in numbers in night catches for size categories between 6.75 and 14.75 mm in length (Fig. 6). The data are given in Table 6. It can be seen that day-caught larvae exceed the diminution in numbers of night-caught larvae for the two smaller size categories shown (6.75 and 7.75 mm), and thereafter are uniformly lower in numbers. Although the trends are similar, I would hesitate to conclude that day-caught larvae could be used as a measure of larval mortality of the Pacific sardine.

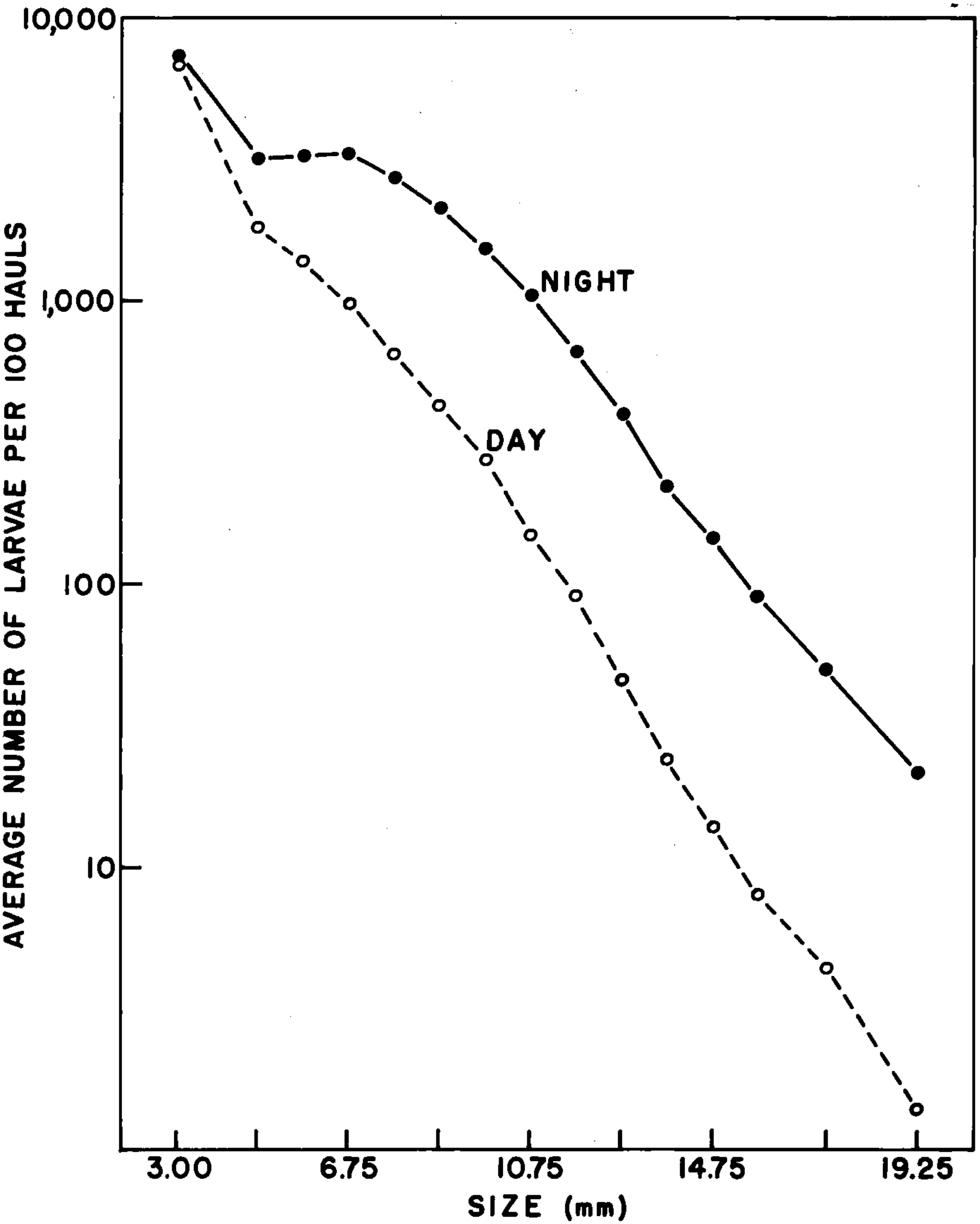

Fig. 5. Relative abundance of day-caught and night-caught anchovy larvae, by size, based on the average number of larvae per 100 positive hauls during 1950 to 1959.

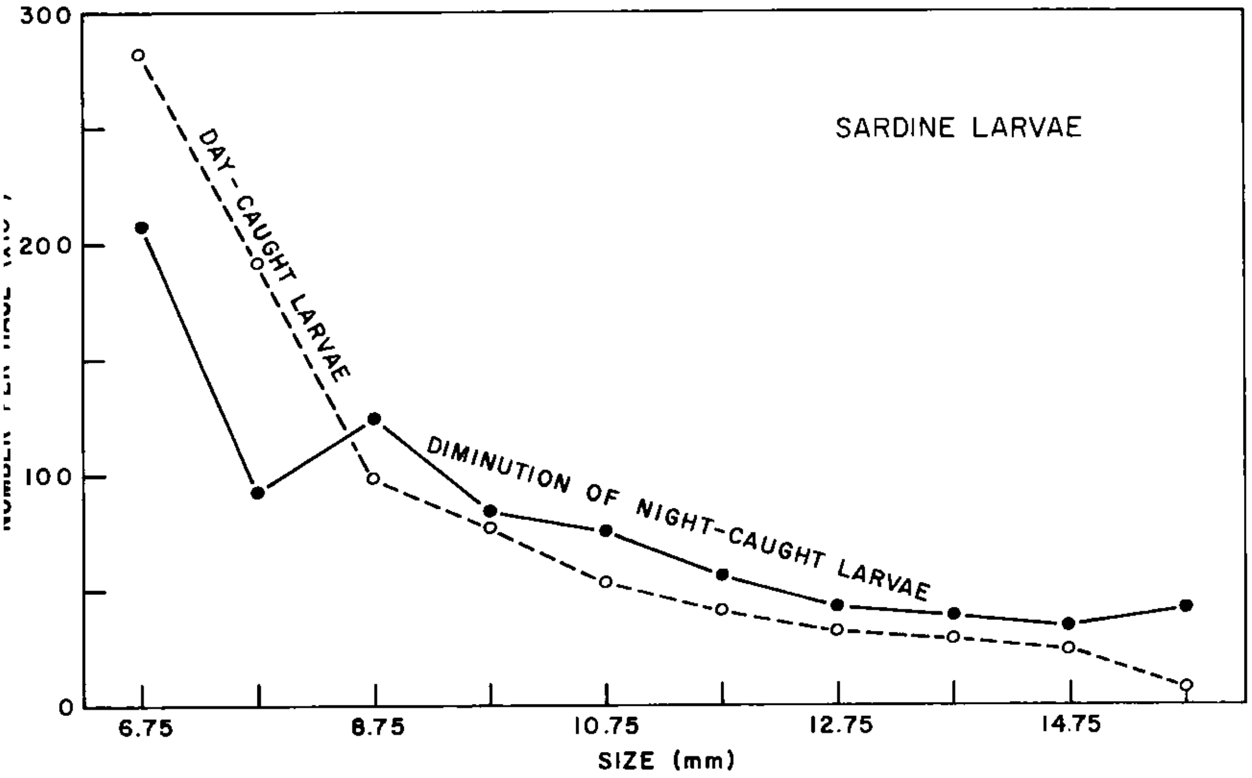

Fig. 6. Average number per standard haul (x 10^2) of day-caught sardine larvae for each 1.0 millimeter size interval between 6.75 and 15.75 mm, compared to the diminution in numbers of night-caught larvae per millimeter of length over the same size range.

TABLE 7. AVERAGE NUMBER PER HAUL (X 10^2) BY SIZE OF NIGHT-CAUGHT AND DAY-CAUGHT ANCHOVY LARVAE, AND THE DIMINUTION IN NUMBERS OF NIGHT-CAUGHT LARVAE, 1950-1959.

Size category	Night-caught larvae	Difference	Diminution in numbers of night-caught larvae	Day-caught larvae
6.75	3,320			973
		535		
7.75	2,785		570	647
		605		
8.75	2,180		606	423
		608		
9.75	1,572		506	273
		512		
10.75	1,060		454	151
		396		
11.75	664		328	90
		260		
12.75	404		216	46
		173		
13.75	231		128	24
		83		
14.75	148		70	14
		57		
15.75	91		48	8
		40		
17.25	51			

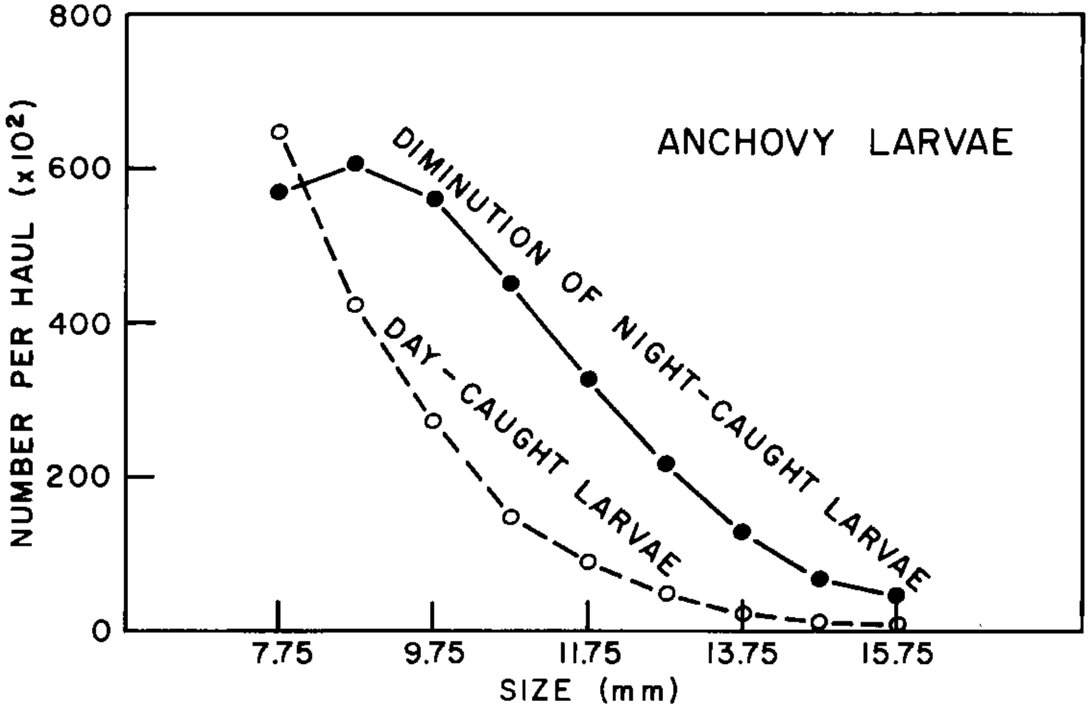

Fig. 7. Average number per standard haul (x 10^2) of day-caught anchovy larvae for each 1.0 millimeter size interval between 7.75 and 15.75 mm, compared to the diminution in numbers of night-caught larvae per millimeter of length over the same size range.

Similar graphs have been prepared for the anchovy (Fig. 7 and Table 7). The disparity between night and day hauls is greater for the anchovy than the sardine. There are proportionately fewer day-caught larvae, and consequently one would never be led to assume that they could represent a meaningful measure of larval mortality.

The picture that is emerging from our investigations is that the primary environmental condition affecting the sardine population is the flourishing anchovy population. I briefly commented in an earlier section about the marked increase in anchovy abundance that has occurred during the period of our CalCOFI surveys. I would like to use my remaining time in looking at the problem of competition between species within a trophic level.

Unfortunately we do not have much information about the comparative strength of the sardine and anchovy populations during the years when the sardine was at a high level of abundance. We made sardine egg and larval surveys in 1939 to 1941, but these were mostly limited to the waters off southern California. During these years the sardine population was in a fairly healthy state. The 1939 year class was the largest of which we have record, for example. At that time anchovy larvae were slightly more abundant than sardine larvae (Marr and Ahlstrom, 1948). We collected 1.2 times as many anchovy larvae as sardine in 1940, 1.7 times as many in 1941. In terms of biomass we know from John MacGregor's investigation that a kilogram of spawning female anchovies will produce twice as many eggs as an equivalent weight of spawning sardines. We also know that anchovies are shorter-lived than sardines.

The relative strength of the sardine and anchovy populations may not have changed much during the decade of the 1940's inasmuch as anchovy larvae were only 2.2 times as abundant as sardine in 1950.

During the decade of the 1950's the picture is quite otherwise. There has been a continuing increase in the size of the anchovy population relative to the sardine as deduced from larval abundance. In 1951 anchovy larvae were 2.6 times as numerous as sardine, by 1955 they were nearly 9 times as numerous. The disparity widened in succeeding years. By 1959 anchovy larvae outnumbered sardines by about 46 to 1, and in 1962 the difference may be as great as 80 to 1.

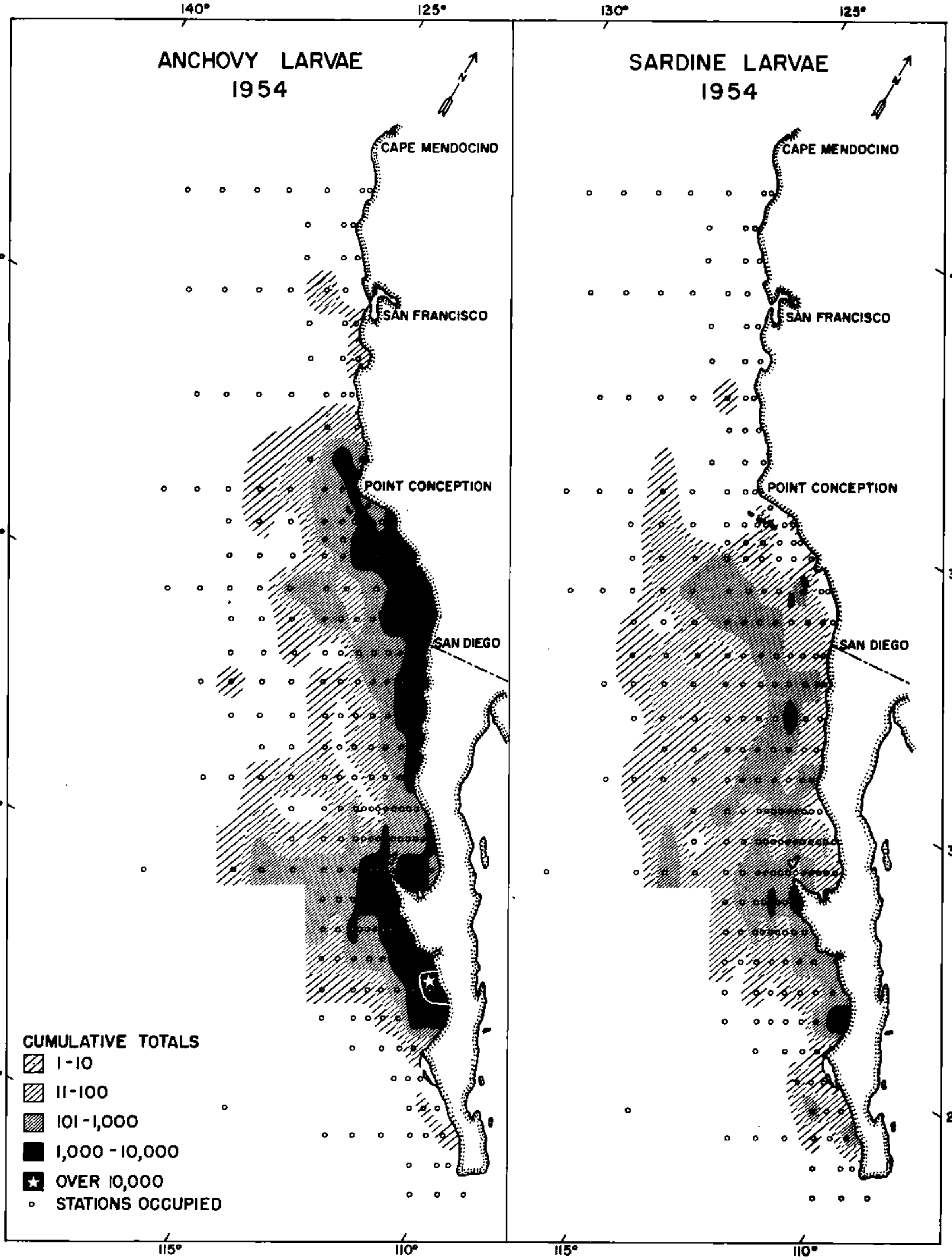

Fig. 8. Distribution and relative abundance of sardine and anchovy larvae in 1954.

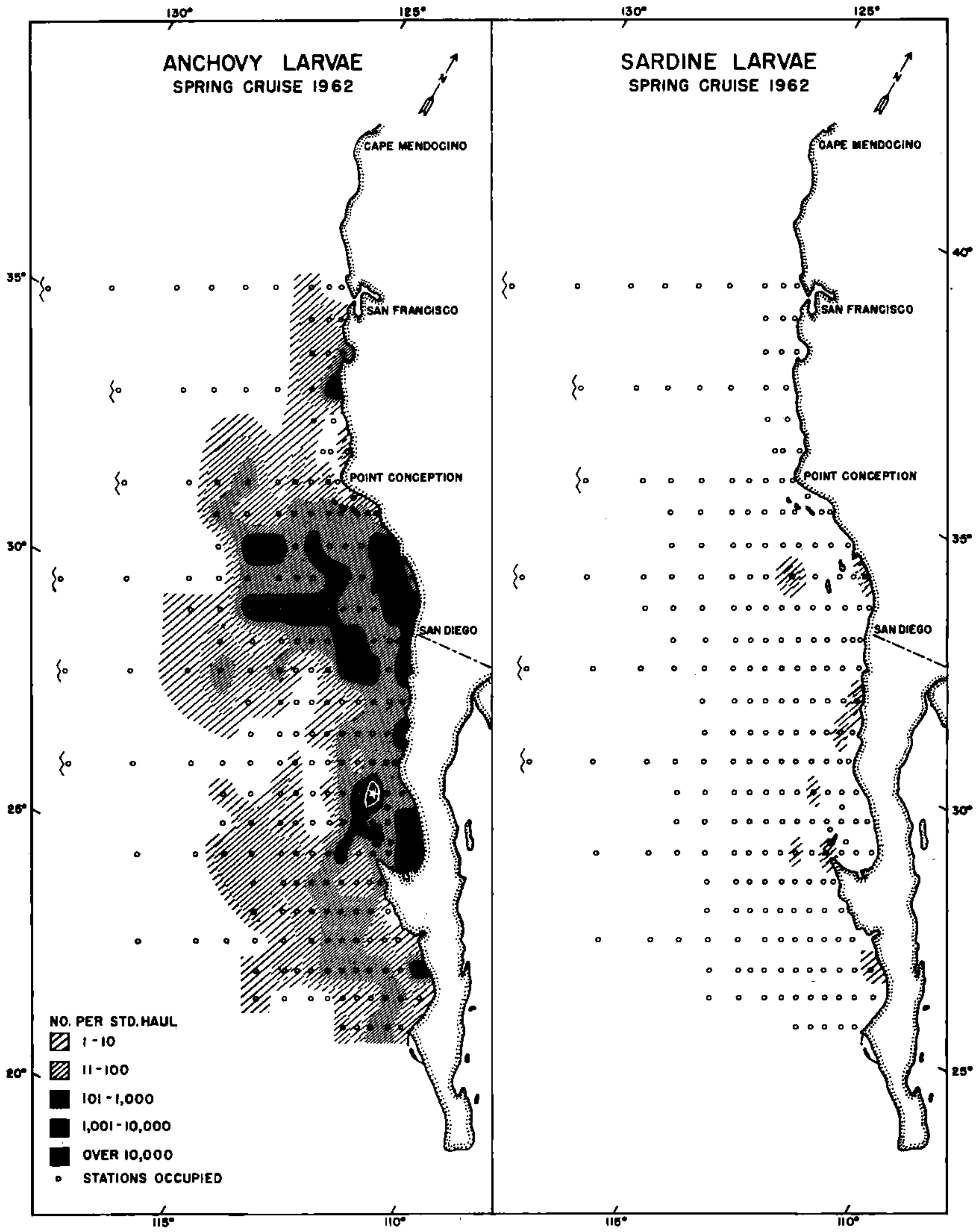

Fig. 9. Distribution and relative abundance of sardine and anchovy larvae during the spring 1962 CalCOFI survey cruise.

Ratios such as the above are striking but also tend to be misleading. The anchovy population, based on census estimates of larvae, more than trebled between 1951 and 1958 (Table 5).

During the same period the sardine population had a brief resurgence in 1954 and then declined to barely one-sixth of this abundance by 1959.

In more recent years, such as 1962, the abundance of anchovy larvae is considerably greater than in 1959, and the abundance of sardine larvae considerably less.

It is interesting to look at some aspects of this change. I have previously contrasted the distribution of sardine eggs in 1953 and 1954. I also wish to contrast the distribution of sardine and anchovy larvae in 1954 (Fig. 8). Note that sardine larvae are even more widespread than anchovy, and that anchovy larvae do not extend as far seaward off southern California as do the sardine larvae. However, note that both species have widespread distributions.

Anchovy larvae, as they increased in abundance, were spread over a larger area. This is strikingly shown in the spring survey cruise of 1962 (Fig. 9). Anchovy larvae are now abundant in offshore waters off southern California where they were barely represented in 1954. Sardine larvae, on the other hand, are exceedingly sparse. Furthermore, they are mostly distributed along shore. The number of anchovy larvae taken on this one cruise was as great as the total number taken in all cruises of 1956, and greater than the combined totals of anchovy larvae for 1950, 1951, and 1952, so great has been the increase in abundance of this species.

As the anchovies have become more widespread, they have tended to co-occur more frequently with sardines. In 1958, 94% of sardine larvae were taken in hauls containing anchovy larvae. A significant reason why the anchovies now have a competitive advantage is their sheer numbers. There were 10 anchovy larvae, on the average for each sardine larva in hauls where they co-occurred in 1958. In the spring cruise of 1962, the few occurrences of sardine larvae were in hauls swarming with anchovy larvae (Fig.9): sardine larvae averaged 19 per haul, anchovy larvae in the same hauls averaged 900. Sardine larvae seldom had the opportunity to see one of their own kind.

As noted above, we do know the time sequence of the increase in anchovy abundance. It began about 1951. The reasons why it occurred are somewhat speculative, but three factors seem to be quite important: 1) a decrease in the abundance of the sardine population due to the coincidence of two exceptionally poor year classes, the 1949 and 1950 classes, 2) a selective fishery which exploited one element of the trophic level, the sardine population, and left the anchovy resource almost alone, and 3) the prevalence of oceanographic conditions that favoured anchovy spawning.

The sardine spawning stock is made up principally of three age groups, two through 4-year old fish. The occurrences of three very poor year classes in succession could have a disastrous effect on the population and even two poor classes in succession could reduce the population to a low level of abundance. The 1949 and 1950 year classes were exceptionally poor ones. Survival during these years was at a rate which was barely an eighth of the average rate for sardine year classes. The increase in anchovy abundance began at about the time that these sardine year classes were recruited. The anchovies were able to fill a hole that developed in their trophic level; there is no evidence that they helped create the hole. The effect of the selective fishery was to give the anchovy a competitive advantage over the sardine. Oceanographic conditions also favoured the anchovy during much of the 1950's. (Marr, 1960, has discussed this problem at some length). Anchovies can spawn at somewhat lower temperatures than sardines. For the sardine, 13°C has been shown to be a limiting temperature; sardine spawning does not ordinarily occur below this. The threshold temperature is lower in the anchovy, being about 11.5° or 12°C.

The difference may not seem large, but it was enough to permit anchovies to spawn earlier off southern California—in some years as much as three months earlier and to spread the spawning over a longer spawning season.

We can quite definitely establish that sardine and anchovy larvae co-occur. We assume from this that the two species compete. The mechanisms of competition are less clear. I have earlier noted that the young stages of sardine and anchovy larvae compete for food. When food is inadequate, this could be a source of mortality. However, the chief source of mortality appears to be predation rather than competition—predation of adults on their own young and the young of other species with planktonic eggs and larvae. Filter-feeding fish are indiscriminate feeders—they feed on whatever they can strain from the water. We have the basic problem that many pelagic fishes have a planktonic phase in their life history, yet depend on plankton for food. Their young are part of this food. This seems to be the mechanism of population control, and it does not really matter whether the predator is a sardine or an anchovy or some other filter-feeding fish.

I have purposely avoided the problem of the relation of survival to spawning stock size. This is a problem that could have taken all the time available to me. Radovich (1962) pointed out that there is a relation between stock sizes and survival, with best survival at middling stock sizes (refer especially to his Fig. 8 on p. 134). Workers on sardines now generally concede this (MacGregor, in press). The spawning stock cannot be dismissed as unimportant. Fishery biology is full of wishful thinking and none more so than in the area of the non-importance of stock size. We in California now know that small spawning stocks produce only small year classes. A year class, on the average, is only about 4/10 as large as the spawning stock. An exceptional year class may be 3 x as large as the parent stock, but a very poor year class may be only 1/20 or 1/25 as large as the parent stock. We have had three abundance regimes, and this relation has held in all three.

And so to conclude. We have found that the chief environmental conditions in our area are biological, not physical or chemical, and that they concern other fishes in the same trophic level with the Pacific sardine. One of the prime accomplishments of CalCOFI surveys has been the documentation of changes in abundance of the younger stages of pelagic fishes in the California Current System during the decade of the 1950's. The value of systematic egg and larval surveys for resource evaluation cannot be overemphasized. On the other hand, we have found an unanticipated uniformity in the survival pattern of sardine and anchovy larvae from year to year.

REFERENCES

AHLSTROM, ELBERT H. 1943. Studies on the Pacific pilchard or sardine (*Sardinops caerulea*). 4. Influence of temperature on the rate of development of pilchard eggs in nature. U.S. Fish and Wildlife Service, Special Scientific Report No. 23, 26 p.

1954. Distribution and abundance of egg and larval populations of the Pacific sardine. *Fish. Bull., U.S.* 93, 56: 83-140.

1959*a*. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. *Fish. Bull., U.S.* , 161, 60: 107-146.

1959*b*. Distribution and abundance of eggs of the Pacific sardine, 1952-1956. *Fish. Bull. U.S.*, 165, 60: 185-213.

1960. Fluctuations and Fishing. Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species. Food and Agriculture Organization of the United Nations, III: 1353-1371.

MS. Kinds and abundance of fishes as determined from larvae. Paper delivered at Larval Fish Biology Symposium of the 1963 California Cooperative Oceanic Fisheries Investigations Conference. To be published in CalCOFI Reports, vol. X.

AHLSTROM, ELBERT H., J. ISAACS, J. THRAILKILL, L. KIDD. 1958. High-speed plankton sampler. *Fish. Bull. U.S.*, 132, 58: 187-214.

ARTHUR, DAVID K. 1956. The particulate food and the food resources of the larvae of three pelagic fishes, especially the Pacific sardine, *Sardinops caerulea* (Girard). Doctoral Dissertation, University of California, Scripps Institution of Oceanography.

BRIDGER, J.P. 1956. On day and night variations in catches of fish larvae. *J. Cons.* 22(1): 42-57.

GULLAND, J.A. 1964. Survival of the youngest stages of fish, and its relation to year-class strength. This Symposium, p.363-371.

ISAACS, JOHN D. MS. Larval sardine and anchovy interrelationships. Paper delivered at Larval Fish Biology Symposium of the 1963 California Cooperative Oceanic Fisheries Investigations Conference. To be published in CalCOFI Reports, vol. X.

LASKER, REUBEN, 1964. Effect of temperature on incubation time, development and growth of embryos of the Pacific sardine, Copeia, No. 2: 399-405.

MACGREGOR, JOHN S. 1957. Fecundity of the Pacific sardine (*Sardinops caerulea*). *Fish.Bull. U.S.*, 121, 57: 427-449.

1964. The relation between anomalies of spawning stock size and year-class size for the Pacific sardine, *Sardinops caerulea* (Girard). *Fish. Bull. U.S.*, 63 (2): 477-491.

MARGALEF, RAMON. 1960. Fluctuations in abundance and availability caused by biotic factors. Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species. Food and Agriculture Organization of the United Nations, III: 1265-1285.

MARR, JOHN C. 1960. The causes of major variations in the catch of the Pacific sardine, *Sardinops caerulea* (Girard). Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species. Food and Agriculture Organization of the United Nations, III: 667-791.

MARR, JOHN C. and ELBERT H. AHLSTROM. 1948. Observations on the horizontal distribution and the numbers of eggs and larvae of the northern anchovy (*Engraulis mordax*) off California in 1940 and 1941. U.S. Fish and Wildlife Service, Special Scientific Report No. 56, 13 p.

NAKAI, ZINZIRO, 1960. Fluctuations in abundance and availability of sardine populations caused by abiotic factors. Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species. Food and Agriculture Organization of the United Nations, III: 1327-1352.

RADOVICH, JOHN. 1962. Effects of sardine spawning stock size and environment on year-class production. *Calif. Fish and Game*, 48 (2): 123-140.

RUSSELL, E.S. 1926. The vertical distribution of marine macro-plankton. III. Diurnal observations on the pelagic young of teleostean fishes in the Plymouth area. *J. Mar. biol. Ass. U.K.*, 14: 387-414.

SAVILLE, ALAN. 1964. Estimation of the abundance of a fish stock from egg and larval surveys. *Rapp. Cons. Explor. Mer.* 155: 164-170.

SETTE, OSCAR E. 1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part I. Early life history, including growth, drift and mortality of the egg and larval populations. *Fish. Bull. U.S.*, 38, 50: 149-237.

1960, The long term historical record of meteorological, oceanographic and biological data. California Cooperative Oceanic Fisheries Investigations Reports, VII: 181-194.

SETTE, OSCAR E. and ELBERT H. AHLSTROM. 1948. Estimations of abundance of the eggs of the Pacific pilchard (*Sardinops caerulea*) off southern California during 1940 and 1941. *J. Mar. Res.*, VII (3): 511-542.

SHELBOURNE, JAMES E. 1957. The feeding and condition of plaice larvae in good and bad plankton patches. *J. Mar. biol. Ass. U.K.*, 36 (3): 539-552.

SILLIMAN, RALPH P. 1946. A study of variability in plankton tow net catches of Pacific pilchard (*Sardinops caerulea*) eggs. *J. Mar. Res.*, VI (1): 74-83.

SPRAGUE, LUCIAN and ANDREW M. VROOMAN. 1962. A racial analysis of the Pacific sardine (*Sardinops caerulea*) based on studies of erythrocyte antigens. Annals of the New York Academy of Sciences, 97, article 1: p. 131-138.

TAFT, BRUCE A. 1960. A statistical study of the estimation of abundance of sardine (*Sardinops caerulea*) eggs. *Limnol. & Oceanogr.* 5 (3): 245-264.

VROOMAN, ANDREW M. 1964. Serologically differentiated subpopulations of the Pacific sardine. *J. Fish. Res. Bd. Canada,* 21 (4): 691-701.

WALFORD, L.A. 1946. Correlation between fluctuations in abundance of the Pacific sardine (*Sardinops caerulea*) and salinity of the sea water. *J. Mar. Res.* VI (1): 48-53.

A REVIEW OF THE EFFECTS OF THE ENVIRONMENT ON THE TUNA

By

Vernon E. Brock[1]

INTRODUCTION

Tuna are among the most pelagic and mobile of fishes. Their distribution and movements mirror the oceanic regions of favourable environment and changes in these with an apparent precision, now largely beyond the human oceanographer, but slowly coming within his reach.

The present review is concerned with the results of recent work which have added significantly to our understanding of the effects of the environment on this interesting and important group of fishes. A short lecture, such as this, is not suitable for an exhaustive review.

The environment is considered as all the external or internal foreign elements that may affect the tuna. However, one complex of elements, the tuna fisheries and their effects on tuna populations, is not dealt with here.

Attention has been given to those species of tuna for which environmental effects have been reported in some detail. Mention is made of other species of tuna which include altogether, following nomenclature of Collette and Gibbs (1963), the albacore (*Thunnus alalunga*), the Atlantic bluefin tuna (*T. thynnus thynnus*), the Pacific bluefin tuna (*T. thynnus orientalis*), the yellowfin tuna (*T. albacares*), the bigeye tuna (*T. obesus*), and the skipjack (*Euthynnus pelamis*).

Environmental changes that may affect tuna include its physical deterioration or improvement, availability of prey, suitability of a region for the survival of eggs and larvae, and the competition or predation of other species. Other changes in the quality of the environment may occur relating to parasites, diseases, and subtle changes in the marine community of which the tuna are a part.

Environmental effects to be significant must, of course, evoke a response. The response may be either active or passive. Active responses may involve translocation, schooling, or other behavioural changes. These may also change with changes in size and maturity.

The passive responses are ones of endurance, and are detectable by changes in mortality or recruitment rates. Survival in these cases is not through appropriate patterns of behaviour or movement, but by the reproductive, physiological, or ecological resilience of the species.

The problems of obtaining adequate data on environmental changes together with the accompanying responses of the tunas have not been frequently solved. The effects of the environment on the tuna have been deduced largely from data concerning tuna fisheries, studies of the fish landed, and work at sea, both aboard fishing and fisheries research vessels. Environmental data have also been obtained from fishing and fisheries research vessels. However, most of these data are from a diversity of sources such as sea surface temperatures from merchant ships; oceanographic observations from oceanographic research and survey ships, weather station ships, naval ships, and others; and data from shore stations.

Not much of the data on the environment and on the tuna are collected simultaneously in space and time. To varying degrees the adequacy of their juxtapositioning is inferential. In addition, the major source of data concerning the effects of the environment on the tuna, the tuna fisheries, provides information that is also largely inferential in character. A recent contribution by Shibata (1963) suggests that the inferences made from catch data may sometimes not be true. He reported on the comparison of catch rates by long-line gear and density of tuna estimated from a sonic fish finder operated at the same times and places where fishing was done. He found no relationship between the two methods for estimating abundance.

Regardless of what fishing success measures, it can sometimes be related to changes in a given

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environmental parameter. However, it may be only inferential that changes in the environmental parameter measured are directly responsible for changes in fishing success. The existence of a chain of causal relationships between the cue to which the fish respond and the measured property will make the observed relationship of unknown reliability depending upon the invariability of the causal linkages involved. These are some of the sources of error in the data.

The environment of the tuna is the pelagic realm of the temperate and tropical ocean. The complex of ocean currents composing the equatorial circulation and the great current gyres poleward of the equator are the important habitats. Various species also occur in seas located at suitable latitudes.

The distributions and abundances of tuna and changes in these are related to the pattern of ocean currents and their changes. The basic pattern of surface currents for the major ocean basins at low and mid latitudes is a transport of water to the western side in the equatorial region, a flow towards the poles along this side, a return flow across the ocean basin to the east at middle latitudes, and a flow towards the equator on the eastern side. Various portions of these great gyral currents have various names such as the Gulf Stream, the North Atlantic Current and the Canary Current in the North Atlantic. Corresponding current segments in the North Pacific are the Kuroshio, the North Pacific and the California Currents. The flow of these currents, by the movement of tropical water poleward on the western margin of the ocean basin and by the movement of temperate water towards the equator on the eastern margin, broadens the band of tropical water in the western oceanic regions and narrows it in the eastern oceanic regions. The depth of the isothermal surface layer of warm water in the tropics is also greatest in the west, and least in the east. The broad band of cool water of the temperate latitudes in eastern oceanic regions is further cooled and enriched by coastal upwelling of greater or lesser intensity. The seasonal temperature change of the surface waters in this part of the ocean is not great, while in contrast the relatively narrow band of cool water in temperate latitudes on the western margin of the oceans shows a marked change in temperature between winter and summer. This description of the major features of the oceanic surface circulation of the temperate and tropical regions is a great simplification of the situation obtaining, but should suffice as a background for considering the effects of the environment on the tuna.

The availability of some species of tuna to various fishing gears may depend upon transitory or permanent features of the ocean. Brock (1959) suggested that the relatively shoal thermocline in the eastern tropical Pacific may be related to the success of surface and near-surface fishing methods such as purse seining. This suggestion implies that the thermocline may serve as a floor to the vertical distribution of the tropical species. Conversely it may also serve as a ceiling for the albacore in the tropics where this species is available to long-line gear, but never apparently in evidence on the surface.

Laevastu and Rosa (1963, Fig. 10) summarize data regarding the temperature tolerance of tunas. The yellowfin appears to tolerate the highest temperatures, and the bigeye, the greatest temperature range. Since this latter species seems to rarely occur at the surface, the surface water temperatures for its fishing areas may not provide a good indication of that of its normal habitat. The albacore and bluefin tunas are considered as temperate water species and possibly the bigeye too, while the skipjack and yellowfin are tropical species. All of these species occur, however, in the tropics to some degree.

THE ENVIRONMENT AND VOLITIONAL RESPONSES OF THE TUNA

During the summer months the poleward movement of many tuna species is a characteristic occurrence which sustains important fisheries. The summer occurrence of albacore and Pacific bluefin tuna off California, skipjack and the Pacific bluefin off Japan, the Atlantic bluefin off northern Europe and New England are examples of this poleward movement. There is no evidence relating these excursions to reproductive activities; in fact, the albacore and Pacific bluefin in California waters are adolescent, immature fish. The most probable hypothesis is that such movements are invasions of a habitat which for reasons of water temperatures or some other is only available seasonally but which affords a more abundant source of prey. In the tropics the seasonal cycle is less evident, at least as far as temperature changes are concerned. However, evidence exists that biologically productive areas have associated higher abundances of tuna. Schaefer (1960) reviews much of this evidence for the eastern and central Pacific, pointing out the association between oceanic processes that stimulate biological productivity such as upwelling and the effects of the equatorial current and countercurrent interaction in bringing nutrient salts into the enphotic zone. The temperature structure of the tropical ocean, with a permanent warm surface layer separated by a density difference from the cooler underlying waters, leads to a depletion of the nutrient salts in the surface layer and its consequent biological impoverishment. The cooler subsurface waters are potential sources of nutrient salts, and any process that moves water of this layer into the illuminated surface layer will stimulate biological productivity.

Blackburn (1963) investigated the association of tuna with variations of biological productivity in the Gulf of Tehuantepec on the west coast of Mexico. He found that the consistent and vigorous northerly winter winds result in the entrophication of the waters of a portion of the Gulf and that the abundance of yellowfin tuna, as estimated by the fishery, was significantly associated with this portion some three months later. A similar association was not found for skipjack; however, the possibility that this species may be excluded during the spring and summer of warm years, thus interfering with the detection of the association, was mentioned but not investigated.

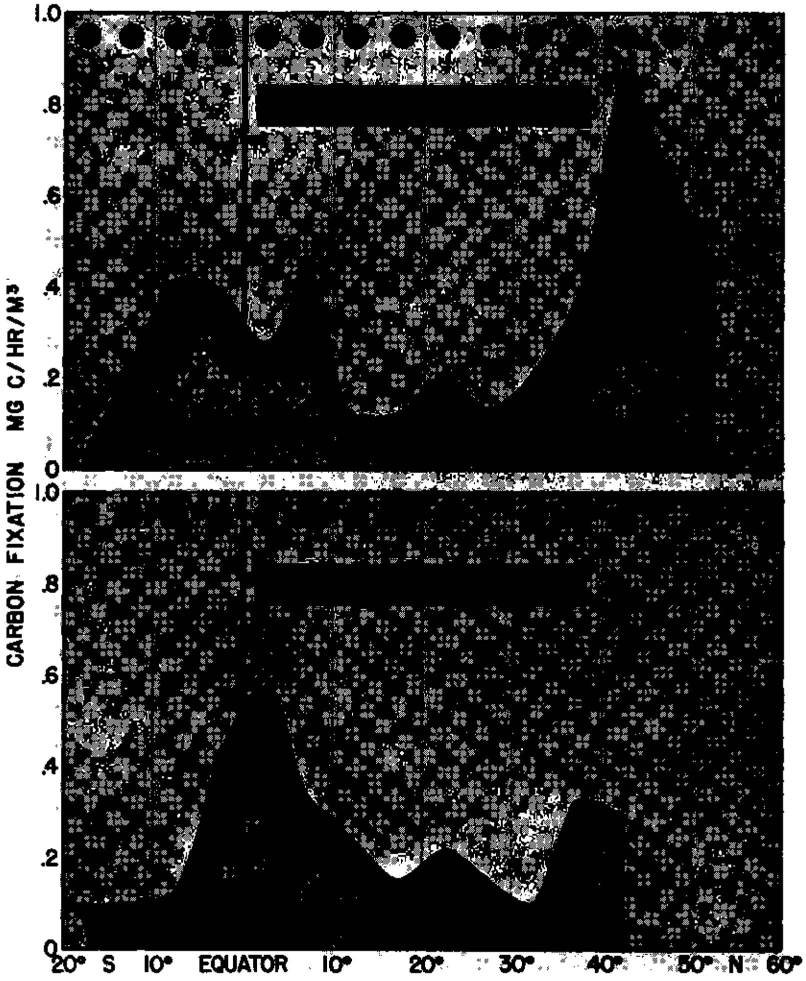
The time lag in the association between the entrophication of a portion of the waters of the Gulf and the abundance of yellowfin tuna was attributed to the time required for the results of entrophication to appear as an increased abundance of tuna prey.

The association of tuna with sea mounts and banks suggests that these features are productive of food for tuna, a suggestion that has not yet been clearly demonstrated to be true. While tuna appear to be more abundant in the vicinity of oceanic islands, a major effect of islands on offshore productivity thereby attracting tuna has not yet been clearly proven. However, an island effect on the composition of the zooplankton for a considerable distance offshore has been shown (Jones, 1962). There is some evidence that yellowfin tuna near islands in the central Pacific are smaller in average size than those further offshore (Shomura and Murphy, 1955).

Austin and Brock (1959) examined the relationships among primary productivity as estimated by C-14 uptake, the standing crop of zooplankton, the standing crop of zooplankton predators from midwater trawl hauls, and of climax predators from long-line catches from lat 20° S to 40° N. Productivity was high in the equatorial and mid latitude regions, low in lat 10° - 20° band as measured at these trophic levels (Fig. 1, 2). The tuna provided an identical pattern when all species were lumped except for the high latitude stations. However, in the equatorial region the only species whose abundance coincided with the regions of highest biological productivity was the yellowfin; the greatest abundance of albacore and bigeye was at higher latitudes where primary productivity was less (Fig. 3). While these data may reflect some artifacts of gear selectivity or differences in vertical distributional patterns among these species, there is a suggestion of differences in habitat requirements which do not, in all cases, coincide with the region of highest biological productivity. The equatorial distributional patterns of albacore may be related to the habitat requirements of the eggs and larvae rather than that of the adults. The ready availability of skipjack to the local Hawaiian fishery during the summer months appears to be a departure from the relationship between the abundance of tuna and their prey. While it can be hypothesized that the skipjack appear in the Hawaiian region, which is in the subtropical belt of low marine productivity, to spawn, they appear to grow rapidly during their season of abundance (Shippen, 1961).

The seasonal poleward movements of some species of tuna are apparently quite sensitive to anomalies of the ocean climate. These anomalies, being unexpected to a degree, and causing shifts in the customary times and places where tuna occur, may occasion serious economic loss to tuna fisheries. An understanding of their effects and predictions of their occurrence are, therefore, greatly desired. Uda (1962) discusses anomalous events in the ocean climate on both sides of the North Pacific and in the North Atlantic together with the linkage mechanisms provided by the atmosphere. Changes in the deep-water circulation in the western North Pacific which may shift the position of the Kuroshio off Japan are also discussed. The possibility of a periodicity in these events related to the sunspot cycle is considered. The apparent reciprocal relationship between the yields from skipjack and albacore fisheries off Japan and the west coast of the United States is discussed in relation to these anomalous situations.

Radovich (1963) discusses the anomalous warming of the ocean off California and the associated poleward movements of warm water fishes including various species of tuna which brings them into regions far beyond their normal ranges. Radovich concludes that these movements are a direct response to temperature change. It is of interest, in this connection, that skipjack appear to leave the warmest areas in the eastern tropical Pacific, when summer temperatures exceed 28° C, during the warm years (Anon., 1963).



CARBON FIXATION

Fig. 1 .

Hester (1961) made a study of the areas of seasonal catch of albacore and Pacific bluefin tuna off the coasts of California and Lower California. He found, during years of below normal sea surface temperatures, a large part of the catch came from the waters south of California, off Lower California. Bluefin tuna are taken south of the best albacore fishing localities ordinarily, apparently preferring somewhat warmer water than the albacore. The center of the fisheries for both species move northward as the season advances. Hester's Fig. 1, recopied here as Fig. 4, shows the center of the seasonal bluefin fishery for a selected cold period (1952-53) largely south of Point Eugenia, about midway along the coast of Lower California, and in contrast for a warm period (1957-58) off Southern California, a latitudinal shift of 350 - 400 miles.

Johnson (1963) also studied the eastern North Pacific Ocean albacore landings during the 1952 cold period and the 1958 warm period on the basis of sea surface temperatures and salinities for a large part of the eastern North Pacific Ocean. During the 1952 albacore season the coastal zone where fish were found was from lat 27° to 45° N. The 1958 coastal fishing ground was from lat 31° to 48° N. The fishery began at the southern end of the ground, usually in June, progressing northward as the season advanced. Johnson related the more southerly occurrence of albacore at the beginning of the fishing season in 1952 to the more vigorous flow and consequent stronger southern penetration of the California Current. In 1958, when the fishery began further to the north, the California Current flow was weaker. The water type characteristic of the California Current could be identified by a combination of lower temperature and salinity, and the general area where the

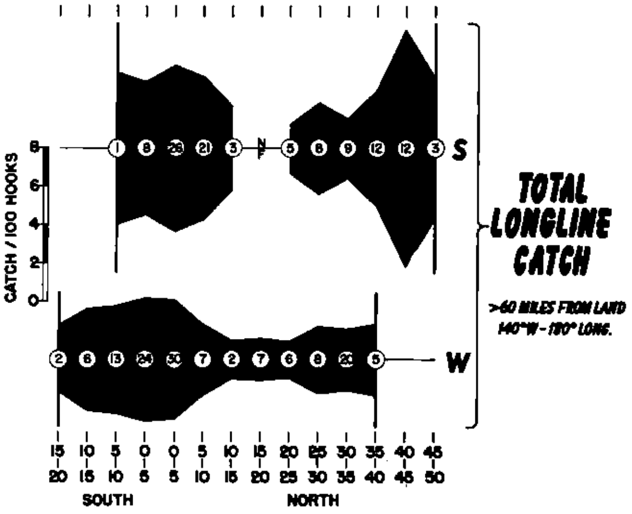

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Fig. 2.

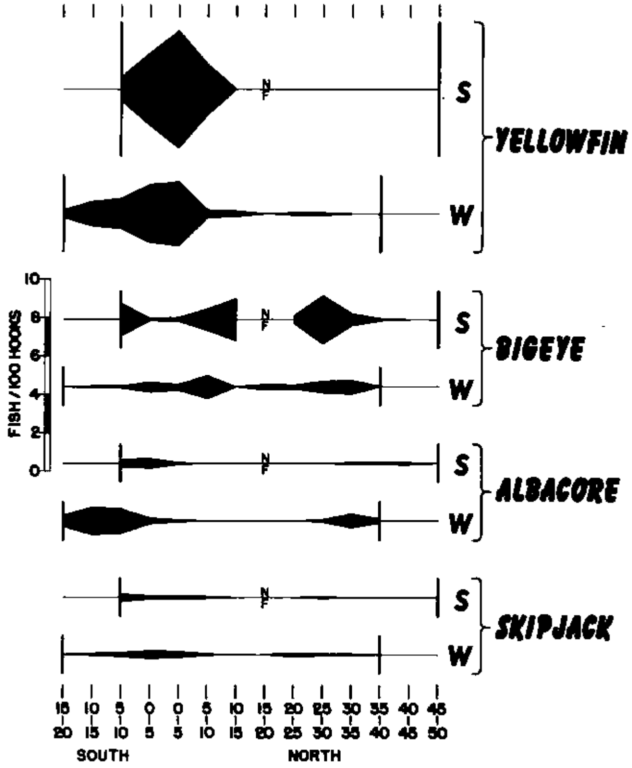
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Fig. 3.

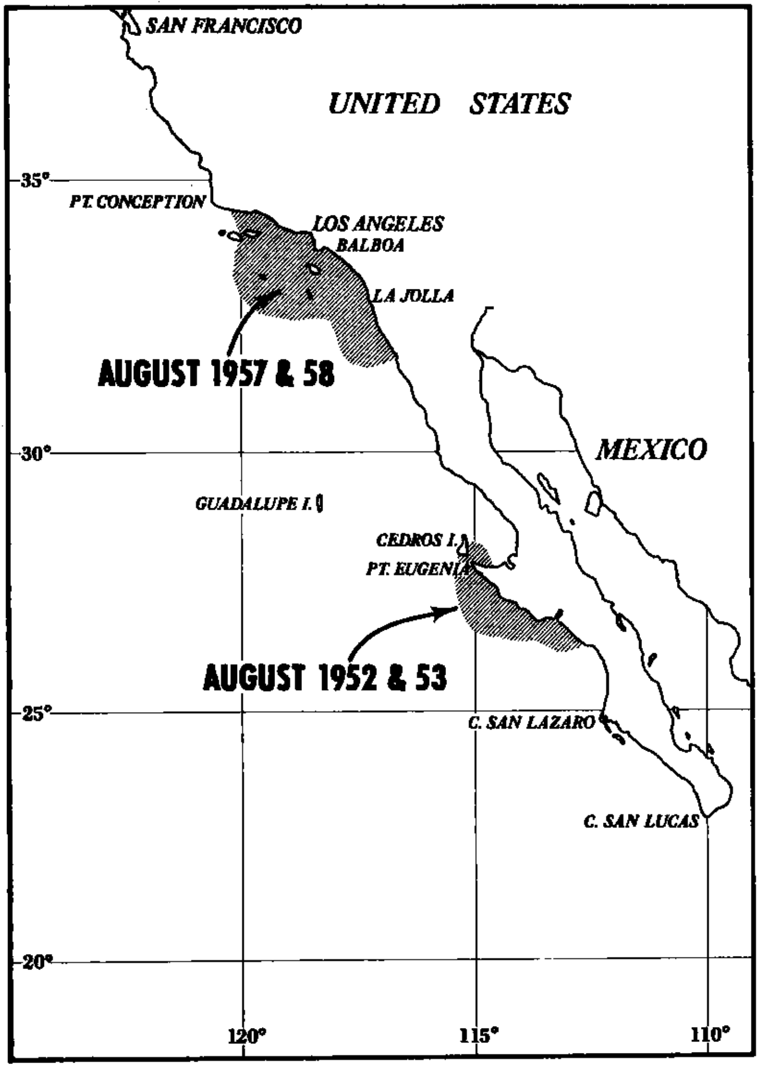


Fig. 4, from Hester, 1961

coastal fishery could be anticipated to begin corresponded to that where this water type approached the coast. The distribution of isotherms in this part of the eastern north Pacific tends to roughly parallel the coast, approaching it obliquely in the south. The movement of albacore, judging from tagging experiments (Otsu, 1960), begins in the central north Pacific in spring towards the American coast in the 13° to 18° C band of water of the Transition Zone lying between the Subarctic and Subtropic Zones. As the fish approach the coast they migrate in the California Current.

Johnson found the anomalously cold conditions for 1952 characterized a large part of the eastern north Pacific and could be related to a more vigorous pattern of wind flow which strengthened the flow of the California Current and increased the degree of coastal upwelling. These associated phenomena were evident several months prior to the beginning of the albacore fishery. He also found in 1958, the wind patterns were such as to weaken the flow of the California Current and that an anomalously warm period was also in evidence several months in advance of the albacore fishing season.

The area where albacore would first appear could be anticipated to a degree by the spring sea surface temperature and salinity distributions in the Southern California - Lower California region. The California Department of Fish and Game has made spring cruises in this region and used the sea surface temperature data as a basis for predicting the locale of the initial albacore catches of the season (Clemens, 1961).

The shifts in the coastal fishing grounds for albacore as related to shifts in ocean climate suggest that the species can detect and remain in a particular water type. The success of the seasonal fishery may depend in part on the relation of the position of the water type, the location of the fishing ports, and the range of the fishing vessels.

The albacore fishery of the eastern north Pacific has experienced major fluctuations in yield in the past, including a virtual disappearance of landings for a time. The mean annual California landing for the years 1916 - 25 was about 17,000 tons; for 1926 - 41, about 2,400 tons; and for the subsequent period, 1942 - 61, about 31,000 tons. During this latter period an additional 10,000 tons or so was landed annually in Oregon and Washington ports to the north of California. Whether the period of scarcity following 1925 was related to major anomalies in the ocean climate or changes in the abundance of the north Pacific albacore stock is not known. Beginning in 1936, an albacore fishery developed to the north of California which continued following the resurgence of the fishery in California. Uda (1962) reported that the 1930 - 40 period was one of good fishing off Japan, and the 1941 - 49 period as one of poor fishing. Figure 5 depicts the albacore fishing areas for the North Pacific.

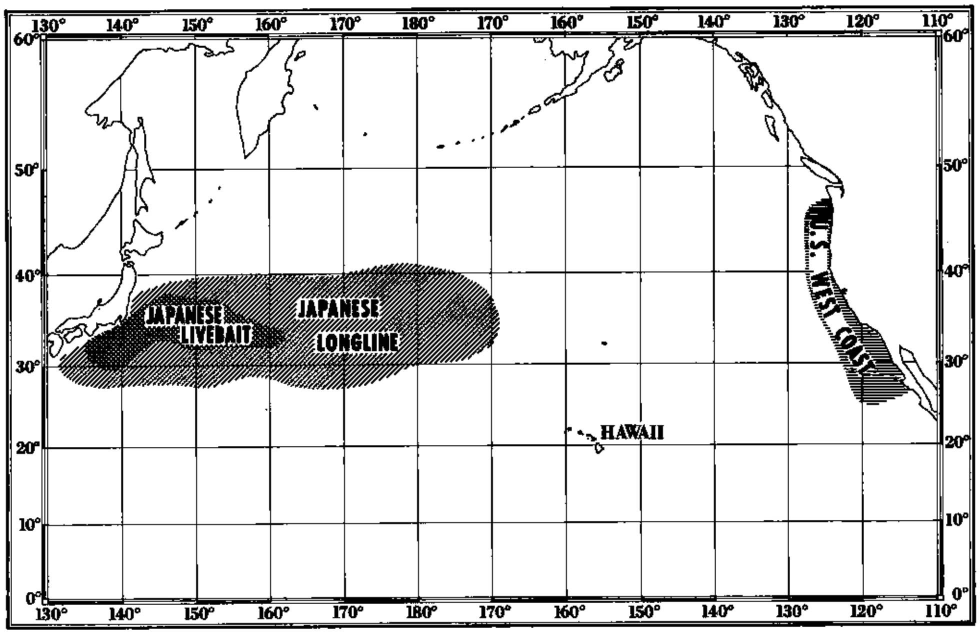


Fig. 5, from Otsu, 1963.

In addition to the bluefin tuna and albacore, there are seasonal fisheries for skipjack in the middle latitudes. The duration and developmental pattern of the large skipjack fishery off Japan is strongly affected by the Kuroshio system and its dynamic interaction with the Oyashio (Anon., 1963). A fishery for this species is also beginning in the analogous current systems in the western north Atlantic.

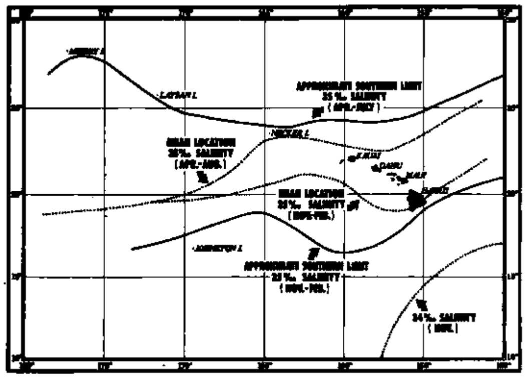


Fig. 6, from Seckel, 1963.

While the seasonal association of tuna with summer warming is well known, studies of the seasonal changes in abundance of skipjack in Hawaiian waters and their anomalies suggest the possibility of more subtle environmental responses. Seckel (1963) described the seasonal cycle in the ocean climate for the Hawaiian region, its anomalies, and the associated changes in the availability of skipjack. The seasonal change at the latitude of the Hawaiian Islands is a gentle one, and the marine environment never becomes unsuited for skipjack which is, indeed, a resident species. Nevertheless, the summer catch may exceed that of winter by as much as twenty times, and the proportion of large fish in the landings greatly increases during the summer.

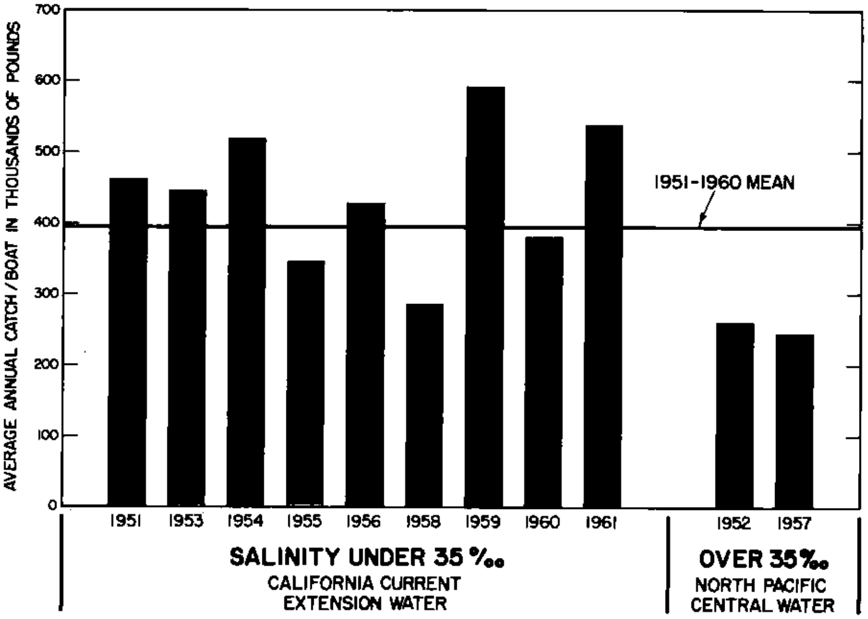


Fig. 7, from Seckel, 1963.

Coincident with the seasonal changes in the availability of fish is a change in the origin and character of the water in the Hawaiian region. During the summer period of good fishing, the water is of transitional character between the North Pacific Central and the North Pacific Equatorial Water Types. This transitional water type has been referred to as the California Current Extension by Seckel. It is separated from the North Pacific Central Water Type by a well defined salinity gradient. This salinity gradient (from 34.8°/00 to 35°/00) is located to the north of the main islands from April through August or September, and to the south from November through February (Fig. 6). At other seasons of the year it is in transit through these islands. This rhythmic seasonal movement of the salinity gradient through the Hawaiian Archipelago, marking the replacement of one water type by another, varied from year to year in the precise time of the advance and retreat and in the vigor of the change. In some years, the more saline waters remained in the Hawaiian area through the summer, and during such years the catch of skipjack was roughly half that of the best years (Fig. 7).

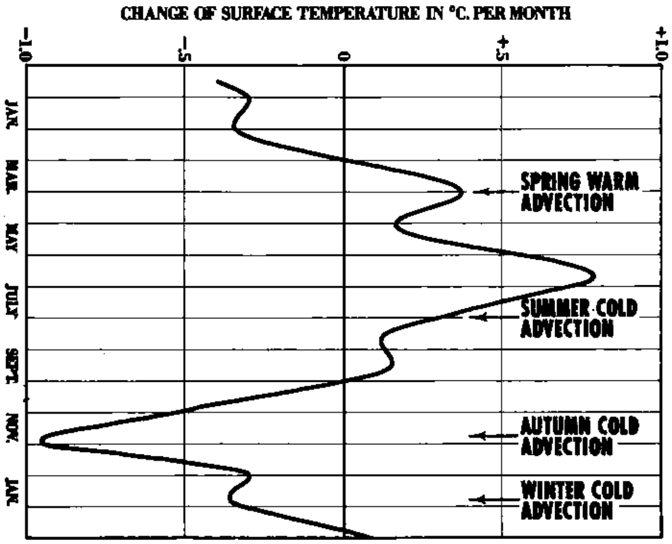


Fig. 8, from Seckel, 1963.

The change in the water types was detectable not only by salinity changes, but by temperature changes also. The seasonal change of sea surface temperatures followed a characteristic pattern, best expressed as a rate of change of temperature with time (Fig. 8). The changes in the observed temperatures reflected, in part, the advection of water through the Hawaiian region, and the time when the rate of temperature change reversed direction from negative to positive indicated a reversal in the direction of advection and provided an advanced notice that the California Current Extension had begun its seasonal march towards Hawaii (Fig. 6). The reversal of advection usually occurred between the latter half of February and the middle of March. The earlier it did occur, the earlier was the beginning of summer in the sea and the appearance of large skipjack in abundance, characteristic of this season. In this situation was the means of predicting during the early spring the probable quality of the fishing for the next summer. Such predictions have been made on this basis since 1959 by the staff of the Honolulu Biological Laboratory, Bureau of Commercial Fisheries. Figure 9 shows the relationship between the time of the reversal in the temperature trend and the annual average catch by boat and that for the year. The reversal from cooling to warming of the ocean surface layers had been followed, as previously mentioned, when this change occurred early in the spring, with a correspondingly earlier replacement of the high salinity North Pacific Central Water by that of the lower salinity California Current Extension for the period for which data were available. In 1963, although the early spring reversal in the trend of sea surface temperatures did occur, it was not followed with the replacement of the first mentioned water type by the second. Apparently the dynamic seasonal processes began with vigor, but became much weaker,

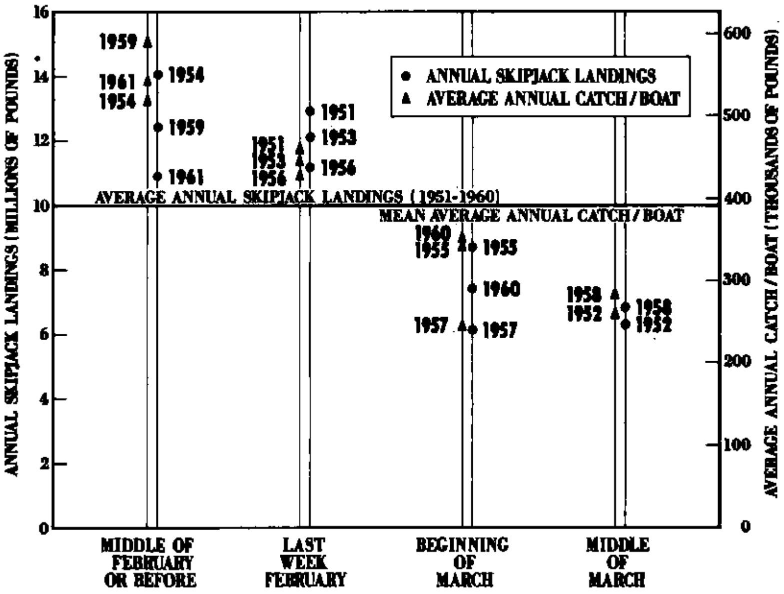


Fig. 9, from Seckel, 1963.

for some reason, prior to summer. The substantially lower than average yield of skipjack for the Hawaiian fishery for 1963 also indicated that the availability of skipjack responded to the anomalous development of the season as might have been anticipated.[1] Interestingly enough, the two water types did not differ significantly in their standing crops of zooplankton or other evidence of productivity aside from that provided by the fishery.

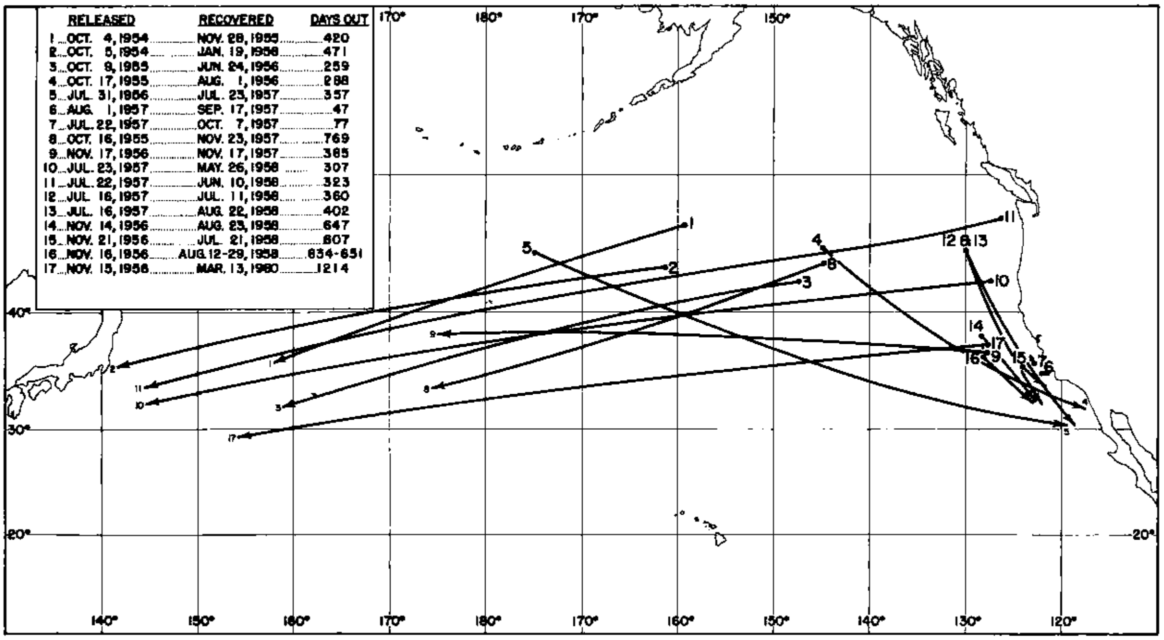
The stock of skipjack associated with the California Current Extension in Hawaii has not exhibited any immunological differences, based on serological tests, from those of the Mexican coast (Dr Lucian Sprague, personal communication). The skipjack present in Hawaiian waters during the winter months do exhibit differences in this regard, suggesting the occurrence of two independent stocks of this species replacing each other seasonally, each associated in Hawaiian waters with a different water type. A related bit of evidence, the recovery of two skipjack in the summer Hawaiian fishery two years after being tagged off Mexico, further strengthens the possibility that the summer Hawaiian skipjack and the skipjack of the eastern Pacific belong to the same stock.

SIZE CONNECTED ACTIVE ENVIRONMENTAL RESPONSES

Studies of the environmental responses of some species of tunas have suggested a change in such responses with growth. These produce a differential distribution of the fish by size or age. In the Pacific this appears to be the case for albacore, bluefin and skipjack tunas.

Brock (1943) found that the albacore fishery of the eastern Pacific off Oregon took adolescent fish and reported that the Hawaiian longline fishery took much larger fish including an occasional mature one. He suggested the possibility that the spawning stock may be in the tropical central Pacific with the adolescent fish entering the temperate eastern Pacific on a feeding migration.

Subsequently the successful tagging of albacore by the California Department of Fish and Game (Wilson, 1953) and later by the Honolulu Biological Laboratory of the Bureau of Commercial Fisheries (Otsu, 1960) (Fig. 10) suggested a complex pattern of migration across the Pacific, with the smaller fish reaching the central north Pacific during the winter months but returning to the eastern side during the summer. To an increasing degree the larger fish continued across the Pacific, being taken



RELEASED	RECOVERED	DAYS OUT
1. OCT. 4, 1954	NOV. 28, 1955	420
2. OCT. 5, 1954	JAN. 19, 1956	471
3. OCT. 8, 1955	JUN. 24, 1956	259
4. OCT. 17, 1955	AUG. 1, 1956	288
5. JUL. 31, 1956	JUL. 23, 1957	357
6. AUG. 1, 1957	SEP. 17, 1957	47
7. JUL. 22, 1957	OCT. 7, 1957	77
8. OCT. 16, 1955	NOV. 23, 1957	769
9. NOV. 17, 1956	NOV. 17, 1957	365
10. JUL. 23, 1957	MAY. 26, 1958	307
11. JUL. 22, 1957	JUN. 10, 1958	323
12. JUL. 16, 1957	JUL. 11, 1958	360
13. JUL. 16, 1957	AUG. 22, 1958	402
14. NOV. 14, 1956	AUG. 23, 1958	647
15. NOV. 21, 1956	JUL. 21, 1958	607
16. NOV. 16, 1956	AUG. 12-29, 1958	634-651
17. NOV. 15, 1956	MAR. 13, 1960	1214

Fig. 10, from Otsu, 1963.

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[1] Article in Commercial Fisheries Review, Vol. 25, No. 12, pp. 24-25.

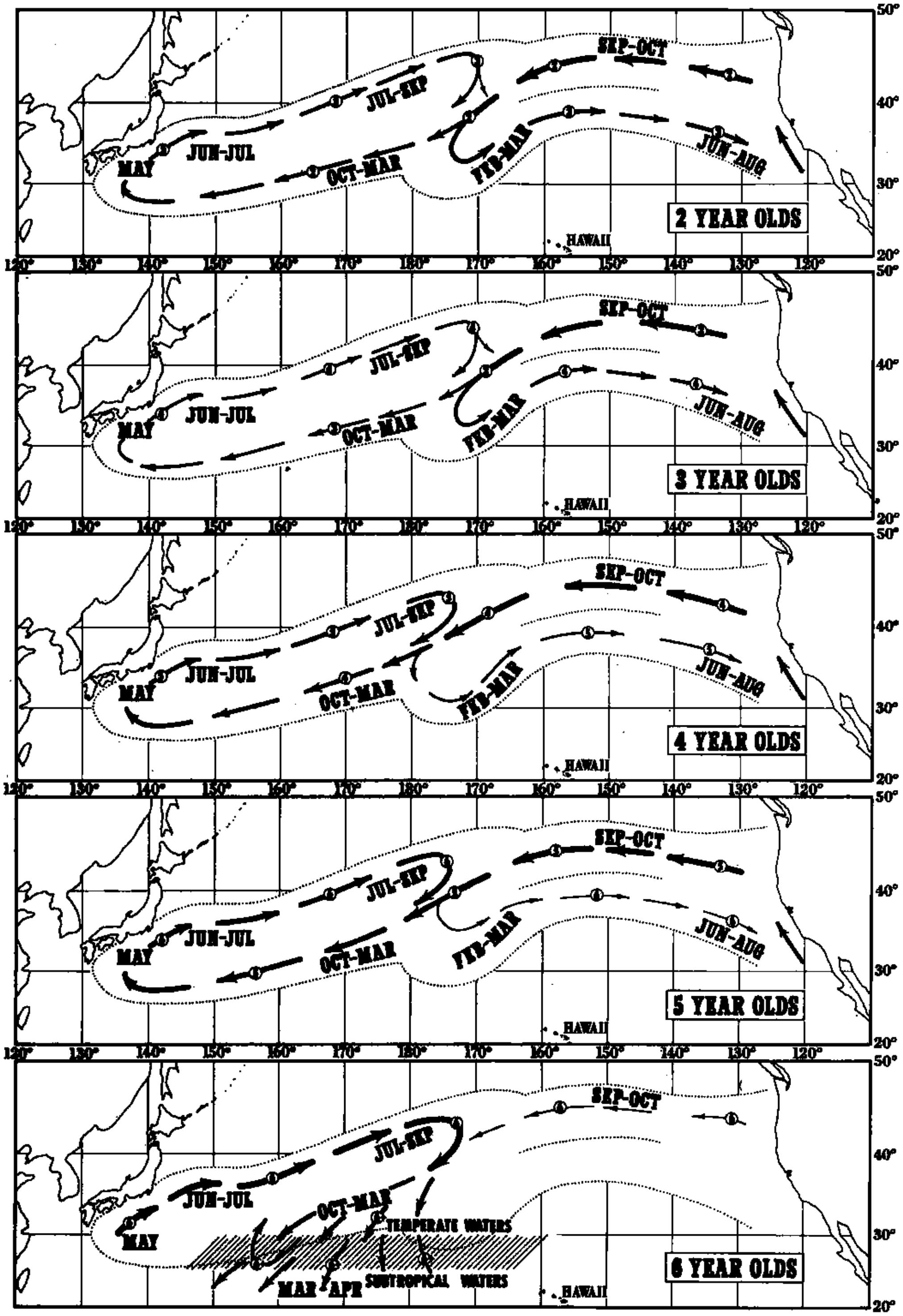

Fig. 11, from Otsu, 1963.

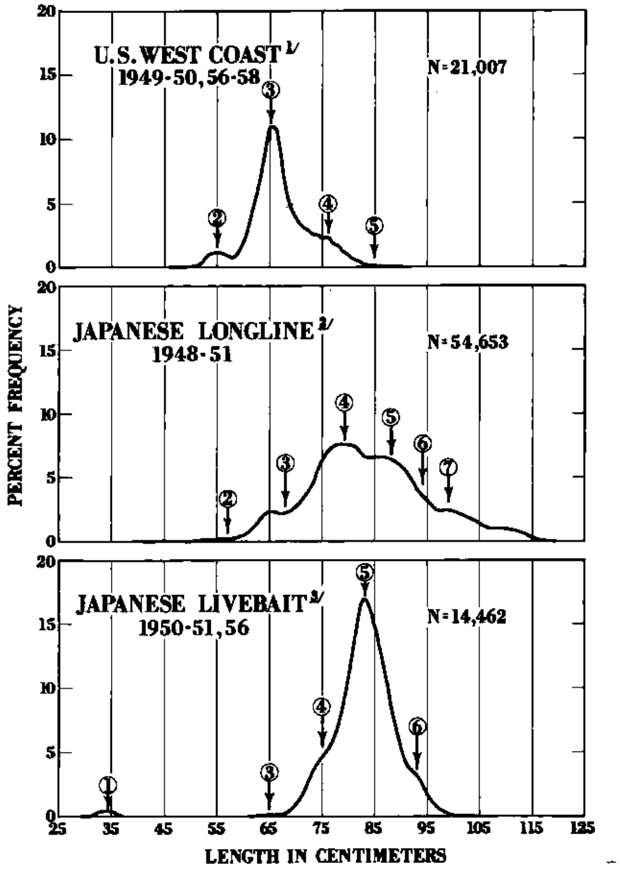

Fig. 12.

in the Japanese fishery and finally appearing in the North Equatorial Current below the surface water from the central to the western side where spawning apparently occurred. Otsu (1960 and 1963) (Fig. 11) described the back and forth migrations in terms of the ages of the fish; both Clemens (1961 and 1963) and Suda (1963) published essentially similar accounts. This migratory pattern did not involve the whole of the north Pacific albacore stock since fish of all sizes did occur in the western Pacific (Fig. 12).

Japanese data on the latitudinal variation in the sizes of albacore taken in the South Pacific suggests a similar pattern there with the adolescent fish in temperate latitudes in the mixed layer and the mature fish in the tropics below the thermocline. The albacore stock of the South Pacific appears to be distinct from that of the North Pacific (Suda, 1963).

The stock of bluefin tuna of the Eastern Pacific is also composed of immature fish. Unlike the bluefin tuna of the Western Pacific and of both the eastern and western North Atlantic, the fish are not large, the abundant sizes being from 4.5 to 20 kg (Roedel, 1953). Recently Orange and Fink (1963) reported the recapture of a bluefin tagged off Lower California about 300 miles south of Tokyo. It was presumably about 16 kg in weight when tagged, and about 121 kg when recaptured some five years later. Of course, the trans-ocean movements of bluefin tuna in the Atlantic were found earlier than those reported by Mather (1963). Here the direction of movement was from west to east.

The coastal stocks of skipjack in the Pacific are composed of individuals usually less than 7 or 8 kg in weight. The fisheries for these species in both Hawaii and Tahiti take, predominately during the summer seasons, a high proportion of large fish from 10 to 20 kg in weight. As previously indicated, there is evidence, including the capture of tagged fish, that the skipjack stock of the West Coast of Mexico and Hawaii, in the summer, are identical. This suggests that an unusually high proportion of the largest individuals in the stock are concentrated at the western or offshore boundary of the range.

The act of translocation is, of course, one of a number of possible responses to environmental changes. It is, through the effects on yields of fisheries, an easily inferred response. Some of the apparent effects of growth or age on this response have been discussed. The effects of changes in size or age on other responses to environmental changes may be less readily detected, depending upon the nature of the response. However, other responses should occur simply by reason of the shift in trophic level that major changes in fish size bring. Such responses may be detected through an appropriate analysis of fishery data if, on theoretical grounds, the nature of the response can be anticipated.

Brock and Riffenburgh (1960), through the use of a simple model, explored certain aspects of prey-predator relationships as these may be affected by schooling. They concluded that, for a given number of schooled prey, the encounter rate with a predator would be greatly reduced as compared to an equal number of scattered prey. If the reduced encounter rate were not to result in a reduced consumption of schooled prey, the predator would need to consume more prey on the occasion of an encounter. This could occur by consuming a large enough quantity immediately on encounter or remaining with the school for an extended period. Considering the quantities of prey that a predator would need to consume to negate the schooling advantage, estimated from reasonable models of school sizes, a strong possibility existed that schooling did confer a real survival advantage, at least in terms of the simple model used. The same model, considered in reverse, suggested that predation would be more efficient by scattered rather than by schooled predators.

The Brock-Riffenburgh hypothesis suggests that predators which are also prey of another predator would be subjected to a survival pressure to school, and a hunger pressure to scatter. With abundant food resources and heavy predation pressure, large schools should occur which should decrease in size as the food resources became less or predation was reduced, or both.

Tunas, like many other groups of fishes, rise through a number of trophic levels during their growth. As larvae they are part of the zooplankton and feed on a selected portion of it. With increasing size they feed on zooplankton predators, including their own young, and on higher predators, until for the larger species, they may approach or become members of the small assemblage of climax predators in the sea. With increasing size, the number of predators for which they are prey diminishes. However, as they become larger their prey may be, to an increasing degree, made up of larger organisms too. These, being in part at least members of higher trophic levels, may be relatively less abundant, requiring in turn more efficient predation by the larger tunas. Such considerations, together with the conclusions drawn from the schooling model, suggested that school size should be an inverse function of fish size within some limits of fish size and school size.

Some of the fishing methods for taking tuna, such as purse seining and live-bait fishing, depend upon schooling fish at or near the surface of the water. The longline method does not depend upon fishermen finding schools by sight. Longline fishing gear is a floating set line with, in some common versions, a hook spacing of 30 fathoms. The hooks are ordinarily baited with frozen fish or squid of appropriate size and the gear set for a day or a sizable portion thereof. Sets of the gear from a large longline vessel may involve upwards of a thousand baited hooks. The wide spacing of the hooks suggests that this gear should be particularly effective for scattered fish, but since no more than a single fish can occupy a hook, not as effective for schooled fish. Additionally, longline gear seems to fish selectively for the larger tuna which in a stable population should be less

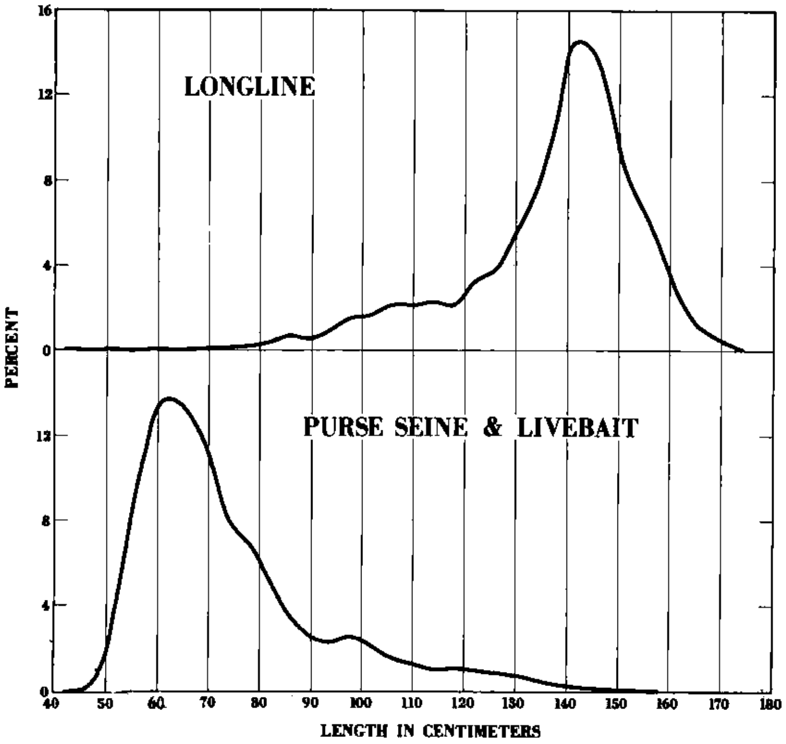

Fig. 13, from Brock, 1962.

numerous than the smaller ones (Fig. 13). However, the gear is ordinarily set to fish well below the surface, depending upon the principal species sought, between 20 and 70 fathoms.

Brock (1962) in a study of the nature of the size selectivity of longline gear for yellowfin tuna analyzed the relation between the size of fish hooked and the number hooked in a run. Runs were defined as fish of the same species taken on adjacent hooks in an uninterrupted sequence. The likelihood of getting runs of various numbers from scattered, solitary fish was computed and compared with that found in longline catches of yellowfin tuna taken in the central equatorial Pacific by the Bureau of Commercial Fisheries Laboratory in Honolulu where accurate records were kept of the species and size of each fish hooked and the hook position in the set of gear. The number of runs was found to occur more frequently than could be accounted for on a chance basis, assuming that the fish were scattered. This suggested that runs of fish may occur as a result of a school of fish encountering a set of longline gear and that the number of fish in a run and the size of the school from which they came would vary in the same direction. If both this and the Brock-Riffenburgh schooling model hold, the average size of the fish in a run should vary inversely with the number of fish in the run. This proved to be the case for the yellowfin catch data employed in the study.

The use of longline catches is an awkward way to investigate the relationship between the number of fish in a school and their size. I suggested to Dr M.B. Schaefer, then Director of Investigations of the Inter-American Tropical Tuna Commission, that this may be conveniently investigated using selected purse seine catches where presumably the entire school was captured. He reported (1963) such an analysis for the yellowfin tuna purse seine catches in the Eastern Pacific Ocean which clearly showed the predicted inverse relationship between the number of schooled fish and their size (Fig. 14).

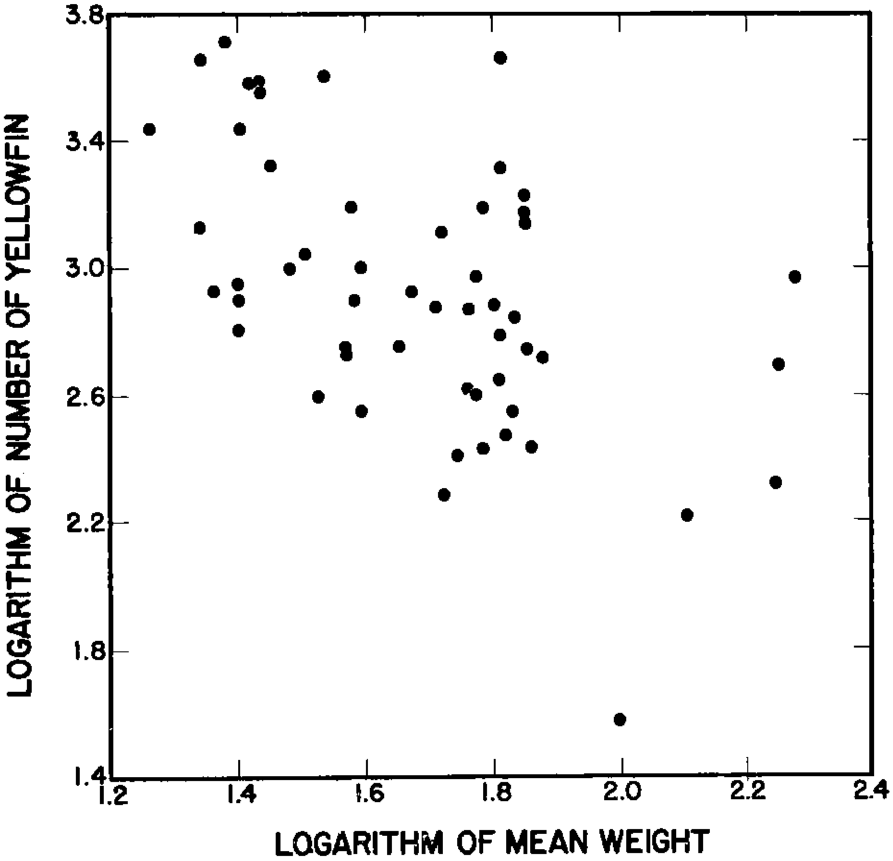

Fig. 14; from Schaefer, 1963

PASSIVE RESPONSES TO THE ENVIRONMENT

These may be difficult to distinguish from active ones, or, in the absence of good records relating to the fisheries, from fishery caused changes.

The predictive success of the model used by Dr Schaefer in estimating the effects of the fishery on the stocks of yellowfin tuna in the eastern Pacific, considering yields and fishing effort, but not environmentally induced changes in recruitment, suggests that these latter changes are not of great magnitude or significance for this species, at least over the extensive fishing grounds of the fishery.

Suda (1963), using primarily the catch and effort data for the winter longline fishery for albacore in the north Pacific, concludes that variations in recruitment are the most significant element in determining the magnitude of the catch per unit effort. He noted that large year classes were associated with a smaller mean size of recruits, and suggested that this was related to competition for sustenance. There was little evident relationship between the estimated number of spawners and resulting recruits. Large year classes of albacore and bigeye tuna seemed to occur during the same years. These relationships suggested that environmental factors were of substantial importance in determining the number of annual recruits to the population. He found no relationship, however, between the apparent abundance of albacore as measured by the fishery in the eastern north Pacific and by the Japanese fisheries, suggesting as a cause that the former fishery did not encompass the whole range of the fishable stock.

A number of workers have used tuna length frequency data as a means of estimating age and growth. Evidence that size groups were age groups was often not complete, but was difficult to interpret on other grounds. In general, tuna growth studies have indicated a rapid growth rate and a short life span for the tropical species and a longer life for bluefin tuna and albacore and a slower growth rate for the latter species. The age determination of these latter two species has also been done by the use of presumed annual marks on hard parts. Some differences have been found in estimates of age and growth of eastern Pacific albacore for the two methods.

The distinct modes and relatively modest range in size of a presumed age group in length frequency distributions for some species of tunas suggests the possibility of a short period of effective spawning. Brock (1943) found that the increase in modal length between the first major group in the length frequencies of albacore landed at San Pedro and the second major group in the landings for the following year was much alike for a number of years of these data, while this same difference for these length groups in the same years was decidedly more variable. This effect would be expected if the first group for one year were sampled from the same year class as that of the second group sampled a year later. Hamre (1963) suggested that the difference found here in the modal position of length of fish of the same age but belonging to different year classes may represent a difference in spawning time. However, Suda (1963) considering the inverse relationship between the mean size of recruits and the magnitude of the year class from which they came for Japanese data, concluded that a difference of this kind may be the result of an initially reduced growth rate through competition for food among the fish of the larger year classes.

Brock (1954), using modes of length frequency curves for the summer Hawaiian skipjack fishery, estimated the growth rate of this species. Recoveries of tagged skipjack showed somewhat less growth but substantially confirmed these estimates. He also found that spawning appeared to occur during the summer months with no evident short period of high intensity. Yet the sharp modes occurring in the length frequency curves, which considering the high rate of growth, suggested a relatively short period of effective recruitment from the apparently extended summer spawning. The possibility existed that the spawning season effectively blanketed an environmental situation that favored a high survival of the young for only a brief period. If this were true, and if the brief period of good survival occurred at different periods of the summer for different years, fish belonging to different year classes should exhibit correspondingly different average lengths at the same nominal ages. This has not yet been investigated.

THE NAVIGATION PROBLEM

The extensive movements of some species of tuna and their apparent ability to detect and associate with specific water types raise some interesting problems concerning how these fish navigate. Albacore, for example, appear in the eastern Pacific off the west coast of Lower California, the three Pacific coast states of the United States, and Canada during the summer as adolescent fish. They move offshore to the north central Pacific during the winter, and some of the older members of this group of adolescent fish continue on to the western Pacific while others return to the eastern Pacific during the following summer. As the older fish that move to the west approach maturity, which occurs at a length of 90 cm, they move towards the equator into the water of the North Equatorial Current where presumably spawning occurs. While the albacore of the North Pacific remain in the great current gyre between the middle latitudes and the equator, they do not simply ride the flow of the current. At times they move with it and at other times against it in a regular pattern related to the age of the fish and the season.

For the albacore to successfully orient themselves to the waters of this gyral current system would imply that they can identify its water by some cue. What the cue may be has yet to be demonstrated. However, Bull (1952) found that some species of marine fish could detect temperature differences of 0.03°C and salinity differences of 0.2 o/oo. Hasler (1960) and others found that fish can detect very slight changes in the odor or taste of water.

Navigation by the location of water masses would seem to play an important role since the anomalous movement of these seems to result in the anomalous movements by the tuna. The nature of gradients in the properties of the ocean suggests that their sole use as a means for navigation and orientation may be difficult, and certainly confusing and inefficient. Due to the effects of local air-sea interaction processes, gradients will not be uniform and may be reversed in a given area for a time. It is difficult to see what properties of the water itself would reveal the direction of current motion. While current boundaries are often sharply defined, their position and direction may be erratic and changeable with islands of water from one water mass becoming isolated in the other (Iselin, 1960).

The ability of many animals, including fishes, to use the azimuth of the sun as a compass has been demonstrated by a number of workers. Hasler (1960) and his co-workers, Braemer (1960), Schwassmann (1960), and Schwassmann and Braemer (1961) have published results of their work on the sun compass, utilizing several species of freshwater fishes and an anadromous one. Since the azimuth direction changes not only during the course of the day, but seasonally and with latitude, a complex response is involved, requiring an accurate time sense, and a change in the orientation pattern seasonally and latitudinally if movements of sufficient length to change latitude significantly are involved. Crossing the equator also involves a reversal of these. Birukow (1963) has provided a short general review of the problem. Adler (1963) studied the accuracy of the sensory abilities of a few species of birds, involved in the use of the sun's azimuth for navigation, the psychophysical limits. His results suggest that navigation may not be by sun compass alone, but may depend to some degree on landmarks or other cues.

There is little information on the abilities of tuna to detect changes in the properties of the ocean and none on their ability to use the sun's azimuth as a compass. However, evidence does exist concerning their ability to orient to the structure of the ocean in a complex way which suggests that they may be able to detect slight changes in the ocean, to navigate great distances accurately, and to anticipate the march of the seasons by appropriate earlier responses. Their means of accomplishing these feats would be of great interest, and their investigation, a challenge.

REFERENCES

ADLER, H.E. 1963. Psychophysical limits of celestial navigation hypothesis. *In* Animal Orientation. *Advances in Biology*, Vol. 26, Berlin.

ANONYMOUS, 1963. Skipjack - a world resource. Cir. 165. Fish and Wildlife Ser. May 1963, pp. 1-28.

AUSTIN, T.S. and V.E. BROCK. 1959. Meridianal variations in some oceanographic and marine biological factors in the central Pacific. Internat. Ocean. Cong. Preprints, pp. 130-132.

BIRUKOW, G. 1963. Time-compensated sun orientation in animals. Proc. 16th Internat. Cong. Zool., Vol. 4, pp. 346-350.

BLACKBURN, M. 1960. Distribution and abundance of tuna related to wind and ocean conditions in the Gulf of Tehuantepec, Mexico. Proc. World Sci. Meet. Biol. Tunas Rel. Sp., *F.A.O.Fish.Rep.*, (6) Vol. 3: 1557-1582.

BRAEMER, W. 1960. A critical review of the sun-azimuth hypothesis. Coldspring Harbor Symp. Quant. *Biol.*, 25, pp. 413-427.

BROCK, V.E. 1943. Contribution to the biology of the albacore *Germo alalunga* of the Oregon coast and other parts of the North Pacific. *Stanford ichthyol. Bull.* 2(6), pp. 199-248.

1954. Some aspects of the biology of the aku; *Katsuwonus pelamis* in the Hawaiian Islands. *Pacif. Sci.* 8 (1), pp. 94-104.

1959. The tuna resources in relation to oceanographic features. In Tuna Industry Conference Papers, May 1959, U.S. Fish and Wildlife Service., Cir. 65, pp. 1 - 11.

1962. On the nature of the selective fishing action of longline gear. *Pacif. Sci.* 16 (1), pp. 3-14.

BROCK, V.E. and R.R. RIFFENBURGH. 1960. Fish schooling: a possible factor in reducing predation. *J. Cons. Explor. Mer*, 25(3), pp. 307-317.

BULL, H.O. 1952. An evaluation of our knowledge of fish behaviour in relation to hydrography. *Rapp. Cons. Explor. Mer*, 131, pp. 8-23.

CLEMENS, H.B. 1961. The migration, age, and growth of Pacific albacore (*Thunnus germo*), 1951-1958. Dept. Fish and Game Fish. Bull. 115.

1963. A model of albacore migration in the North Pacific Ocean. Proc. World Sci. Meet. Biol. Tunas and Rel. Sp., *F.A.O. Fish. Rep.*, (6), Vol. 3: 1537-1548.

COLLETTE, B.B. and R. H. GIBBS. 1963. A preliminary review of the fishes of the family Scombridae. Proc. World Sci. Meet. Biol. Tunas and Rel. Sp., *F.A.O. Fish. Rep.*, (6), Vol. 1: 23-29.

HAMRE, J. 1963. Size and composition of tuna stocks. Proc. World Sci. Meet. Biol. Tunas and Rel. Sp., *F.A.O. Fish. Rep.*, (6), Vol. 3: 1023-1039.

HASLER, A.D. 1960. Guideposts of migrating fishes. *Science*, 132 (3430), pp. 785-792.

HESTER, F.J. 1961. A method of predicting tuna catch by using coastal sea-surface temperatures. *Calif. Fish. Game*, 47(4), pp. 313-326.

ISELIN, C. O'D. 1960. The Gulf Stream system. *Oceanus*, 6(4), pp. 20-23.

JOHNSON, J.H. 1963. Changes in availability of albacore in the eastern Pacific Ocean. Proc. World Sci. Meet. Biol. Tunas and Rel. Sp., *F.A.O. Fish. Rep.*, (6), Vol. 3: 1227-1235.

JONES, E.C. 1962. Evidence of an island effect upon the standing crop of zooplankton near the Marquesas Island, Central Pacific. *Jour. du Cons.*, 27(3), pp. 223-231.

LAEVASTU, T. and H. ROSA, Jr. 1963. Distribution and relative abundance of tunas in relation to their environment. Proc. World Sci. Meet. Biol. Tunas and Rel. Sp., *F.A.O. Fish. Rep.*, (6) Vol. 3: 1835-1851.

MATHER, F.J., III. 1963. Game fish migrations. *Oceanus*, 10(2), pp. 16-19.

ORANGE, C.J. and B.D. FINK. 1963. Migration of a tagged bluefin tuna across the Pacific Ocean. *Calif. Fish Game*, 49(4), pp. 307-308.

OTSU, T. 1960. Albacore migration and growth in the North Pacific Ocean as estimated from tag recoveries. *Pacif. Sci.*, 14(3), pp. 257-266.

OTSU, T. and R.M. UCHIDA. 1963. Model of the migration of albacore in the North Pacific Ocean. *Fish. Bull., U.S.* , 63(1), pp. 33-44.

RADOVICH, J. 1963. Effects of water temperature on the distribution of some scombrid fishes along the Pacific coast of North America. Proc. World Sci. Meet. Biol. Tunas and Rel.Sp., *F.A.O. Fish. Rep.*, (6), Vol. 3: 1459-1475.

ROEDEL, P.M. 1953. Common ocean fishes of the California coast. *Fish. Bull. 91, State of California*, Department of Fish and Game.

SECKEL, G.R. 1963. Climatic parameters and the Hawaiian skipjack fishery. Proc. World Sci. Meet. Biol. Tunas and Rel. Sp., *F.A.O. Fish. Rep.*, (6), Vol. 3: 1201-1208.

SCHAEFER, M.B. 1960. Tuna oceanography programs in the tropical central and eastern Pacific. Calif. Coop. Oceanic Fish. Invest. (CalCOFI) 8, 1 July 1959-30 June 1960, pp. 41-44.

1963. Report on the investigations of the Inter-American Tropical Tuna Commission for the year 1962.

SCHWASSMANN, H.O. 1960. Environmental cues in the orientation rhythm of fish. Coldspring Harbor Symp. Quant. *Biol.*, 25, pp. 443-450.

SCHWASSMANN, H.O. and W. BRAEMER. 1961. The effect of experimentally changed photoperiod on the sun-orientation rhythm of fish. *Physiol. Zool.*, 34(4), pp. 273-286.

SHIBATA, K. 1963. Analysis of the fish finder records II some acoustic and ecological information on tuna and others. *Bull. Fac. Fish. Nagasaki*, No. 14, February 1963, pp. 15-24.

SHIPPEN, H.H. 1961. Distribution and abundance of skipjack in the Hawaiian fishery, 1952-53. *Fish Bull.* 188, Vol. 61.

SHOMURA, R. and G.I. MURPHY. 1955. Longline fishing for deep-swimming tunas in the Central Pacific. *Sp. sci. Rep. Fish.* 157, September 1955, pp. 1-70.

SUDA, A. 1963. Structure of the albacore stock and fluctuation in the catch in the North Pacific areas. Proc. World Sci. Meet. Biol. Tunas and Rel. Sp., *F.A.O. Fish. Rep.*, (6), Vol. 3: 1237-1277.

UDA, M. 1962. Cyclic correlated occurrence of world-wide anomalous oceanographic phenomena and fisheries conditons. *J. oceanogr. Soc. Japan*, 20 Ann. Vol. 1962. pp. 368-376.

WILSON, ROBERT C. 1953. Tuna marking, a progress report. *Calif. Fish Game*, 39 (4) pp. 429-442.

A REVIEW OF THE EFFECTS OF THE ENVIRONMENT ON THE HERRING

By

B. B. Parrish[1]

NOTE:

"The substance of Mr Parrish's paper will be included within a longer review which is being prepared in conjunction with Mr A. Saville of the Marine Laboratory in Aberdeen, under the title "The biology of north-east Atlantic herring populations", for publication in the review journal "Oceanography and Marine Biology", edited by Dr H. Barnes (published by George Allen and Unwin Ltd.). It is expected that Parts 1 and 2 of this joint review will appear in volume 3, to be published in 1965, and other parts subsequently".

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SECTION

A

A-1

RELATION OF TEMPERATURE TO FISH ABUNDANCE AND DISTRIBUTION IN THE SOUTHERN NEW ENGLAND AREA.[1]

By

R. L. Edwards[2]

ABSTRACT

Information is presented on the distribution of a number of species of southern New England fishes that typically migrate offshore during the winter months. Depth and temperature preferences are discussed. Seasonal changes in the abundance of eight species on an inshore fishing ground, the Southwest Ground near Block Island, are described for the period 1956-58. The relation of these changes to temperature is discussed. The seasonal changes observed on the Southwest Ground demonstrate that these species tend to be most abundant on inshore grounds when water temperatures are the same as those in which they occur most abundantly offshore. Some of the factors that complicate the analysis of seasonal changes in abundance are briefly discussed. These include size, sex, and the effect of temperature or other hydrographic events such as the fall overturn on availability.

INTRODUCTION

The first United States Commissioner of Fisheries, S. F. Baird, undertook an investigation of the life histories of various commercial species common to the southern New England area by soliciting the testimony of knowledgeable fishermen, trap operators and others. To the question concerning the seasonal movements of scup, Mr W. E. Whalley of Newport, Rhode Island, replied as follows:

"They expected them in February, and got the seines ready. They had them in the water in March. I always judge by the dandelions; when I see the first dandelion, scup come in; I watch the buds, and when the buds are swelled full, then our traps go in. When the dandelion goes out of bloom and goes to seed, the scup are gone; that is true one year with another, though they vary with the season. I am guided by the blossoms of other kinds of plants for other fish. When high blackberries are in bloom, we catch striped bass that weigh from twelve to twenty pounds; when the blue violets are in blossom—they come early—you can catch the small scoot-bass. That has always been my rule, that has been handed down by my forefathers".

Although this testimony is nearly 100 yr old, it is not easy to improve upon it today.

Fishery biologists tacitly agree that temperature is an important factor in the determination of general distribution and seasonal abundance. It is difficult however to demonstrate and quantify the role of temperature, simply because of the lack of concomitant fishery and temperature data for most marine areas; and because of the difficulty of establishing the causality involved n implied relationships. While much still remains to be desired, the general temperature cycle s well known and abundant fishery data exist for the southern New England area, sufficient at east to justify a study of the relation of temperature to variations in seasonal abundance.

Early in the 1950's, a sizeable industrial trawl fishery developed in New England, particularly at Point Judith, Rhode Island. This fishery was unusual in that all fish taken in the trawl were anded. Food fish were sorted out and sold at the local cooperative, and the rest of the catch old at a nearby reduction plant. The general aspects of this fishery have been reported upon by dwards and Lux (1958). The species composition of that portion of the catch sold for reduction n 1957 and 1958 has been reported by Edwards (1958) and Edwards and Lawday (1960). By 1960 this ishery virtually ceased to exist at Point Judith. The fishing activities had however been careully documented for the period July 1955-60 inclusive.

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Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, Massachusetts, USA.

DIVERSITY INDEX STUDIES

The first attempt to interpret the industrial trawl fishery data involved the calculation of various indices of species diversity, especially Fisher's (Fisher, *et al.*, 1943) alpha[3]. There was a relation between bottom temperature and alpha, particularly on those fishing grounds nearest to land. The values of alpha obtained for one of these, the Southwest Ground, are given in Table 1. Combining samples, as for example the bimonthly combinations given in Table 1 or the combining of samples from nearby grounds of the same depth, tended to strengthen the relation between temperature and alpha, and suggested as well that very large samples were required to obtain reliable values for individual grounds or smaller units of time. As it was, over 55,000 fish were involved in the Southwest Ground samples used for the analysis summarized in Table 1.

TABLE 1. ALPHAS FOR SOUTHWEST GROUND, FOR 1956-58, BY MONTH, FOR ALL MONTHLY SAMPLES COMBINED, AND FOR EACH BIMONTHLY PERIOD, ALL SAMPLES COMBINED.

	1956	1957	1958	Average alpha	Alpha, all samples combined	Alpha bimonthly values, all samples combined		Bottom water temperature °C
Jan.	2.16	3.13	--	2.65	2.55	+Feb.	2.45	6.0
Febr.	1.76	1.98	2.53	2.09	2.01	+Mar.	2.39	3.8
Mar.	2.69	2.36	2.48	2.51	2.42	+Apr.	2.92	3.3
Apr.	3.54	2.67	2.69	2.97	2.80	+May	3.07	4.8
May	2.80	2.78	2.89	2.82	3.00	+June	3.32	7.0
June	2.80	2.56	3.31	2.89	3.30	+July	3.68	11.2
July	2.93	3.23	2.87	3.01	3.55	+Aug.	3.78	12.0
Aug.	2.65	2.86	2.36	2.62	3.22	+Sept.	3.77	13.3
Sept.	2.90	3.09	3.18	3.06	3.38	+Oct.	3.59	14.2
Oct.	2.82	3.26	3.01	3.03	3.58	+Nov.	3.91	14.2
Nov.	2.46	2.28	3.09	2.61	3.35	+Dec.	3.20	12.6
Dec.	2.60	2.41	2.47	2.49	2.45	+Jan.	2.77	7.0

SOUTHERN NEW ENGLAND SPECIES

In very broad terms, the species in the southern New England area may be divided into two groups. The first is a summer or warm water complex, and includes the red hake (*Urophycis chuss*), silver hake (*Merluccius bilinearis*), scup (*Stenotomus chrysops*), butterfish (*Poronotus triacanthus*), fluke, or summer flounder (*Paralichthys dentatus*), angler (*Lophius americanus*) and about twenty additional species of lesser abundance. Most of these species migrate offshore and southward to the edge of the Continental Shelf during the winter months. During the cold months of the year, a second group of species, fewer in number and considerably smaller in biomass, dominate the grounds. The group includes, among others, the cod (*Gadus morhua*), ocean pout (*Macrozoarces americanus*), yellowtail flounder (*Limanda ferruginea*) and the longhorned sculpin (*Myoxocephalus octodecimspinosus*). During the warmer months of the year these species either move offshore or eastward toward the Gulf of Maine.

WINTER DISTRIBUTION

The fishes characteristically occurring inshore during the warm months of the year migrate offshore and southward during the winter months as mentioned above. During winter months as shown in Fig. 1., inshore water temperatures approach 0°C. Temperatures increase rapidly with depth, reaching a maximum of 12° to 14°C. between 100 and 125 m. This warm water zone is characteristic of the shelf edge from Cape Cod to Cape Hatteras. Beyond the warm zone temperatures slowly decrease as depth increases, but seldom decrease to much less than 6°C. at 250 m.

The numbers of individuals of some of the species collected at the time the data for Fig. 1 were obtained are given in Table 2. More extensive distributional data were obtained in 1959 on

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[3] $S = \alpha \ln (N/\alpha+1)$, where S is the number of species and N the total number of individuals.

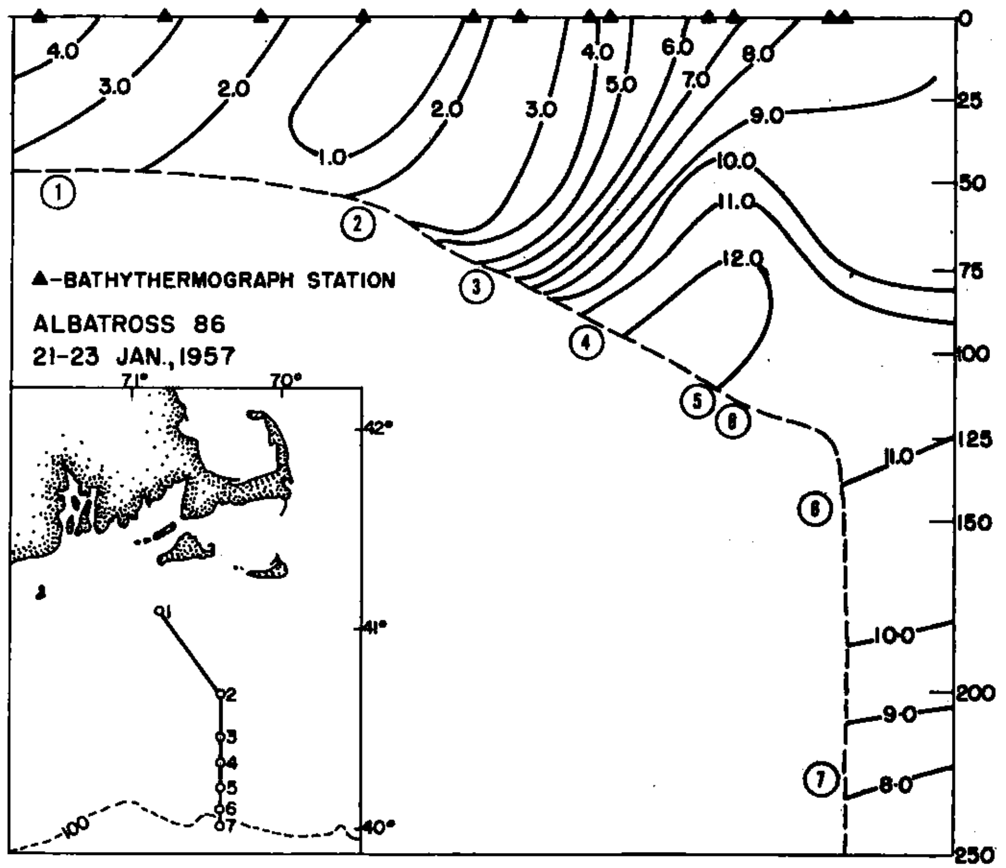

Fig. 1. Water temperatures and fishing station locations (circled), based on data collected on *Albatross III* cruise 86, 21-23 January, 1957. Transect runs south from Martha's Vineyard.

lbatross III Cruise 126 (Edwards, *et al.* 1961). These data are presented diagrammatically in Fig. . The values given represent the relative (percent) number per tow for each temperature interval iven. The number of tows was insufficient to break down the data for temperatures less than 10°C.

Two species, the scup and fluke, were most abundant in the warmer water and both were more bundant on the shoaler side of the warm water zone. The fluke was not often taken on this par-icular cruise and the data obtained indicate a sample bias toward colder water not in accord with ther observations, as for example those of Cruise 86 given in Table 2.

The butterfish was most abundant in waters with a temperature of about 11° C , regardless of epth. Similarly distributed, but with a preference for even colder water (9° to 10°C), the red ake also appeared to disregard depth.

While the angler was most frequently taken in water of any depth with temperatures from 8° to °C , it was clearly more abundant at depths of 125-200 m. Silver hake as well tended to be more ɔundant in deeper water but generally did not occur where temperatures were much below 9°C except ɔr young-of-the-year silver hake which were taken only in the relatively cold shoal water. A eneral tendency for this species to prefer progressively warmer water as it increases in size was ɔserved.

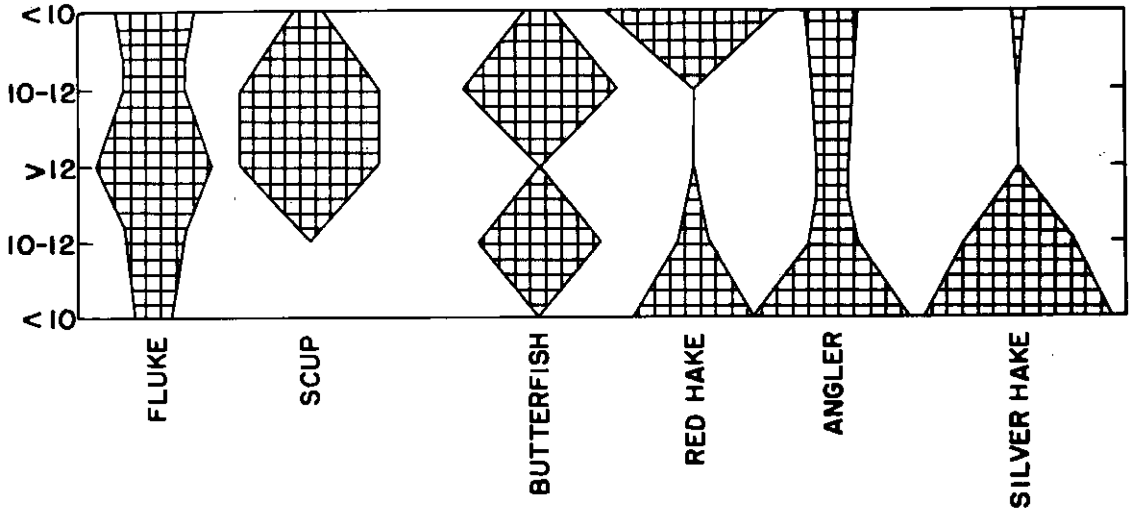

Fig. 2. Diagrammatic presentation of the relative (percentage) catch/tow data. Depth increases from top to bottom, the warmest water occurs between 100-125 m.

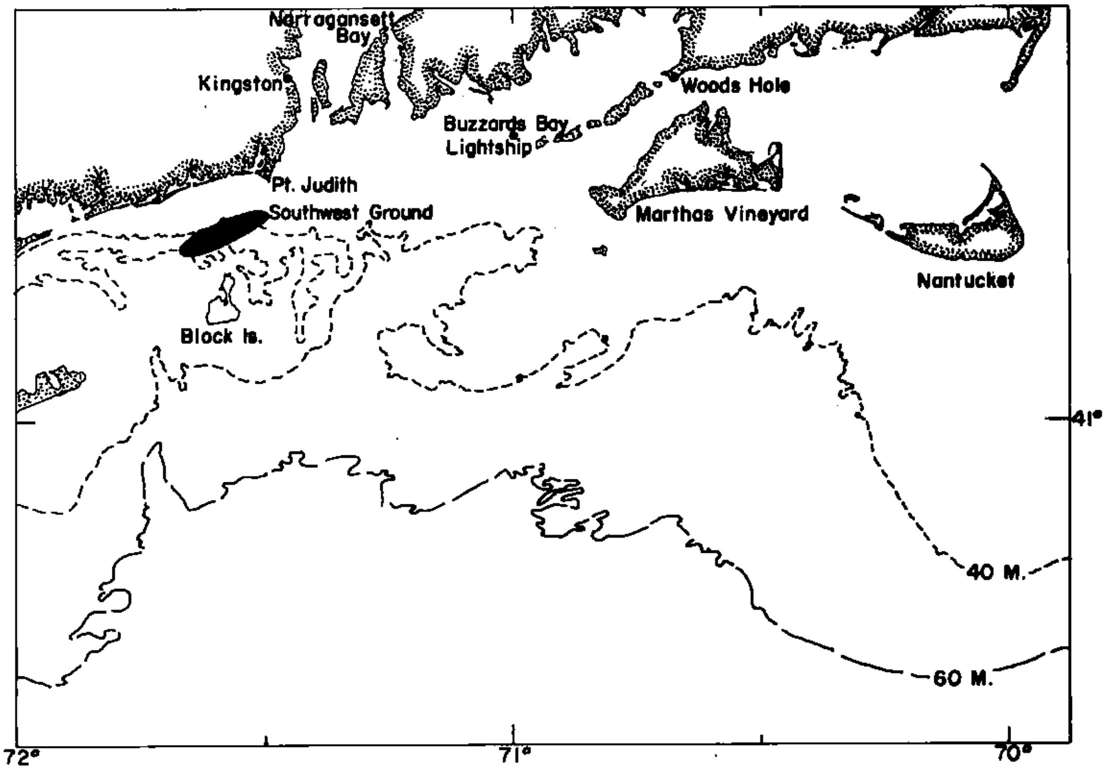

Fig. 3. Map of the southern New England area showing location of Southwest Ground and surface temperature stations.

TABLE 2. NUMBERS OF SELECTED SPECIES CAUGHT AT STATIONS SHOWN ON FIG.1. ASTERISK INDICATES YOUNG-OF-THE-YEAR.

	STATION NUMBER							
	1	2	3	4	5	8	6	7
Bottom temperature °C	2.8	2.2	6.7	11.1	11.9	11.6	11.0	8.4
Depth (m)	50	60	70	85	110	115	145	230
Fluke				12	5			
Scup				19	1			
Butterfish				695	21			
Red hake		18	102	1				
Silver hake	*6	*560	223	11		1		28
Angler	2	6	7	1		1		6
Cod		9						
Ocean pout	1	2						

SEASONAL CHANGES ON THE SOUTHWEST GROUND

Water temperatures.

The Southwest Ground (Fig. 3) lies between Block Island and the coast of Rhode Island. The depths fished by commercial fishermen varied from 40 to 50 m. The seasonal cycle of temperature for waters 50 m in depth in this immediate area is shown in Fig. 4. Temperature minima of about 3°C occur in late February or early March, and maxima of about 20°C at the surface in August and 15°C at the bottom in September and October. Overturn begins toward the end of September and usually is complete by the end of October. Intrusions of colder bottom water in late summer almost certainly occur from time to time.

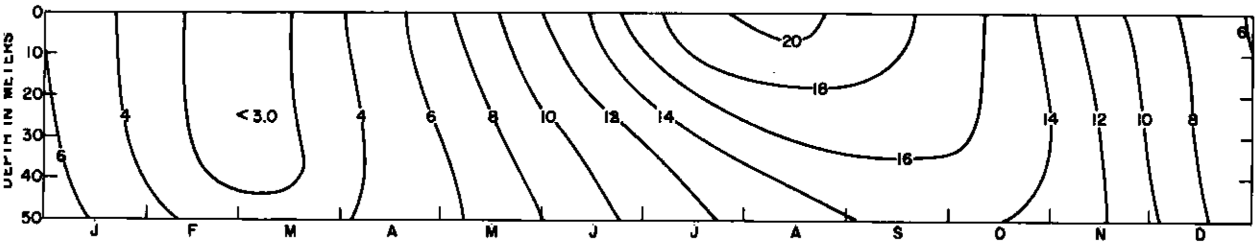

Fig. 4. Seasonal cycle of temperature for waters 50 meters in depth north of Block Island. Based on all bathythermograph data available for the period 1941-1960.

Fishery data will be presented below for the years 1956-58. The only consistently useful temperature data for this period are to be found in the surface temperature and lightship observations reported by Bumpus (1957) and Day (1959*a*, *b*). The year 1957 was a relatively warm year throughout the area south of Cape Cod. Day noted several instances of cold bottom water intrusion along the middle Atlantic coast in 1957. The data for 1958 show a tendency toward much colder water than was recorded in the previous several years. Surface temperatures at Woods Hole show the same general trends as do those at the Buzzards Bay Lightship and Kingston, Rhode Island. The records for the latter two stations are, unfortunately, incomplete for the period 1956-58.

Woods Hole surface temperature deviations for the period 1956-58 are presented in Fig. 5. The data have been smoothed by 3's to emphasize trends and reduce strictly local variations.

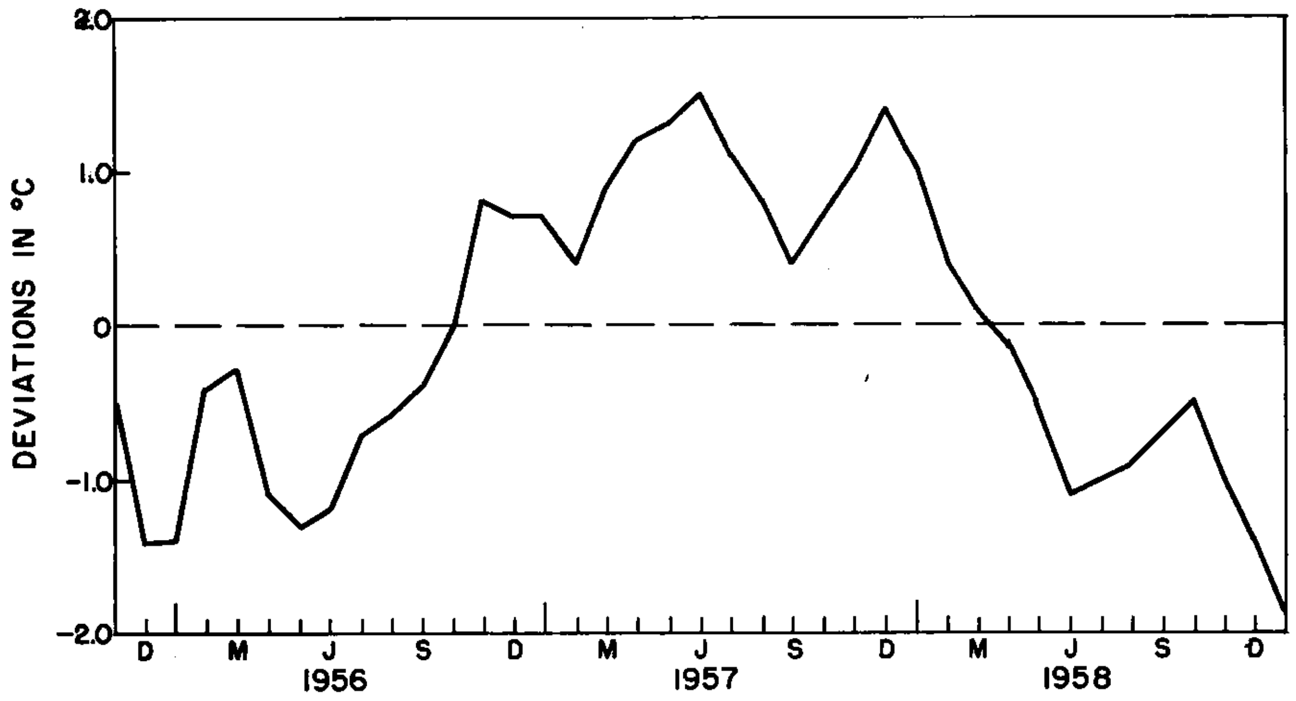

Fig. 5. Monthly deviations of Woods Hole surface temperatures, smoothed by 3's, for the period November 1955 to January 1959.

To the extent that these Woods Hole temperature deviations may also represent trends on the Southwest Ground, the following points should be kept in mind in connection with the discussions that follow. The year 1956 began relatively cold but warmed up gradually and ended with above normal temperatures. Conditions during 1957 were consistently warmer than normal. The sharp decline in the deviations for the summer months may indicate that the cold water intrusions mentioned earlier occurred in the southern New England area as well. The combination of warmer than average surface conditions and intrusions of colder bottom water would tend to delay overturn. Beginning with temperatures significantly above normal, 1958 temperatures became progressively colder than average and the year ended with below normal temperatures. It may be assumed that bottom temperatures varied in much the same manner except for that period (June - September) when thermal stratification was marked.

Catch/hour data

Table 3 lists the average monthly catch/hour for the eight species discussed below. Data are presented for the period 1956-58. The Southwest Ground is fished only during daylight hours; thus no adjustment was required for diurnal variations in availability. The vessels that prosecuted this fishery were all small otter trawlers, mostly less than 20 m in length. The codends of the trawls were invariably lined with netting having a stretched mesh size of 5 - 6 cm.

For the purposes of discussion, these data were transformed into relative (percentage) catch/hour figures for each year separately to eliminate the bias caused by variation in year class strength.

Fluke;Fig. 6,7

Fluke first arrive in moderate abundance in May and June and are most abundant on the Southwest Ground at the time of maximum bottom temperatures as shown in Fig. 6a. The data for each year separately show essentially the same changes, September in each case showing maximal relative abundance. Fish were on the grounds for the longest period in 1957, arriving in measurable numbers in March. They were present for the shortest period in 1958. In the spring these fish move through the grounds to other areas that are both shoaler and warmer at this time. As temperatures increase, the fluke gradually leaves the shoaler waters and the abundance again slowly increases on the Southwest Ground. At or about the time of overturn (data to establish the exact dates of overturn for the Southwest Ground do not exist) there is usually a marked increase in the catch/hour for a short period of time after which fluke rapidly depart from the ground. The bar diagram of the changes in catch/hour on a 5 day period basis, Fig. 7, illustrates this point. The somewhat anomalous data for 1957 are especially interesting in view of the postulated delay of overturn.

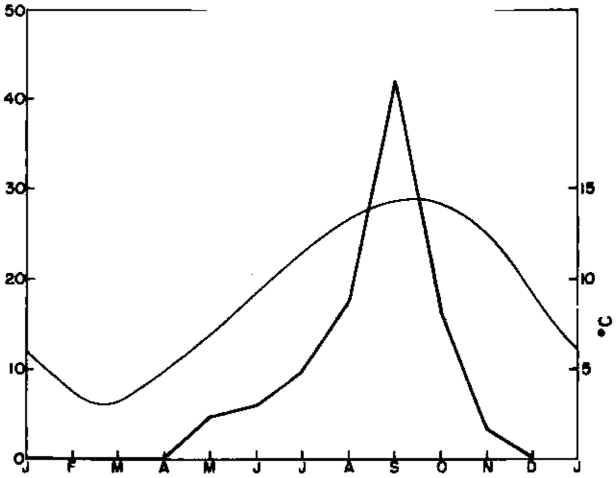

Fig. 6a. Seasonal changes in fluke abundance on the Southwest Ground, for the period 1956 through 1958, and average bottom temperature.

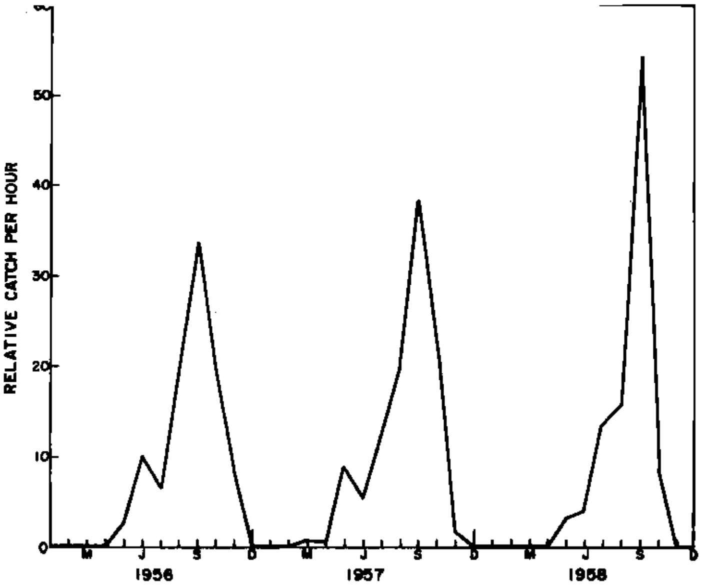

Fig. 6b. Yearly variation in seasonal changes of fluke abundance.

Scup; Fig. 8

The scup shows approximately the same seasonal abundance changes as the fluke. They first appear in number in April or May, at which time they are on their way to inshore spawning grounds where the water temperatures average 8° to 10°C. They move into deeper water as the season progresses and are most abundant at the time of highest bottom temperatures. Again as was the case with the fluke, they were present for the longest period of time in 1957. The offshore migration of the scup also begins at about the time of overturn and they are virtually gone from inshore grounds in November.

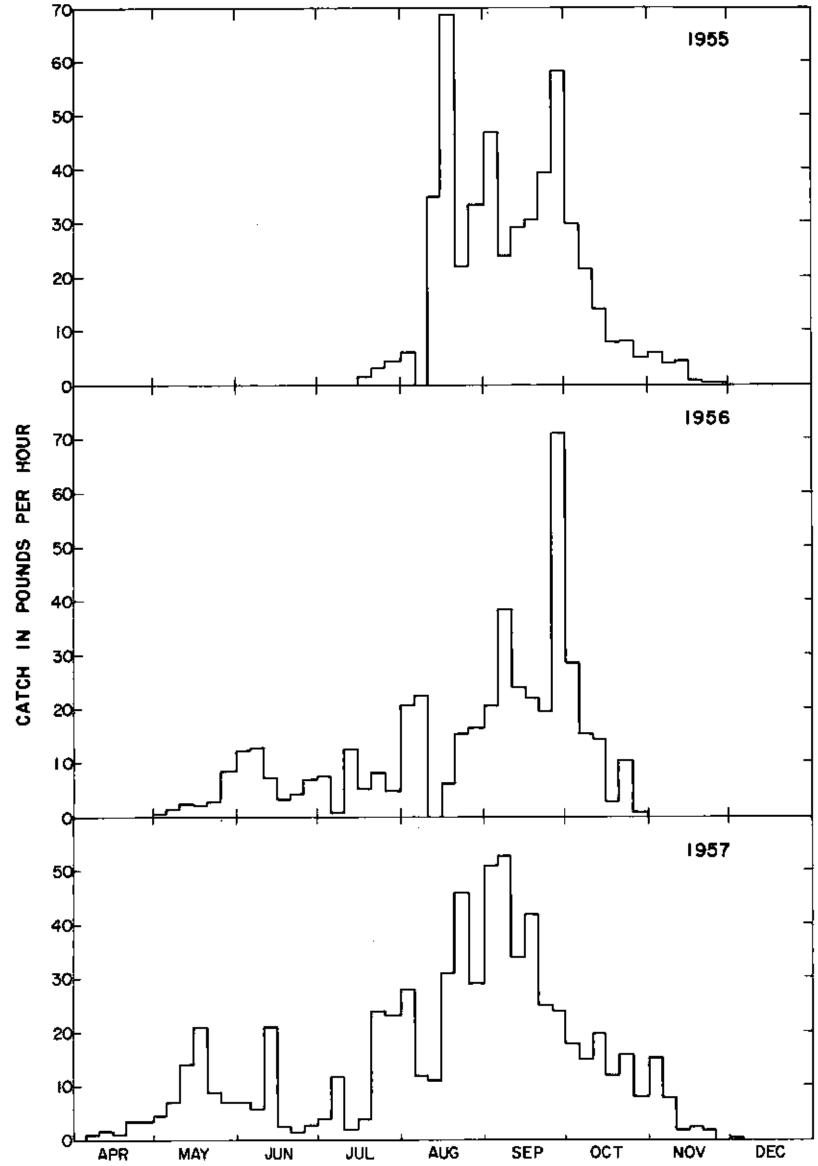

Fig. 7. Variation in the catch/hour of fluke on the Southwest Ground by 5 day periods, July 1955-December 1957.

Butterfish; Fig. 9

The butterfish is a widely ranging, quasi-pelagic species. Unlike the scup and fluke it frequently occurs in considerable numbers during the summer in the Gulf of Maine to the north and east. Historically its occurrence on the Southwest Ground is more erratic than any of the other principal species. Butterfish reach their peak seasonal abundance in November when the water temperature at the bottom is around 12°C. This species showed up earliest (April) in 1957 and generally was more abundant throughout the season in this year.

TABLE 3. CATCH PER HOUR TO NEAREST POUND OF VARIOUS SPECIES ON THE SOUTHWEST GROUND, BY MONTH, 1956 THROUGH 1958.

Species		Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Fluke	'56	--	--	--	+	2	8	6	15	28	17	7	+
	'57	+	--	1	+	7	4	1	16	30	19	1	--
	'58	--	--	--	+	3	4	13	14	50	8	+	--
Average		--	--	+	+	4	5	9	15	36	14	3	+
Scup	'56	--	--	--	--	13	4	17	21	41	76	1	+
	'57	--	--	--	1	6	4	5	12	8	15	2	--
	'58	--	--	--	--	19	26	33	52	82	33	1	+
Average		--	--	--	+	13	12	18	28	44	41	1	+
Butterfish	'56	--	--	--	--	+	4	3	6	2	3	45	19
	'57	+	--	--	+	+	3	3	12	36	46	158	4
	'58	+	--	--	--	+	2	1	10	3	7	4	16
Average		+	--	--	+	+	3	2	9	14	19	69	13
Silver hake	'56	40	--	+	1	183	269	504	557	987	1048	1889	817
	'57	292	285	30	79	356	735	423	865	731	841	624	414
	'58	98	8	3	1	145	187	300	558	603	552	338	507
Average		144	98	11	27	228	397	409	660	774	814	951	579
Red hake	'56	5	--	--	4	512	334	127	256	378	451	580	194
	'57	30	17	10	42	364	529	175	289	70	81	119	43
	'58	--	5	4	9	513	279	117	128	363	456	1167	291
Average		12	7	5	18	463	381	140	224	270	329	622	176
Angler	'56	75	--	19	8	86	123	101	16	54	30	35	167
	'57	60	71	79	57	25	124	88	129	--	47	109	378
	'58	319	24	18	35	169	209	232	114	125	128	161	157
Average		151	32	39	33	93	152	140	86	60	68	102	234
Ocean pout	'56	51	220	392	103	186	37	--	--	--	--	--	172
	'57	223	478	445	296	307	42	16	+	--	--	--	4
	'58	44	378	440	463	212	38	22	+	2	--	5	6
Average		106	359	429	288	235	39	13	+	1	--	2	61
Cod	'56	40	61	56	11	6	4	+	--	+	1	60	41
	'57	25	26	25	9	1	+	+	--	--	+	46	48
	'58	41	71	39	30	9	+	+	+	+	6	70	74
Average		35	53	40	16	5	1	+	+	+	2	59	54

Silver hake; Fig. 10

Seasonal changes in relative abundance closely follow the seasonal temperature changes. Peak abundance is indicated for November but it should be noted (Table 3) that this may be the result of an atypical situation in November 1956. As mentioned before, the larger the silver hake, the warmer the water they appear to prefer. In 1956 the maximum lengths of silver hake sampled on the inshore grounds near Point Judith were as follows:

Jan. - Mar.	28 cm
Apr. - June	40 cm
July - Aug.	50 cm
Sept. - Dec.	40 cm

The fish were on the Southwest Ground for the shortest period in 1956, and year round in 1957 and 1958.

This species also occurs in the Gulf of Maine in commercial quantities during the summer months. During the early 1950's when water temperatures generally showed marked deviations on the warm side, occasional catches of silver hake were recorded from the Gulf of Maine during the winter months. Usually they depart this area early in the fall.

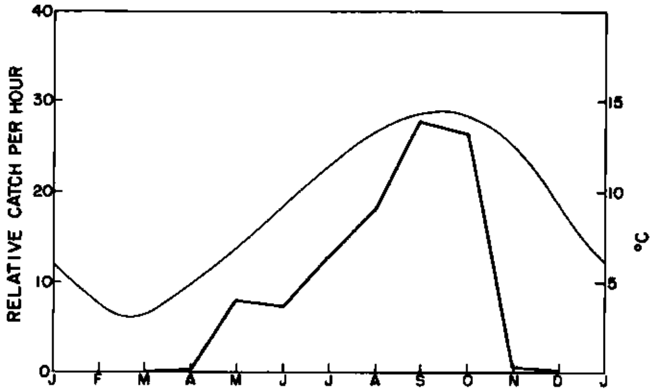

Fig. 8a. Seasonal changes in scup abundance on the Southwest Ground, for the period 1956 through 1958, and average bottom temperature.

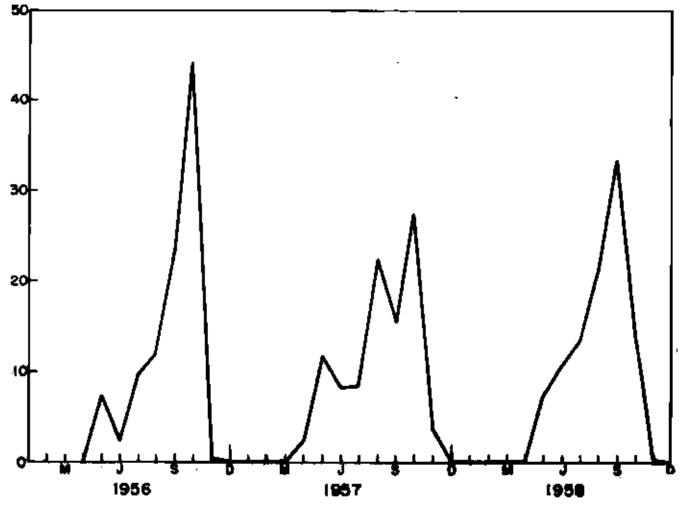

Fig. 8b. Yearly variation in seasonal changes of scup abundance.

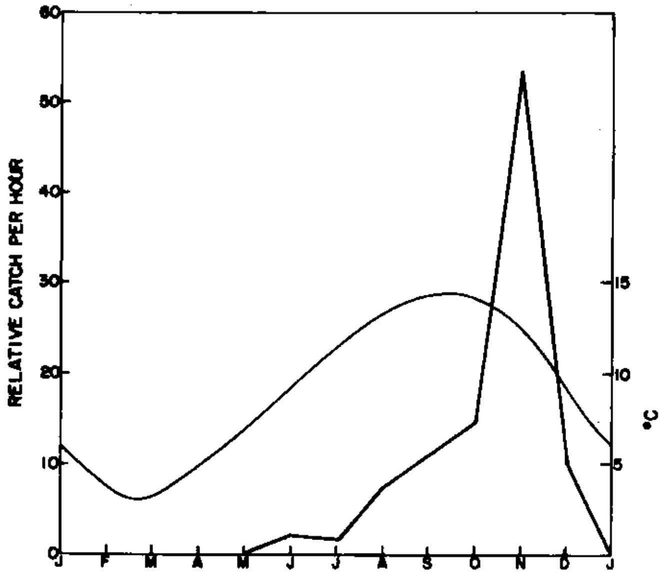

Fig. 9a. Seasonal changes in butterfish abundance on the Southwest Ground, for the period 1956 through 1958, and average bottom temperature.

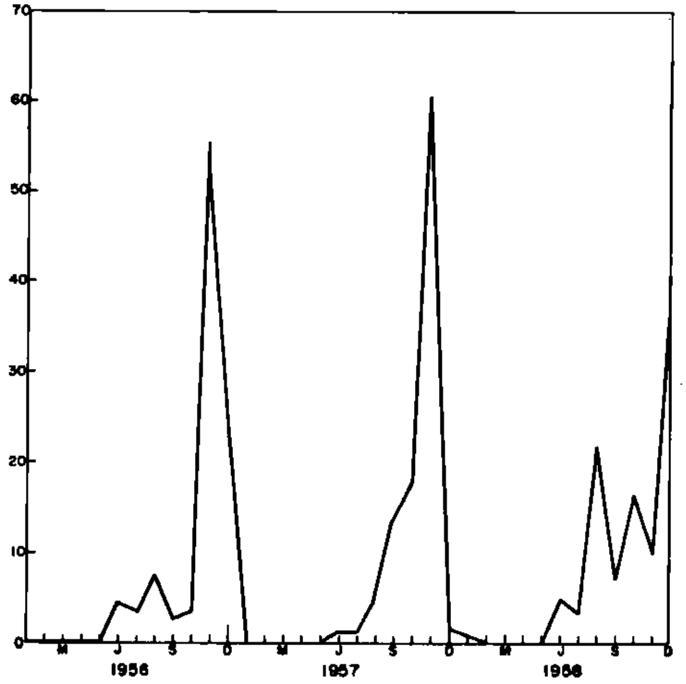

Fig. 9b. Yearly variation in seasonal changes of butterfish abundance.

Red Hake; Fig. 11

Red hake move into the Southwest Ground in great abundance late in April or early in May. As the waters warm this species tends to move into deeper, colder water to return again in number following the time of overturn. The species was on the ground throughout 1957, although generally less abundant than in 1956 or 1958. It did not return to the ground in number in the fall of 1957, probably because of the atypical hydrographic events of the year.

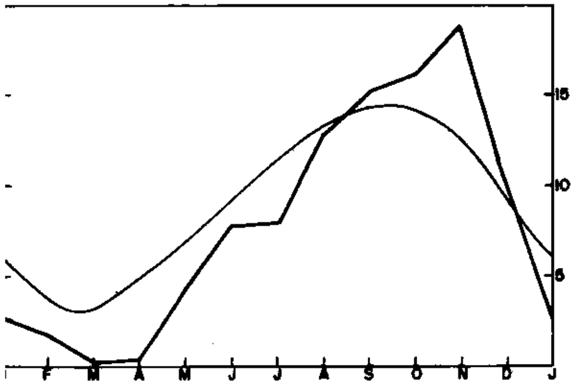

Fig. 10a. Seasonal changes in silver hake abundance on the Southwest Ground, for the period 1956 through 1958, and average bottom temperature.

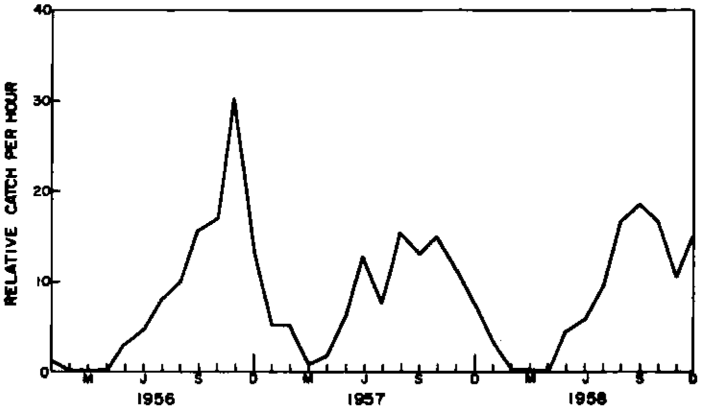

Fig. 10b. Yearly variation in seasonal changes of silver hake abundance.

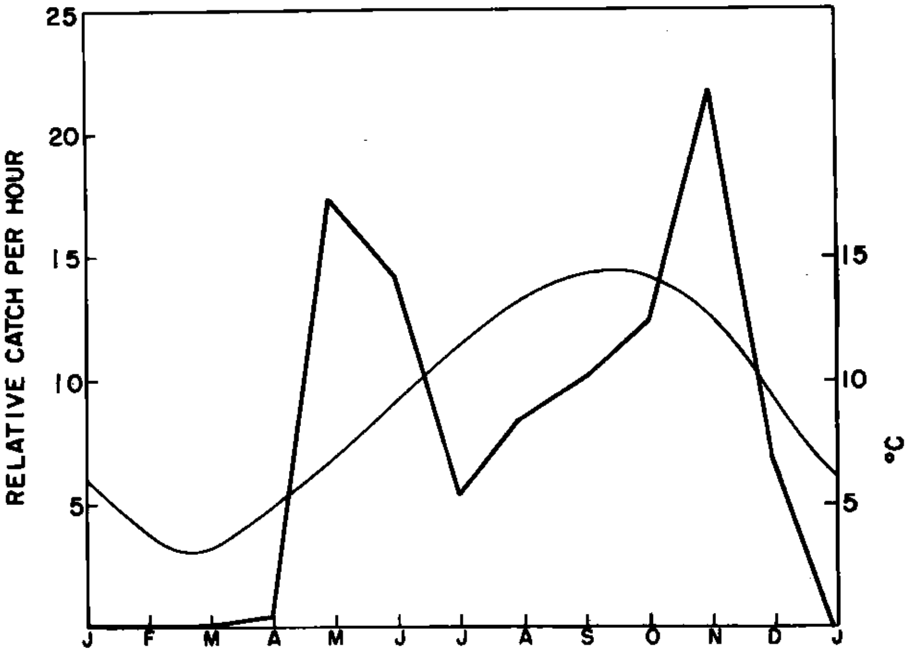

Fig. 11a. Seasonal changes in red hake abundance on the Southwest Ground, for the period 1956 through 1958, and average bottom temperature.

Angler; Fig. 12

The angler shows essentially the same type of seasonal variation in abundance as the red hake but with a preference for colder water. It is most abundant when the temperatures are about 9°C. It was present throughout 1958, the year that began relatively warm and finished on the cold side. It was entirely absent from the ground in September of 1957.

Both the angler and the red hake may occur on the ground throughout some years. Both as well occur as far north at least as the Grand Bank off Newfoundland.

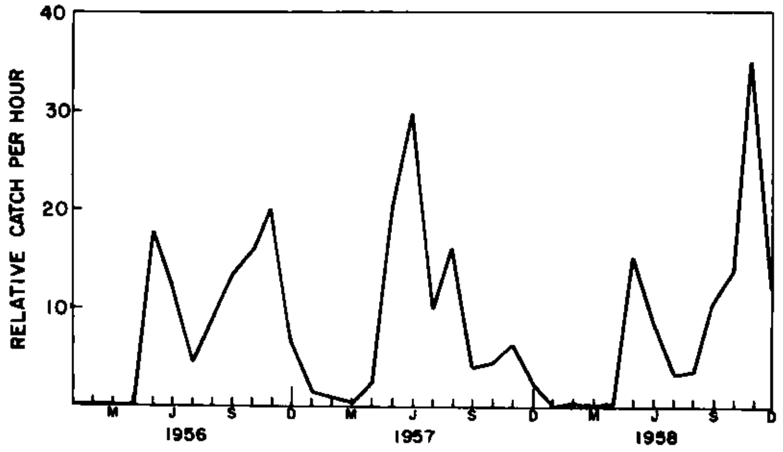

Fig. 11b. Yearly variation in seasonal changes of red hake abundance.

Ocean pout; Fig. 13

The ocean pout is clearly most abundant when water temperatures reach their minimum. They were present longest in 1958, but most abundant in terms of catch/hour in 1957. There is no substantial evidence, observational or otherwise, to suggest that the ocean pout undertakes migrations of any consequence. Olsen and Merriman (1949) have presented evidence that ocean pout are to be found on rougher, rocky bottoms, where they spawn in the summer and fall. It is suggested therefore that the changes observed may represent merely a local shift in habitat in response to temperature changes.

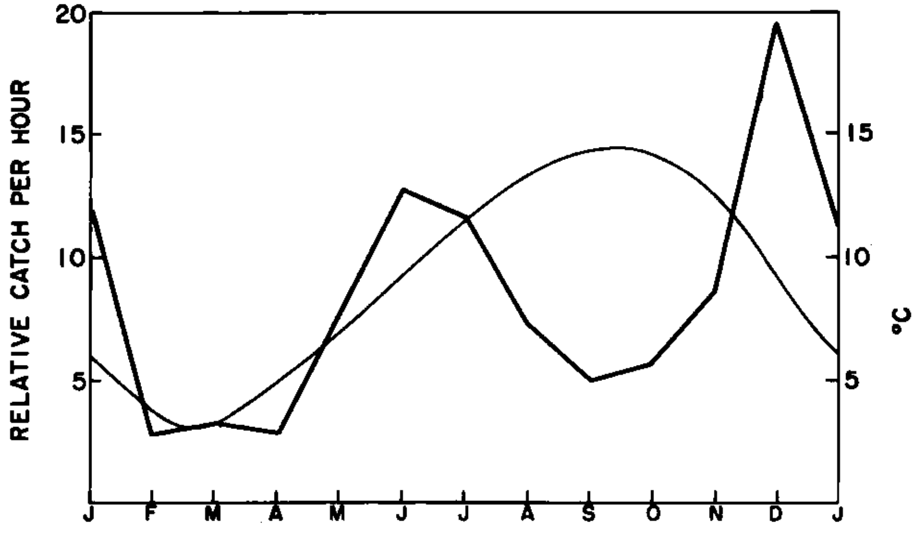

Fig. 12a. Seasonal changes in angler abundance on the Southwest Ground for the period 1956 through 1958, and average bottom temperature.

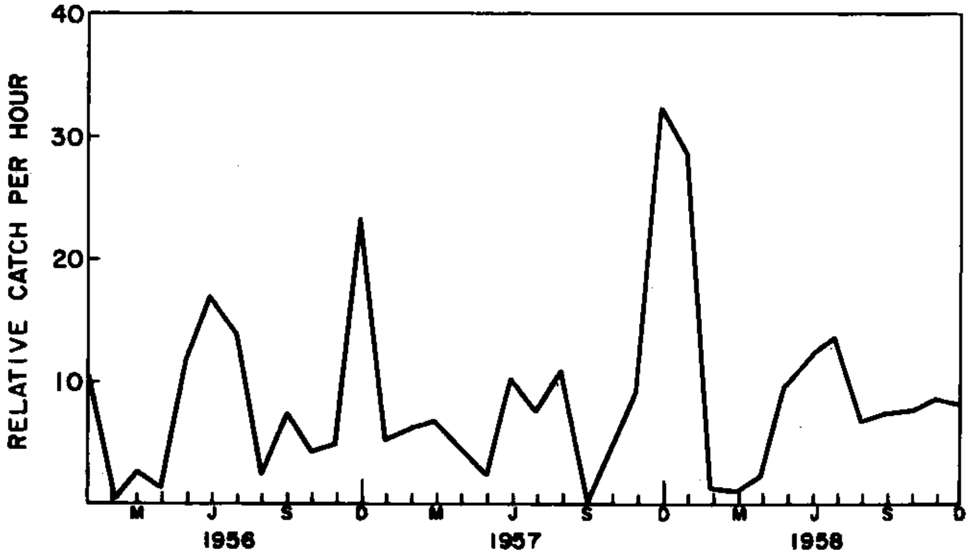

Fig. 12b. Yearly variation in seasonal changes of angler abundance.

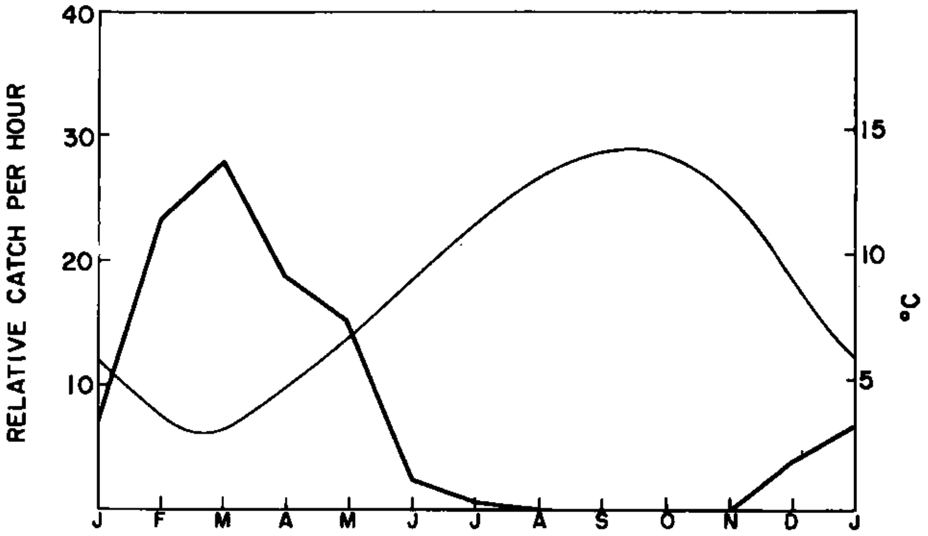

Fig. 13a. Seasonal changes in ocean pout abundance on the Southwest Ground for the period 1956 through 1958, and average bottom temperature.

Cod; Fig. 14

The cod shows essentially the same changes in seasonal abundance as the ocean pout, with the difference however that these changes are clearly associated with movements. The first peak in abundance represents a migratory wave that can be followed to the southern coast of New Jersey where these fish spawn. This group of fish arrives about 1 month after overturn. Occurring with these fish are other cod, possibly a local subgroup, which remain in the area throughout the winter (Bigelow and Schroeder, 1953, p. 186). The cod returning from the New Jersey spawning grounds do not pass through the inshore fishing grounds and thus do not show up on the Southwest Ground. The catch/hour in 1957 was considerably below that of the other 2 yr. Cod were present throughout 1958.

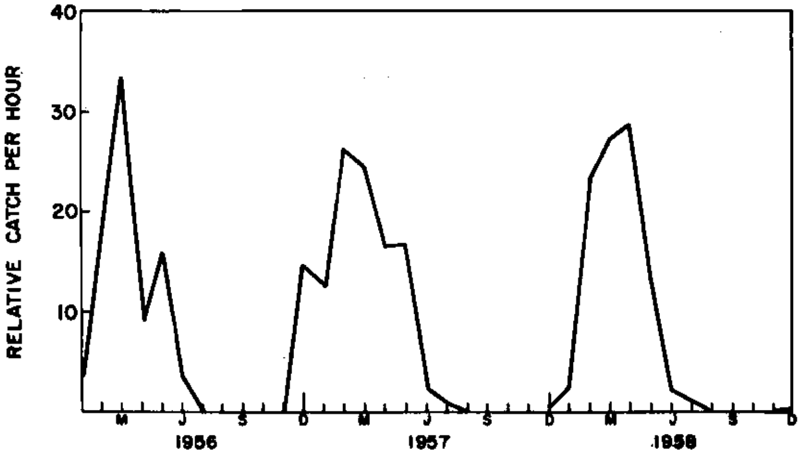

Fig. 13b. Yearly variation in seasonal changes of ocean pout abundance.

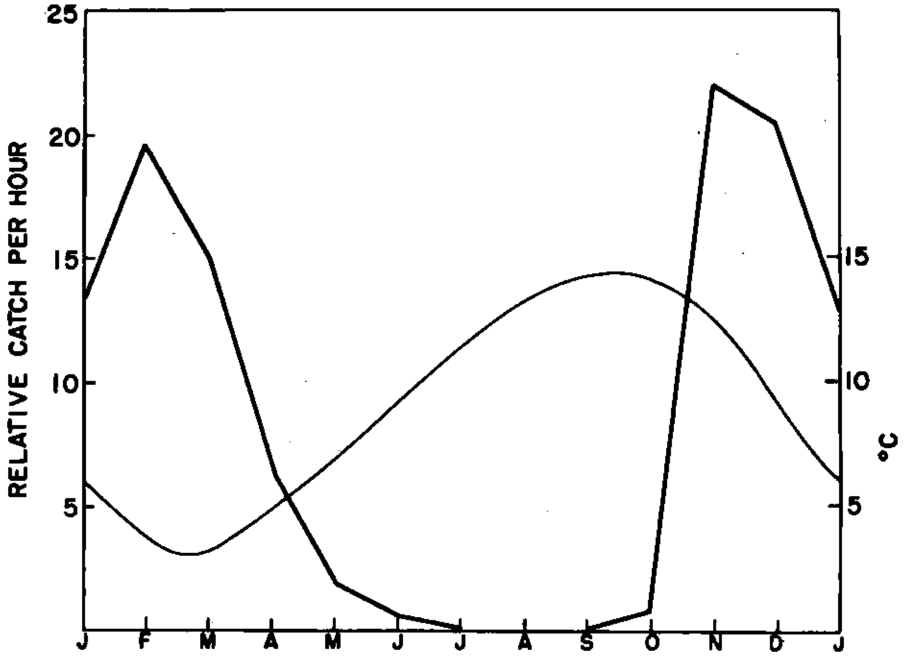

Fig. 14a. Seasonal changes in cod abundance on the Southwest Ground for the period 1956 through 1958, and average bottom temperature.

DISCUSSION

The eight species discussed above illustrate the range of seasonal variations in relative abundance observed on the Southwest Ground. More than 25 species including skates and dogfish, were taken by the industrial trawl fishery on southern New England grounds and landed in quantities greater than 1,000 metric tons a year. With the exception of the winter flounder, skates, and dogfish, these others also show seasonal changes in abundance that one might hypothesize on the basis of winter distributional data. The winter flounder inhabits the bays and estuaries of this coast where it may be found during the colder months of the year. The seasonal changes observed on the Southwest Ground would lead one to believe that it was a fish with preferences similar to those of the red hake or angler. It is however actually moving offshore as temperatures increase. The

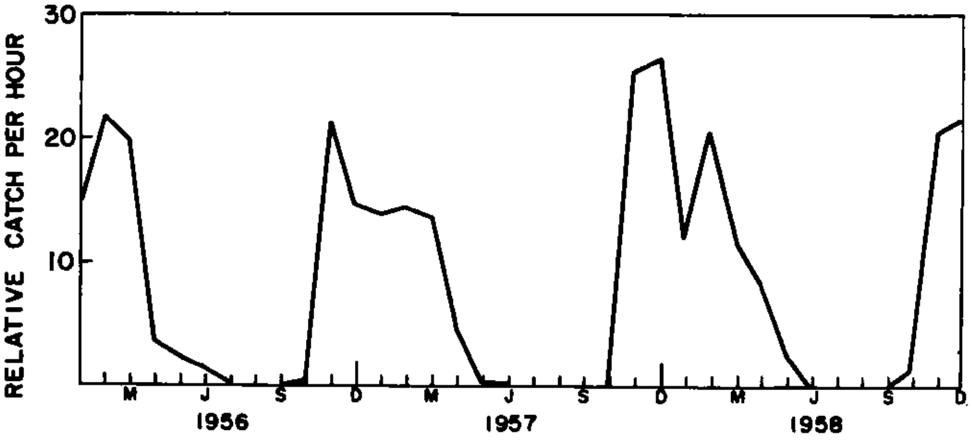

Fig. 14b. Yearly variation in seasonal changes of cod abundance.

analysis of the seasonal movements of skates and dogfish is complicated by differential movements on the parts of the two sexes. Such differential movement of the sexes may also be a factor in bony fish species but is easy to overlook since they are not so readily sexed.

The analysis of seasonal changes in abundance is further complicated by apparent changes in temperature preference on the part of different age groups. As was mentioned earlier, such appears to be the case with the silver hake and there are subtle indications in our data for other species that the phenomenon may be general. Size (or age) and sex are factors that should be considered in the experimental design of any future work.

Although the data presented here suggest that most, if not all, typical Middle Atlantic species tend to seek approximately the same temperature whether inshore in the summer or offshore in the winter, the question of availability has not been resolved. For most species the lack of fish in research vessel and commercial catches does reflect that the species has in fact left an area entirely. In others, as for example the ocean pout, the changes in seasonal abundance appear to represent a local shift to a different habitat that is not adequately sampled by the commercial fleet. The dramatic rise in catch/hour seen in the fluke at the time of overturn and that occurs within a 5 day period can only be interpreted as a change in availability whether due to aggregation or other behavioural change, or a shift in local habitat. Whatever the reason, it raises a question that must be resolved for each species. Most of the species discussed here show marked changes in availability between day and night. Fortunately, as mentioned earlier, the data presented in this paper may be presumed reasonably free of bias due to diurnal variations in abundance, since the Southwest Ground is seldom, if ever, fished after dark.

Most species arrive and depart in a relatively abrupt manner. Between arrival and departure the changes in abundance observed are more gradual and suggest that the fish are moving about the general area in a relatively passive manner with changes in relative abundance reflecting the general suitability of the area.

REFERENCES

BUMPUS, D.F. 1957. Oceanographic observations, 1956, east coast of the United States. *U.S. Dept. Int., FWS, Spec. Sci. Rept. No. 233.*

BIGELOW, H.W. and W.C. SCHROEDER. 1953. Fishes of the Gulf of Maine. *Fish. Bull. U.S., 74.*

DAY, C.G. 1959*a*. Oceanographic observations, 1957, east coast of the United States. *U.S. Dept. Int., FWS, Spec. Sci. Rept. No. 282.*

1959*b*. Oceanographic observations, 1958, east coast of the United States. *U.S. Dept. Int., FWS, Spec. Sci. Rept. No. 318.*

EDWARDS, R. L. 1958. Species composition of industrial trawl landings in New England, 1957. *U.S. Dept. Int., FWS, Spec. Sci. Rept. No. 266.*

EDWARDS, R.L. and L. LAWDAY. 1960. Species composition of industrial trawl-fish landings in New England, 1958. *U. S. Dept. Int. FWS, Spec. Sci. Rept. No. 346.*

EDWARDS, R.L. and F.E. LUX. 1958. New England's industrial fishery. *U.S. Dept. Int., FWS, Comm. Fish Rev.,* 20 *(5).*

EDWARDS, R.L., R. LIVINGSTONE and P.E. HAMER. 1961. Winter water temperatures and an annotated list of fishes—Nantucket Shoals to Cape Hatteras. *U.S. Dept. Int., FWS, Spec. Sci. Rept. No. 397.*

FISHER, R.A., A.S. CORBET and C.B. WILLIAMS. 1943. The relation between the number of individuals and the number of species in a random sample of an animal population. *Anim. Ecol.,* 12 (1).

OLSEN, Y.H. and D. MERRIMAN. 1946. The biology and economic importance of the ocean pout (*Macrozoarces americanus* Bloch and Schneider). *Bull. Bingham Oceanogr. Coll.,* 9 *Art. 4.*

A-2

SEASONAL DISTRIBUTION OF COD (*GADUS MORHUA* L.) ALONG THE CANADIAN ATLANTIC COAST IN RELATION TO WATER TEMPERATURE[1]

By

Yves Jean[2]

ABSTRACT

Seasonal relationships between size, bottom temperature and distribution of cod are described for the western Gulf of St. Lawrence and Nova Scotia Banks.

In summer, in the western Gulf of St. Lawrence, cod are distributed from 35 to 145 m at bottom temperatures from 0° to 6°C. They are most abundant at about 100 m where the temperature is around 1°C. In winter they are concentrated in 130 - 180 m along the western slope of the Laurentian Channel at bottom temperatures from 1° to 3°C.

On the Nova Scotia Banks cod are less abundant than in the Gulf of St. Lawrence. They are found mainly around Banquereau, Middle Ground and the northern edges of Sable Island Bank. Further to the west cod are replaced by haddock as the dominant species. Nova Scotia Banks cod are found in shallower and warmer waters than Gulf cod, both in summer and winter. In summer they are present from 65 to 110 m at bottom temperatures varying from about 1° to 8°C. In winter they are taken primarily at 90 - 135 m at bottom temperatures from 2° to 4°C.

Area and depth distributions of commercial catches reflect the seasonal pattern of cod migrations and distributions demonstrated in surveys and tagging studies.

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[1] Originally Contribution No. A-7, ICNAF Environmental Symposium, Rome 27 January-1 February 1964. Published *in extenso* in the J. Fish. Res. Bd. Canada, 21(3): 429-460, 1964.

[2] Fisheries Research Board of Canada, Biological Station, St. Andrews, N.B.

A-3

DISTRIBUTION OF HADDOCK OFF THE EASTERN CANADIAN MAINLAND IN RELATION TO SEASON, DEPTH AND BOTTOM TEMPERATURE[1]

By

F.D. McCracken[2]

CONTENTS Page

RESEARCH-VESSEL SURVEYS

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[1] Originally Contribution No. A-8, ICNAF Environmental Symposium, Rome 27 January-1 February 1964.

[2] Fisheries Research Board of Canada, Biological Station, St. Andrews, N.B.

ABSTRACT

Haddock stocks off the outer coast of Nova Scotia (ICNAF Subarea 4) are discrete from those of the Grand Banks (ICNAF Subarea 3). Those off the central and eastern part of the Nova Scotia region (ICNAF Divisions 4V and 4W) do not appear to mix extensively with those off the western portion (ICNAF Division 4X).

Otter trawling for haddock produces greatest landings from Division 4W mainly from February to April, and smaller but important landings from Divisions 4V-T mainly in May-July.

In winter, research-vessel survey hauls caught greatest numbers of haddock of all sizes in southern Division 4W (Sable Island-Emerald Bank region) at depths of 70 - 125 m and temperatures of about 4° to 6°C. On top of the banks at depths less than 70 m and temperatures below 2°C haddock were virtually absent. To the eastward in Division 4V haddock were mainly small (<40 cm fork length), less abundant, and occurred considerably deeper (100-250 m) at temperatures around 3° to 4°C.

In summer, haddock return to shallower water and are distributed more widely throughout the region. Haddock, mainly large, migrate inshore to shallower waters off Cape Breton in Divisions 4V and 4T. Others merely move to shallows on top of the banks where small fish (<40 cm) and a few larger fish (>40 cm) are most numerous at depths of 35 - 70 m and at temperatures around 6° to 8°C.

INTRODUCTION

Haddock, *Melanogrammus aeglefinus* L., are found off the North American coast from Georges Bank to the southern Gulf of St. Lawrence, St. Pierre and Grand Banks.

Migrations and interrelationships of haddock stocks off the Canadian Atlantic mainland have been described by Needler (1930) from tagging results and statistics of the commercial fishery. Needler (1931) also presented information about the life-history of the haddock in this region, and McKenzie (1946) described in detail the Canadian fishery there during the late 1930's. Subsequent tagging (McKenzie, personal communication; McCracken, 1956, 1960, 1963) has filled in various gaps in the study of haddock migrations and interrelationships.

These studies relied mainly on records of commercial fishing. The data have limitations, particularly those for the earlier period when much of the fishery was conducted by hook and line, and only large fish were caught and landed. More recent commercial fishing has been mainly by otter trawl, which captures haddock over a greater size range and more extended area, and the new records are free of some of the shortcomings of the old.

This paper presents data on the recent commercial fishery along with the results of Fisheries Research Board of Canada systematic research-vessel surveys, which began in the Gulf of St. Lawrence in 1957 and on offshore banks in 1958. These surveys have the advantage of taking small haddock and fishing in areas at seasons not covered by the commercial fishery. Observations during surveys also relate hydrography to specific areas and catches.

The results presented here will emphasize seasonal changes in distribution of haddock related to area, depth, temperature, and size of fish.

MATERIALS AND METHODS

Data presented in this paper have been compiled from results of research-vessel surveys, log records kept by commercial fishing vessels, and statistics of landings published by the International Commission for the Northwest Atlantic Fisheries (ICNAF). The research-vessel surveys were conducted at various times from 1958 to 1962, both in "winter" and "summer". Jean (1964) has presented details of the vessels and gear used. They were the 25-m *Harengus*, towing a manila No. 36 otter trawl with an 18.3-m headline, for summer surveys, and the 53-m *A. T. Cameron*, towing a manila No. 41 otter trawl with 24-m headline, for winter surveys. In all cases the codend was either covered or lined with 25-30 mm mesh netting.

In 1960 comparative fishing trials were carried out by the two vessels at the same time and place. These showed that, on the average, the *A. T. Cameron* caught twice as many haddock per tow as the *Harengus*. For comparability, *A. T. Cameron* catches have therefore been reduced by a factor of 0.5.

During the 1958 summer and winter surveys two hauls were made at about a half of the fishing stations. Thereafter only single hauls were made. Virtually all haddock in the *Harengus* catches and most of those taken by the *A. T. Cameron* were measured. For sampling some large catches by the *A. T. Cameron* fish were placed in baskets, usually in lots of 3 or 5, and a basket from each succeeding lot was chosen at random for measurement. Fish in the last lot of baskets were normally mixed between baskets before the sample basket was chosen. Paloheimo and Dickie (1963) have demonstrated some bias in this method of sampling; however, none of the *Harengus* catches and only about 20% of the *A. T. Cameron* catches could be affected.

At each fishing station surface and bottom water temperatures were taken along with a bathythermograph cast. Records so obtained have been used to relate temperature and haddock distribution.

Statistics of landings used here are those reported to ICNAF by its member countries and published in its Statistical Bulletin. Distribution of Canadian catches by otter trawlers was obtained from log records kept by captains of these vessels and collected by our field staff.

HADDOCK STOCKS AND THE FISHERY

1. Division of stocks

The haddock stocks considered in this paper are those occurring off central and eastern Nova Scotia and in the southern corner of the Gulf of St. Lawrence. This region has been designated as Divisions 4T, 4V, and 4W of Subarea 4 by ICNAF (Fig. 1). Haddock of this region are separate from those of Subarea 3 (Grand Banks and St. Pierre Bank off southern Newfoundland). Needler (1930) and McCracken (1956, 1960) have shown that the deep-water Laurentian Channel which divides these two subareas is an effective barrier to haddock migrations. Vertebral counts by Clark and Vladykov (1960) (54.1 for eastern and central Nova Scotia banks and 52.9 for St. Pierre Bank) support the conclusion that these stocks are separate.

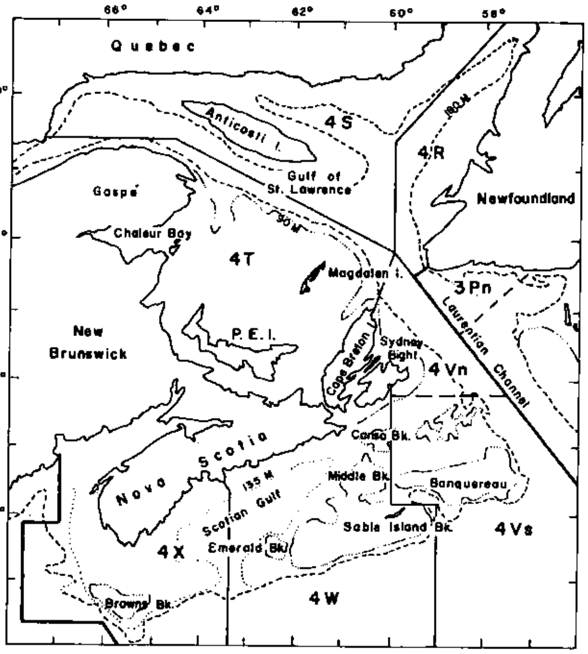

Fig. 1. Map of ICNAF Subarea 4 (including 3Pn and part of 3Ps) showing banks, deeps, and localities mentioned in the text.

Tagging results (Needler, 1930; McCracken, 1956, 1960) indicate only limited mingling of haddock stocks between central and eastern Nova Scotia (4V, 4W) and those of western Nova Scotia (4X). The conclusions from tagging are supported by differences in haddock vertebral counts shown by Clark and Vladykov (1960) for haddock from Divisions 4V-W and 4X. The deep, warm-water Scotian Gulf appears to be the main barrier.

Taggings within Divisions 4T, 4V, and 4W indicate extensive intermixing of commercial-size haddock (40 cm fork length and over). Haddock caught and tagged off inshore Cape Breton (4V) in spring (Needler, 1930) were retaken later that season in the southern Gulf of St. Lawrence (4T). The following winter haddock from the same tagging were recaptured on offshore Sable Island Bank (4W). Similarly, haddock tagged in September in the southern Gulf of St. Lawrence (4T) (McCracken, 1960) were retaken in spring and autumn off Cape Breton (4V) and in winter on offshore banks (4W). Uniform vertebral counts (Clark and Vladykov, 1960) provide further evidence that a single stock occupies all Subarea 4 regions east of the Scotian Gulf. Further evidence for a single stock in Divisions 4T, 4V, and 4W is provided by statistics of landings, seasonal distribution of commercial fishing effort, and results of research-vessel tows.

2. Statistics of landings

Average annual commercial haddock landings by 3-month periods from Subarea 4 for the years 1958-60 are presented in Table 1. They demonstrate the importance of central (4W) and western (4X) Nova Scotia areas in the haddock fishery. Most of the landings came from these two Divisions, and during 1958-60 slightly more were landed from 4W than from 4X. For the region under discussion in this paper (4T, 4V, 4W), 4W (central Nova Scotia) accounted for about 70% of the total landings; 4T (the southern Gulf of St. Lawrence) for about 10%; and 4V (eastern Nova Scotia) for about 20%.

TABLE 1. AVERAGE ANNUAL HADDOCK LANDINGS IN METRIC TONS, ROUND FRESH, BY DIVISIONS, OF SUBAREA 4, FEBRUARY 1958 - JANUARY 1961.

Division	4T		4V		4W		4X		Total	
Period	Can.	For.	Can.	For.	Can.	For.	Can.	For.	Canadian	Foreign
					Otter trawl					
Feb-Apr	19	...	452	197	9549	1258	591	6624	10611	8079
May-July	1409	22	1197	129	1804	159	1498	1069	5908	1379
Aug-Oct	712	...	575	42	3081	169	1848	514	6216	725
Nov-Jan	233	...	621	87	3246	135	324	306	4424	528
Totals	2373	22	2845	455	17680	1721	4261	8513	27159	10711
					Other gears					
Feb-Apr	...	...	31	985	459	915	1297	...	1787	1900
May-July	46	4	330	364	34	34	1297	...	2078	402
Aug-Oct	75	7	161	927	96	96	1263	...	1767	1030
Nov-Jan	33	39	181	157	58	58	911	...	1387	254
Totals	154	50	703	2433	1394	1103	4750		7019	3586
GRAND TOTAL	2639		6436		21898		17524		48475	

For the region 4T-V-W, landings by Canadian vessels predominated, making up about 80% of the total for all nations. Otter trawls accounted for most of the Canadian haddock landings from Divisions 4T-V-W. "Other" Canadian gears were mainly inshore traps operated on the coast of Cape Breton in 4V and 4W. Most haddock landings by other countries can be classified as being produced by towed gear. Haddock taken by "other" foreign gears were mainly from Spanish pair trawlers operating in Divisions 4V and 4W.

TABLE 2. AVERAGE ANNUAL CANADIAN OTTER TRAWL EFFORT BY DIVISIONS, OF SUBAREA 4, FEBRUARY 1958-JANUARY 1961.

Division	4T	4Vn	4Vs	4W	4X	
Period	hr	hr	hr	hr	hr	Total
Feb-Apr	771	1831	2216	17417	1729	23964
May-July	56201	3963	3486	8037	11043	82730
Aug-Oct	57238	985	1643	8271	7287	75424
Nov-Jan	14884	1790	1964	11157	...	29795
Totals	129094	8569	9309	44882	20059	21193

Average annual effort in hours fished by Canadian otter trawlers in areas 4T-4X, from February 1958 to January 1961, by 3-month intervals, is presented in Table 2. These effort data may be compared with haddock landings in Table 1 to show relative abundance of haddock in each of the Divisions. In 4T a large number of hours fished by Canadian otter trawlers from May to October did not produce large landings of haddock. Since haddock is in great demand, the low landings indicate scarcity of haddock in this Division. In the winter period (February-April) relatively large Canadian effort in Division 4V produced small landings compared with the return per unit effort in Division 4W, and indicates much higher abundance of haddock in 4W at that season. For the remainder of the year the difference between 4V and 4W is not so marked.

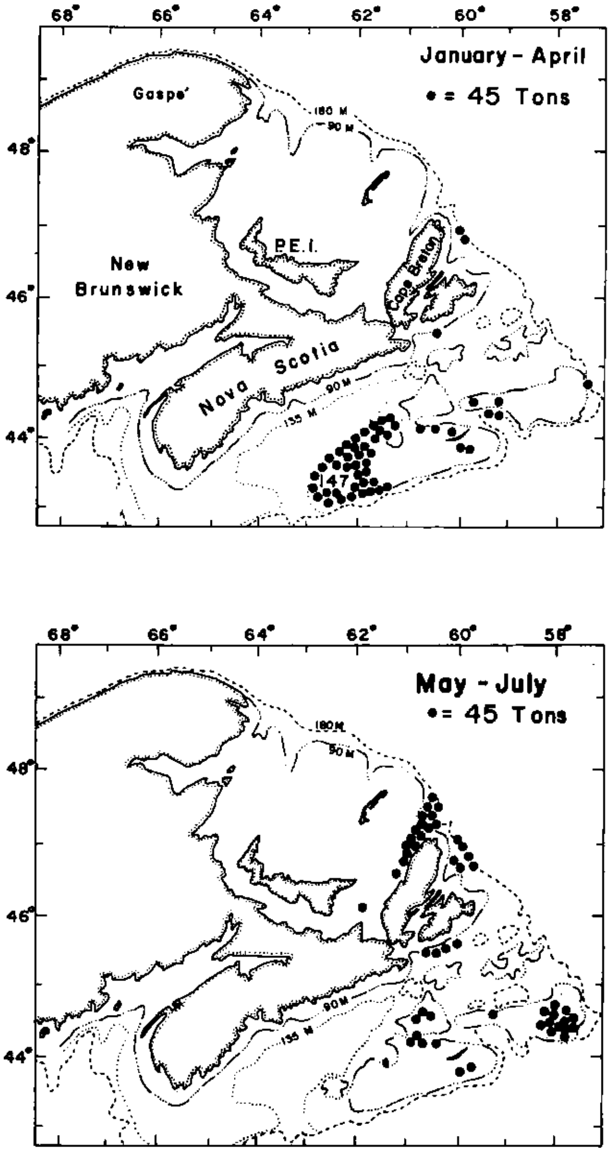

Fig. 2. Distribution of catches of haddock by Canadian otter trawlers in Divisions 4T, 4V, and 4W in January-April and May-July,1959; from log records.

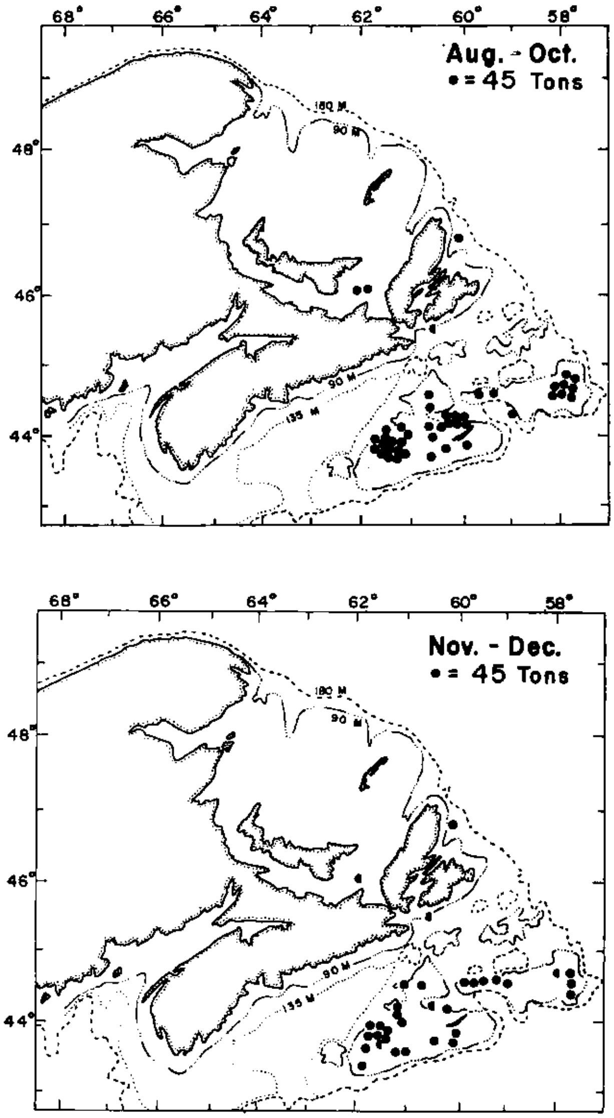

Fig. 3. Distribution of catches of haddock by Canadian otter trawlers in Divisions 4T, 4V, and 4W in August-October and November-December,1959; from log records.

The seasonal nature of the catches presents an interesting pattern, which is generally repeated from year-to year. Records for Division 4W show that the bulk of haddock landings was made in the February-April period. Seasonal differences were less marked in 4V, although most of the landings were made in May-October. Canadian landings from 4V were greatest in May-July. Those from Division 4T were also greatest in the May-July period, although a substantial portion was also landed in August-October.

3. Distribution of commercial catches

Representative 1959 log records for Canadian otter trawlers fishing commercial-size haddock (over 40 cm fork length) are summarized in Fig. 2 and 3. Catches in winter and early spring months (January through April) were mainly from offshore banks (Sable Island and Emerald Banks, 4W), although by April a few catches were made off Cape Breton and on Banquereau (4V).

In May-July, catches were being made around Sable Island and on top of Middle Ground (4W), on top of Banquereau in shallow water and in deep water off the east coast of Cape Breton (4V) and in the deep-water gully on the west coast of Cape Breton (4T). At the same time, statistics records show catches being taken by inshore traps operating on the east coast of Cape Breton (4V and 4W). In other words, the haddock catches were spread throughout the central and eastern Nova Scotia region.

In the August-December period a few haddock were taken off Cape Breton and in the eastern end of Northumberland Strait (4T). However, the bulk of landings still came from the offshore banks, Banquereau and Sable Island. The amounts of haddock taken by otter trawls in the shallow water of 4T vary widely from year to year. Some years much larger amounts are taken than are shown for this period in 1959.

Since otter trawls are the most important gear used, their catches in 4T-V-W indicate the seasonal changes in distribution of the fishery. In winter it centres on offshore banks in 4W and moves inshore in 4V and 4T during spring and autumn. The fact that McKenzie (1946) found the same seasonal distribution of the fishery in 1938-40 suggests that this pattern has existed for a long time. However, landings from the inshore eastern Nova Scotia area in spring were even more important then because trap fishing was more common.

Otter-trawler log records show that haddock fishing is largely confined to depths less than 185 m throughout the year; that the summer fishery tends to be in shallow water, less than 90 m; and that the winter fishery is generally deeper than 90 m with some east-west variation. As will be shown from research-vessel surveys, the fishery reflects the seasonal pattern of haddock distribution.

RESEARCH-VESSEL SURVEYS

1. Distribution by area and season

Research-vessel surveys in 4T-V-W have been carried out in the winters of 1959-62 and in the summers of 1958-60. Results for 1960 and 1962 have been chosen to illustrate winter haddock distribution because, in those years, the survey covered the widest areas. To supplement these, the results of winter hauls from eastern Banquereau in 1959, mainly on top of the bank, have been added to the 1960 data. Results for the 1959 survey have been chosen to illustrate summer distribution, again because these covered the widest area.

1.1. Winter

Winter distribution of haddock in 4T-V-W (Gaspé to Sable Island and Emerald Banks) as deduced by research-vessel catches is shown in Fig. 4 and 5. Both small (<40 cm) and large (>40 cm) haddock were scarce in the Gulf of St. Lawrence (4T) and off the east coast of Cape Breton (4Vn). Those taken were confined to deep water along the edge of the Laurentian Channel. The area off western Cape Breton, where a spring fishery occurs, was not covered by the surveys. However, it is known from January 1962 commercial codfishing efforts in this area that haddock were virtually absent. It seems likely that this is the usual winter situation. Around Banquereau (4Vs) small catches of haddock were taken from deeper water along the southern edge of the bank and in the deeper water region between Banquereau and Sable Island Bank. None were taken on top of the bank. Haddock of all sizes were most numerous around the western end of Sable Island Bank and around

Emerald Bank in the southwestern part of Division 4W. This is also the distribution indicated by winter catches of the commercial fleet (Fig. 2).

Winter research-vessel catches of both small and large haddock were mainly confined to depths less than 185 m on the Scotian Shelf. Around Emerald and Sable Island Banks (4W) most were deeper than 75 m. In the Banquereau region (4Vs) most were deeper than 90 m. Along the Laurentian Channel (4Vn) those haddock taken ranged considerably deeper, about 135-230 m.

Most of the haddock from the Laurentian Channel and Banquereau region were small fish (<40 cm). Around Emerald Bank and western Sable Island Bank large haddock (>40 cm) made up a much larger proportion of the winter research-vessel catch. Again, this is indicated by the distribution of the winter fishery for commercial sizes (>40 cm).

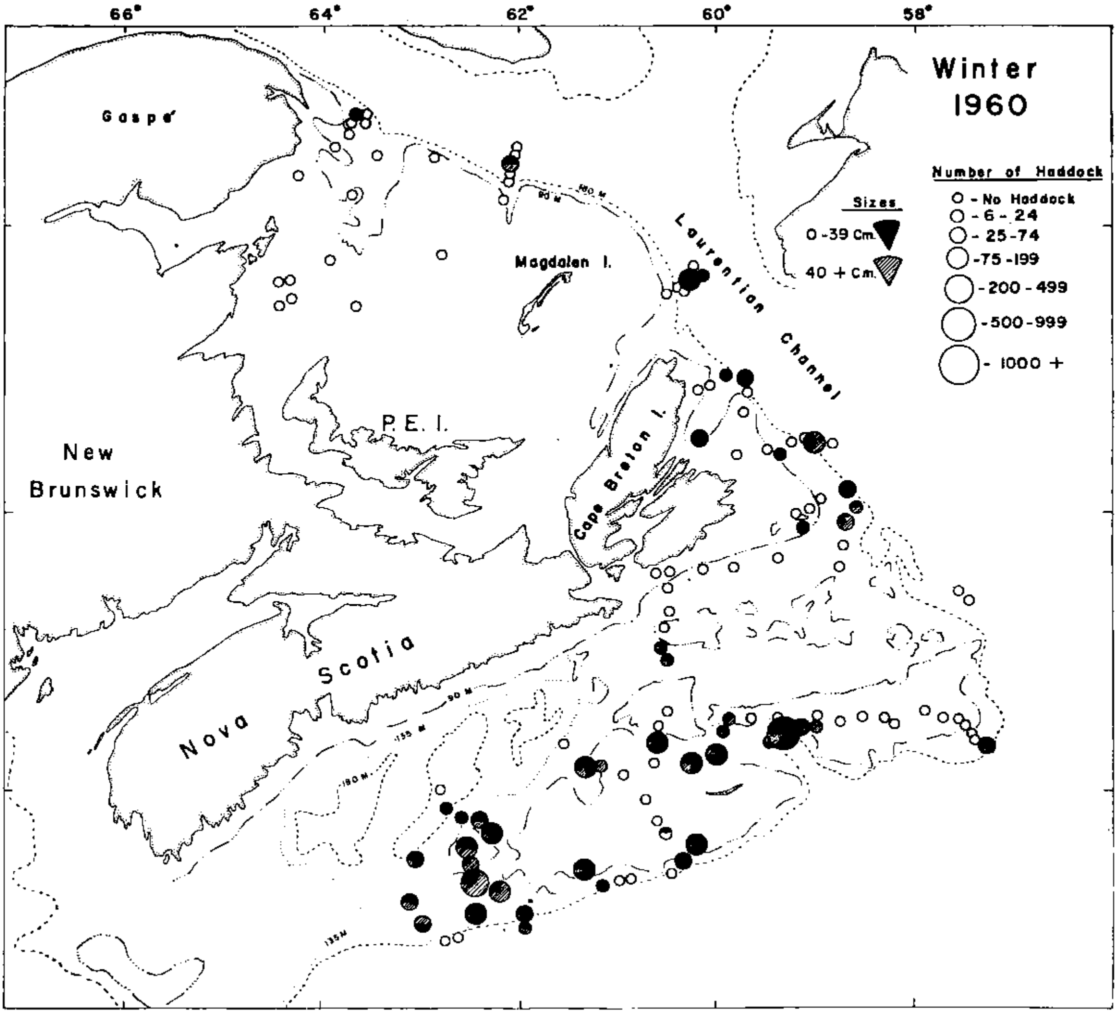

Fig. 4. Distribution of haddock catches by research vessels along the Canadian mainland in the winter of 1960.

1.2. Spring and summer

The 1959 spring and summer research-vessel survey results give a less satisfactory picture than the winter surveys. They are deficient both in timing and area covered. The offshore bank surveys (Banquereau to Emerald) were made in midsummer and, although they covered a large portion of the offshore region, they did not cover the inshore waters of eastern Nova Scotia. The spring surveys off Cape Breton were carried out much earlier and covered only the east coast although there is a spring haddock fishery on the west coast as well. In the Gulf of St. Lawrence the principal area covered in spring and summer was that off Gaspé and northern New Brunswick. Because of these deficiencies, the 1959 research-vessel survey data have had to be supplemented by results of samples of commercial landings and by results of some earlier research-vessel catches in the western Cape Breton region.

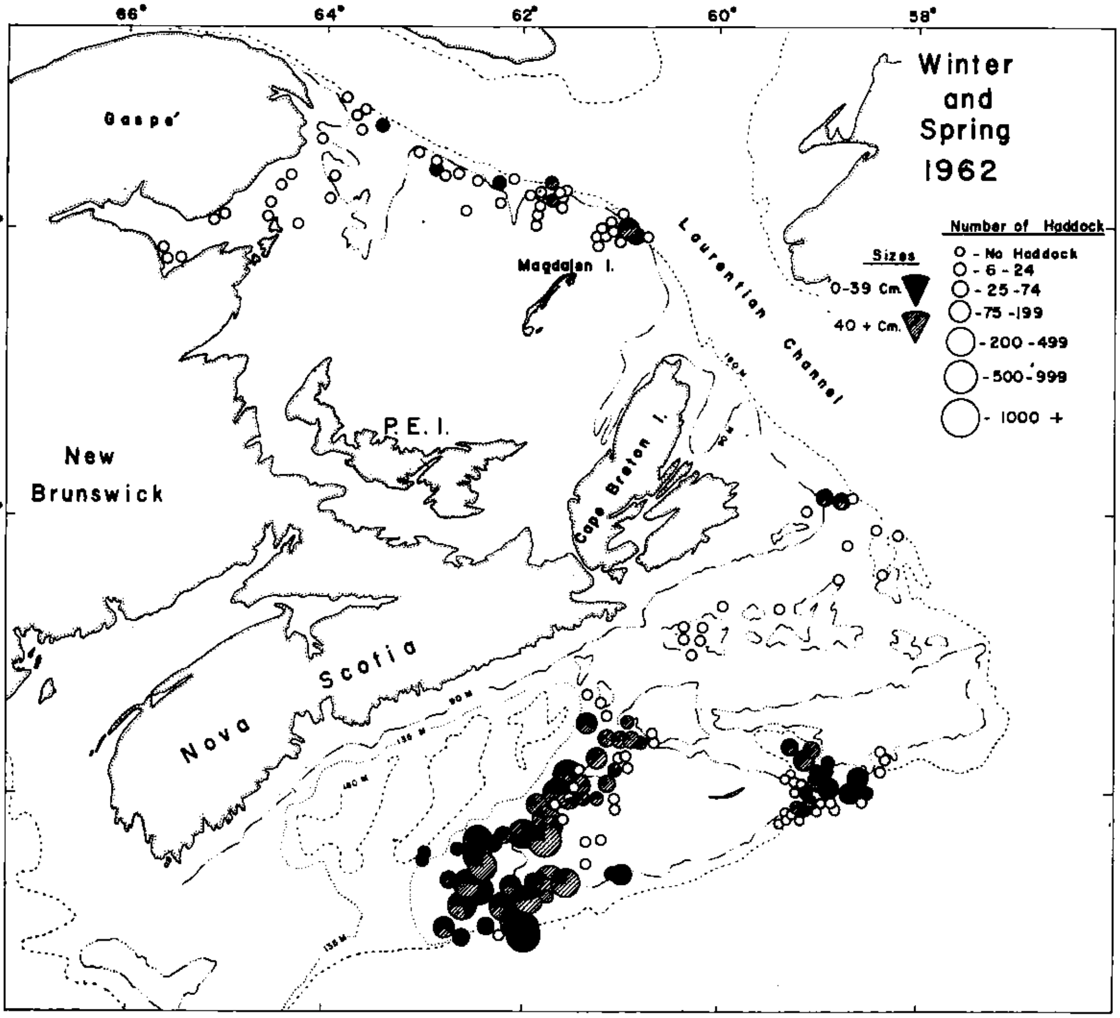

Fig. 5. Distribution of haddock catches by research vessels along the Canadian mainland in the winter (offshore banks) and spring (Gulf of St. Lawrence) of 1962.

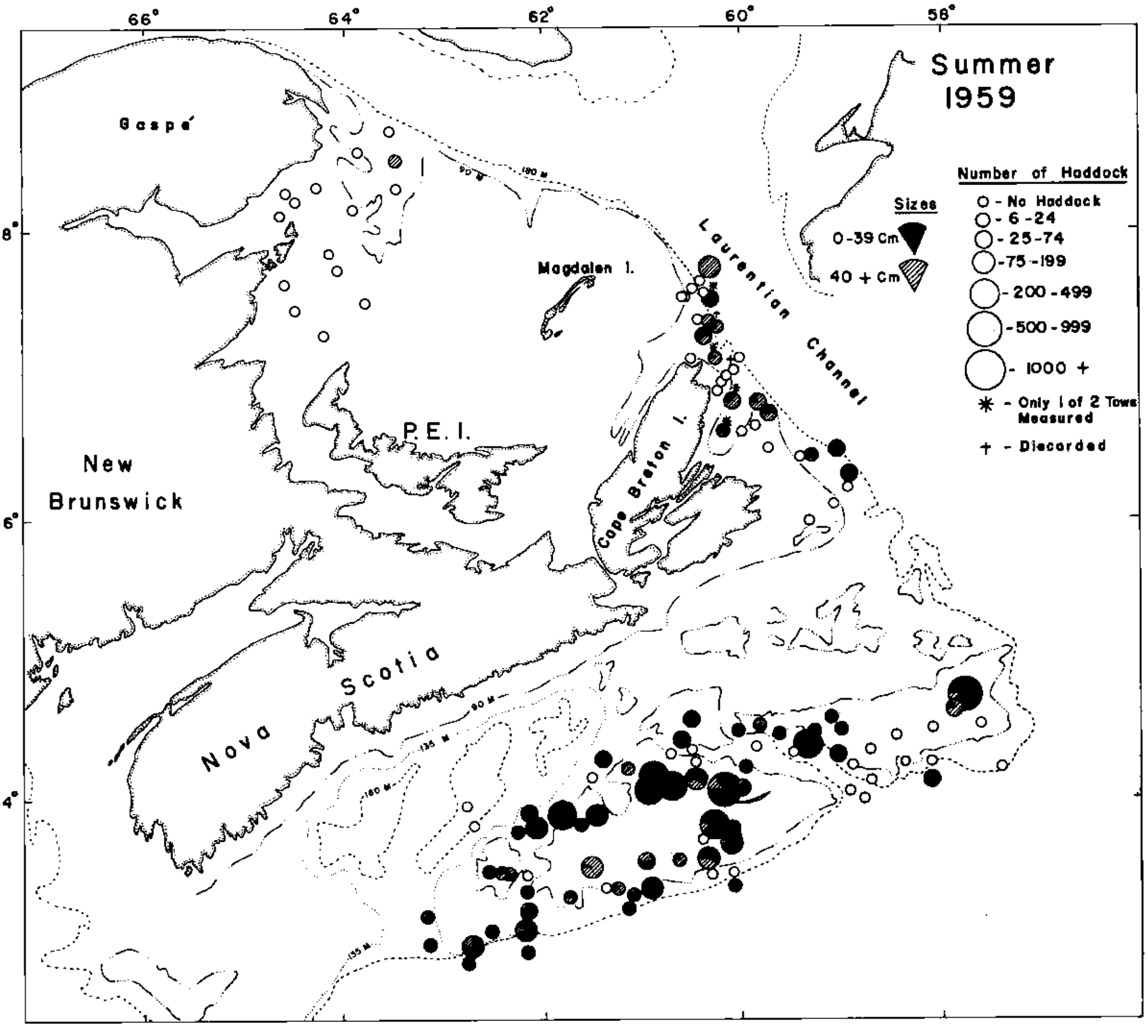

Fig. 6. Distribution of haddock catches by research vessels along the Canadian mainland in the spring and summer of 1959.

The spring research catches in the western Gulf of St. Lawrence took almost no haddock (Fig.6). Landings and log records of commercial vessels also indicated that haddock are virtually absent from this region. Occasional small catches are made, particularly in late summer months and in shallow water around northern New Brunswick (unpublished data). However, the survey results combined with commercial fishing data indicate that haddock are uncommon throughout the south-western Gulf, except for the southern corner around eastern Prince Edward Island and western Cape Breton. Off the east coast of Cape Breton spring survey hauls took small catches of haddock, mainly at depths between 90-185 m along the Laurentian Channel. Sampling was not carried out inshore in this region. However, it is known that at this time traps alongshore on the east coast of Cape Breton were taking haddock. In the offshore Nova Scotia areas, haddock were caught in fair numbers from Banquereau to Emerald Bank. Largest catches came from on top of the banks from depths less than 75 m, particularly around Sable Island and on Banquereau. Although a few haddock were taken throughout the area from deep water (90-185 m), the general distribution was in shallow water, thus contrasting with that in winter when haddock are regularly most abundant at the 90-185 m depths and absent from the shallows.

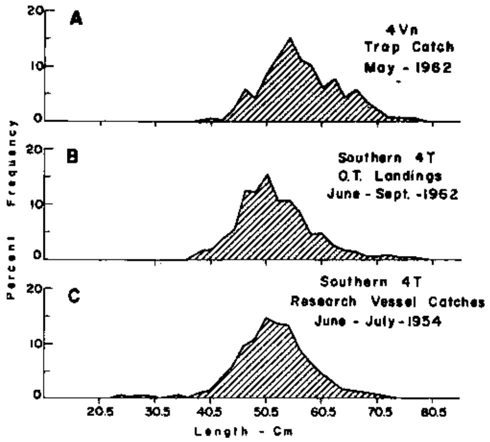

Fig. 7. Size composition of haddock in commercial landings and research-vessel catches from inshore Cape Breton and the southern Gulf of St. Lawrence.

A. Trap-caught haddock, Cape Breton, May 1962.
B. Haddock landings of commercial otter trawlers in July and September 1962 from the southern Gulf.
C. Haddock catches by research vessel in June and July 1954 from the southern Gulf of St. Lawrence.

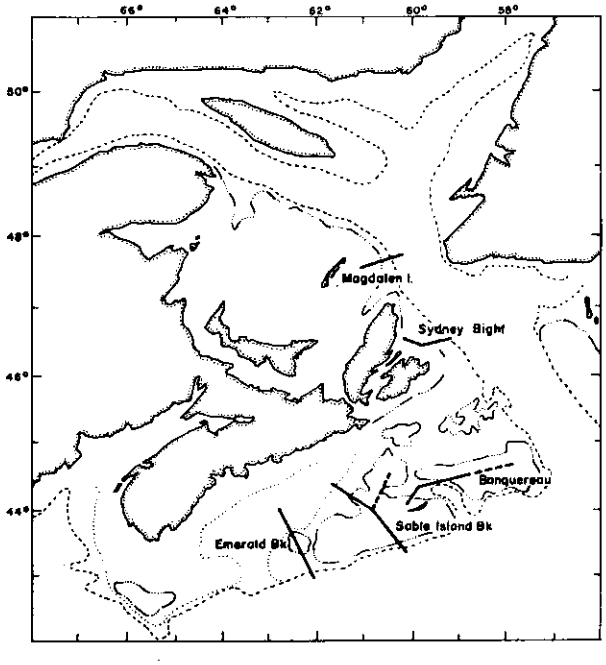

Fig. 8. Location of sections used in comparing distribution of haddock by depth and temperature.

With few exceptions, small haddock (<40 cm) predominated in all the offshore banks catches, both in shallow and deep water. This contrasts with winter conditions when large haddock (>40 cm) predominated in many of the hauls around Sable Island and Emerald Banks. Spring catches in deep water off the east coast of Cape Breton were a mixture of small and large haddock. The survey results suggest that most haddock in inshore Cape Breton and southern Gulf of St. Lawrence waters in spring and summer are large fish. Samples of commercial haddock catches (no fish discarded) from an inshore trap off eastern Cape Breton in May 1962 show that haddock taken were mainly over 45 cm (Fig. 7A). Samples from landed catches of the commercial otter-trawl fishery in the eastern end of Northumberland Strait (southern 4T) in July and September 1962 included only haddock that were over 43 cm long (Fig. 7B). Discard estimates for this region were extremely low in 1962 and 1963 (less than 2% by count; unpublished data). From this it appears that the haddock in the area were practically all large fish. Dragging in the Northumberland Strait region during June to July 1954, using a net with covered codend (during mesh-selection experiments), produced mainly large haddock over 40 cm (Fig. 7C). Thus, we conclude that haddock in these inshore waters during summer are mainly large. Tagging results (Needler, 1930; McCracken, 1963) show that these are part of the winter offshore stocks.

2. Distribution related to depth and temperature

Results of research-vessel fishing along the Laurentian Channel, off the Magdalen Islands and eastern Cape Breton, in the Banquereau region, and in the vicinity of Sable Island and Emerald Banks, have been chosen to show haddock distribution by depth more clearly, and to relate distribution to temperature. While research-vessel surveys in these regions have been carried out for a number of years, those chosen to illustrate summer conditions in the Banquereau region were done in 1959, and those to illustrate winter, spring, and summer in all other areas were done in 1960. The locations of sections chosen are shown in Fig. 8.

2.1. Winter

In January 1960, off the Magdalen Islands in the Gulf of St. Lawrence, haddock were confined to deep water (240-275 m) at temperatures of about 4°C (Fig. 9). They were absent from depths less than 200 m and temperatures of less than 3°C. Catches were light and composed largely of small fish (<40 cm).

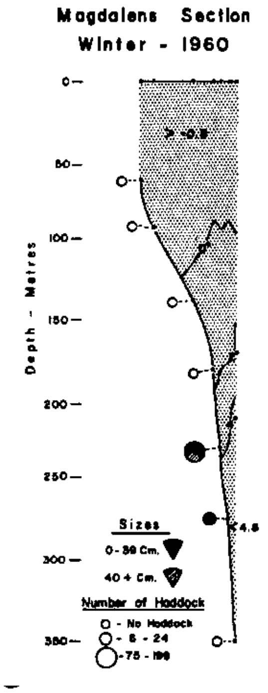

Fig. 9. Distribution of small and large haddock by depth and bottom temperature east of Magdalen Islands winter 1960.

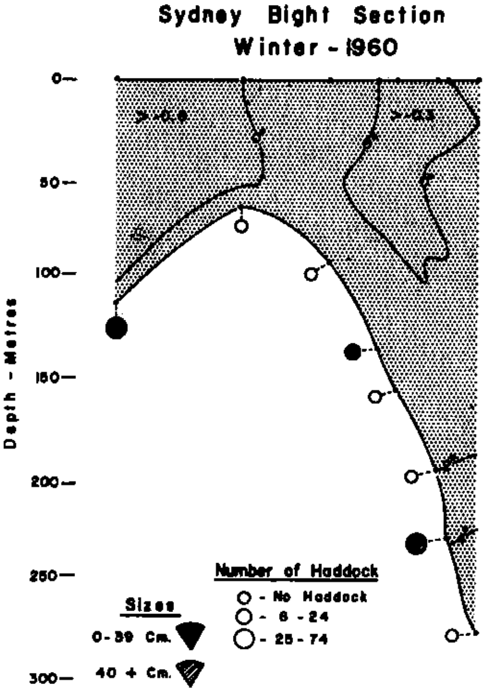

Fig. 10. Distribution of small and large haddock by depth and bottom temperature in Sydney Bight (east Cape Breton), winter 1960.

In the Sydney Bight winter section, eastern Cape Breton, haddock were found at 125 m at a temperature of <1°C (Fig. 10). Catches were light and composed mostly of small fish. In depths about 225 m and at temperatures of about 4°C, catches were also light but contained both small and large haddock.

Along the southwestern end of Banquereau, no haddock were found at depths less than 75 m and bottom temperatures below 2°C (Fig. 11). But good catches of both small and large fish were taken at 90-150 m and at temperatures between 3.5° and 4°C along the steep slope of Banquereau. Only small numbers were taken in the deeper, warmer water of the "gully". Small fish predominated in the catches at depths of 110-135 m and at temperatures of about 4°C on the Sable Island side of the "gully".

In the section across Sable Island Bank there were no haddock at depths less than 75 m and bottom temperatures below about 3.5°C (Fig. 12). However, fair catches of small haddock were taken at depths of 75-110 m and temperatures of 4° to 6°C on both the seaward and shoreward slopes of Sable Island Bank. The largest catches were taken on the seaward slope.

In the Emerald Bank region good haddock catches were made at depths of 75-110 m and temperatures of 4° to 8°C (Fig. 13). On the shoreward slope of the bank mainly small fish occurred in temperatures of 4° to 6°C. Large fish predominated in catches from the "plain" (80-100 m) extending across and south of Emerald Bank where temperatures ranged from about 4.5° to 8°C. Small fish were most numerous again at the seaward edge of this plain at depths around 110-130 m and temperatures of about 7°C.

Thus, in winter, the haddock in the eastward area are mainly small fish and found in deeper water and at lower temperatures than those in the westward area.

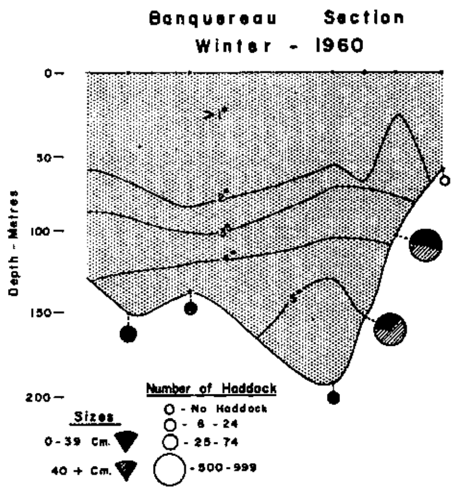

Fig.11. Distribution of small and large haddock by depth and bottom temperature in the western Banquereau region, winter 1960.

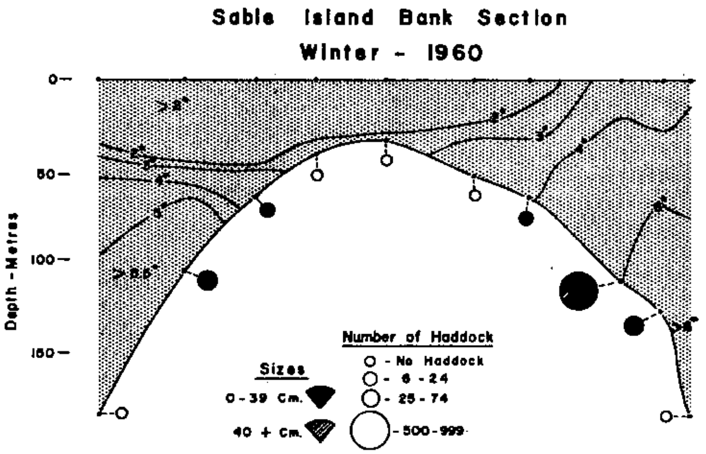

Fig. 12. Distribution of small and large haddock by depth and bottom temperature in the Sable Island Bank region, winter 1960.

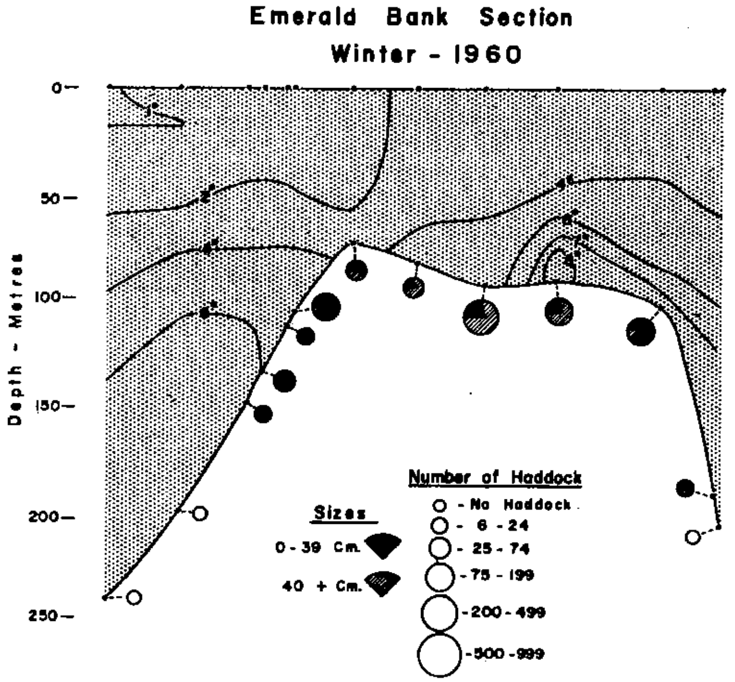

Fig. 13. Distribution of small and large haddock by depth and bottom temperature in the Emerald Bank region, winter 1960.

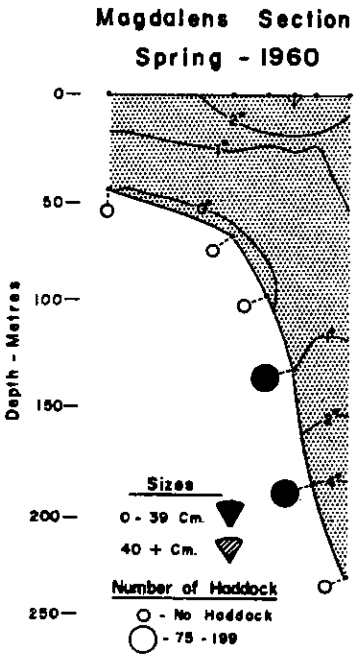

Fig. 14. Distribution of small and large haddock by depth and bottom temperature east of Magdalen Islands, spring 1960.

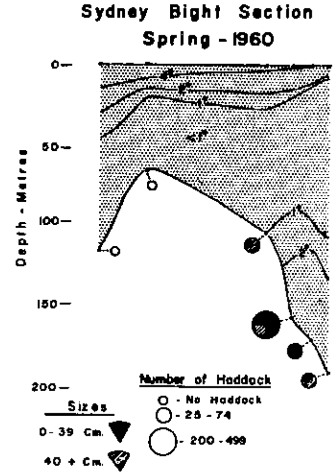

Fig. 15. Distribution of small and large haddock by depth and bottom temperature in Sydney Bight (east Cape Breton), spring 1960.

2.2 Spring and summer

Research-vessel surveys in the various regions during spring and summer were carried out over a longer period than those in winter. Surveys off eastern Nova Scotia and in the Gulf of St. Lawrence were done in May while those on offshore banks were done in July.

Off the Magdalen Islands in May, haddock had moved into slightly shallower water than in winter but small fish were still being taken from depths of 130-185 m at temperatures between 1° and 4°C (Fig.14). They were absent from the coldest, shallowest water (<1°C) at depths of about 45 to 110 m.

In the section off Sydney Bight, haddock catches were larger than in winter and there was a greater proportion of larger fish (>40 cm). They were taken from shallower water (110-190 m) and colder water temperatures (1° to 3°C) than in winter (Fig. 15).

A section across Banquereau in the summer of 1959 (July) showed that haddock were numerous in the shallow, warm-water region at the eastern end of the bank. They were mainly small fish (<40 cm) and were taken from depths of 35-45 m and at temperatures of 5° to 7°C (Fig. 16). There were no haddock of any size over much of the bank at depths around 55-75 m and temperatures under 3°C. On the south-western slope of Banquereau small fish were found at all depths between 75 and 135 m and temperatures around 2°C. On the Sable Island side of the deep gully between Banquereau and Sable Island largest catches of predominantly small fish were made in shallow water less than 55 m at temperatures of 6° to 8°C.

On top of Sable Island Bank largest catches of haddock were taken at depths of 35-65 m and temperatures of 6° to 10°C(Fig.17). These summer catches were much larger than the winter, shallow-water catches, and small fish (<40 cm) predominated. In further contrast to winter conditions, there were few haddock on the slopes of the banks at depths greater than 65 m.

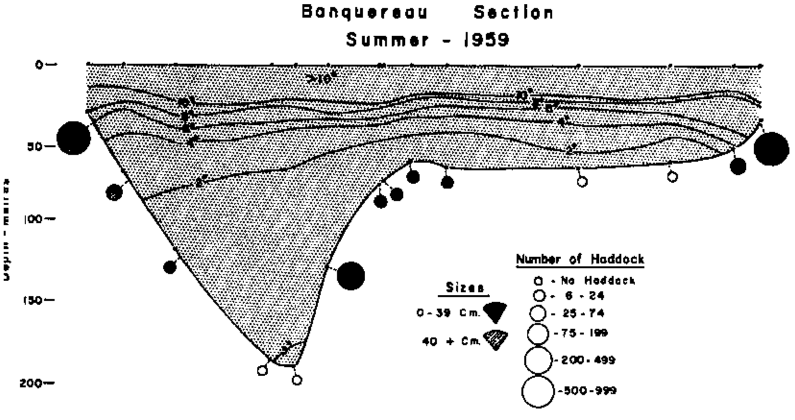

Fig. 16. Distribution of small and large haddock by depth and bottom temperature in the Banquereau region, summer 1959.

Around Emerald Bank, which is further to the westward, the summer catches were light compared to winter, and there were practically no haddock on the Scotian Gulf side of the bank at all depths exceeding 80 m, even though temperatures there were from 4° to 6°C(Fig. 18). Light catches of both small (<40 cm) and large (>40 cm) fish were taken on the plain and slopes seaward of Emerald Bank from 100 to 185 m and temperatures from 7° to 10°C.

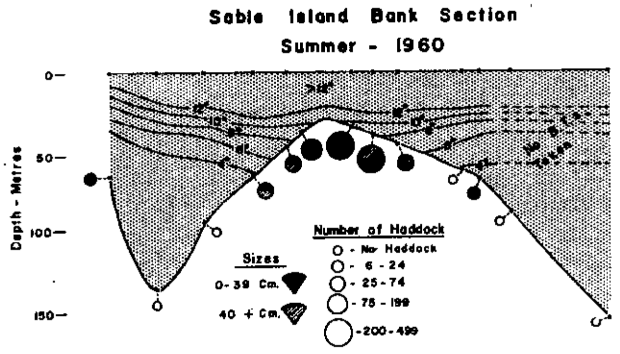

Fig. 17. Distribution of small and large haddock by depth and bottom temperature in the Sable Island Bank region, summer 1960.

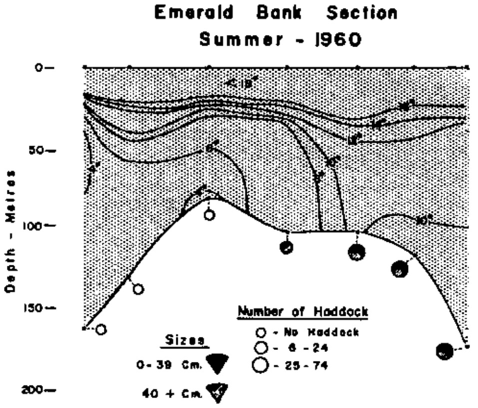

Fig. 18. Distribution of small and large haddock by depth and bottom temperature in the Emerald Bank region, summer 1960.

Thus, summer distribution of haddock on all offshore banks had changed markedly since winter. To the westward the concentrations of commercial-size haddock were no longer found in the Emerald Bank region, and small fish were now most abundant in the shallow, warm-water layer of Sable Island Bank. To the eastward; catches of small haddock had increased by spring and the fish had moved to somewhat shallower water. There were few large haddock at any of the stations fished in the offshore region. It seems likely, as shown by tagging results and statistics of the commercial fishery, that many of the large fish had moved inshore to the eastward off Cape Breton and into the southern Gulf of St. Lawrence. Those remaining offshore were distributed over a much wider area across the top of the banks than in winter.

3. Variation in distribution between years and seasons

The Sable Island-Emerald Bank region where haddock were most numerous has a complex topography (Fig. 1). The Scotian Gulf separates these offshore banks from the inshore grounds. To the eastward the banks deepen into a gully between Middle Bank and Banquereau, and to the westward depth increases gradually in the vicinity of Emerald Bank. Bottom temperatures at similar depths in this region may be widely different, and it is difficult to obtain relationships that are common to the different regions. Sections across the bank, already presented, show some differences in haddock catches for the shoreward and seaward sides of the banks. Further grouping of research-vessel haddock catches in relation to depth and temperature provides interesting comparisons between years and seasons.

Average haddock catches by size and age in the Sable Island-Emerald Bank region for four depth zones for the winters of 1959-60 and the summer of 1959 are presented in Fig. 19 and 20.

3.1 Depth zone <70 metres

In the winters of both 1959 and 1960, bottom temperatures in March-April at these depths were less than 3.5°C and survey catches of haddock were light. In 1959, bottom temperatures were generally below 1.5°C and no haddock were caught. In 1960, bottom temperatures were slightly higher, about 2° to 3°C, and a few small (under 20 cm) and larger (40-50 cm) haddock were taken. Mainly these were fish of ages 1-5 yr. In the summer of 1959 haddock catches were greatest at these depths, in temperatures of about 3° to 7°C. Smaller haddock (<40 cm) of ages 2-4 predominated in the catches.

3.2 Depth zone 70-125 metres

In the winters of both 1959 and 1960, greatest catches of haddock were taken in this depth range. In 1959, larger fish, over 40 cm and ages 5-7, were found throughout this depth range, with somewhat greater numbers in the warmer water (3.5° to 7°C) to the westward. To the eastward, where

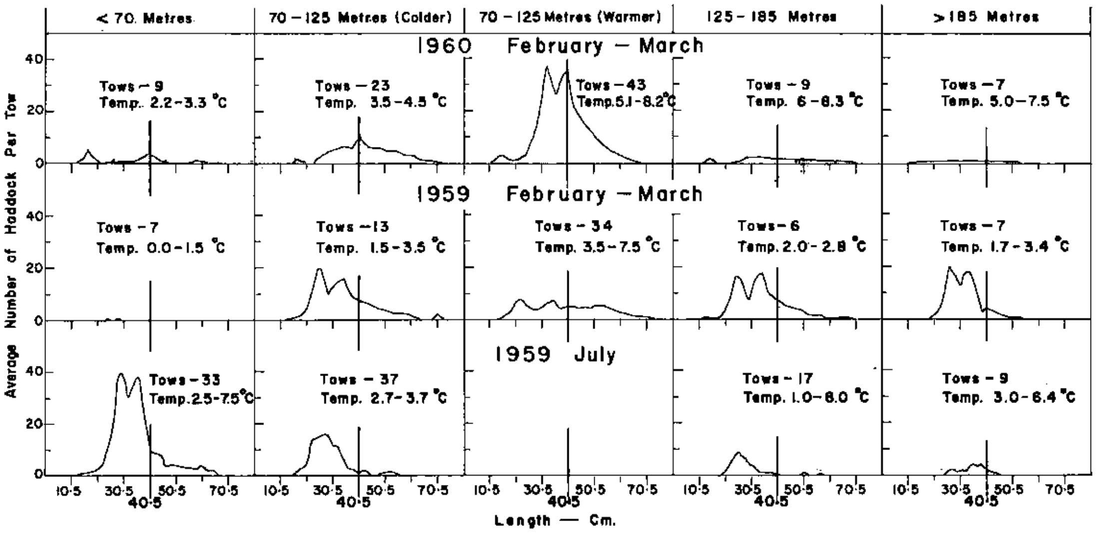

Fig. 19. Average catches and sizes of haddock by depth zones in the Sable Island-Emerald Bank region in winters of 1959 and 1960 and summer of 1959.

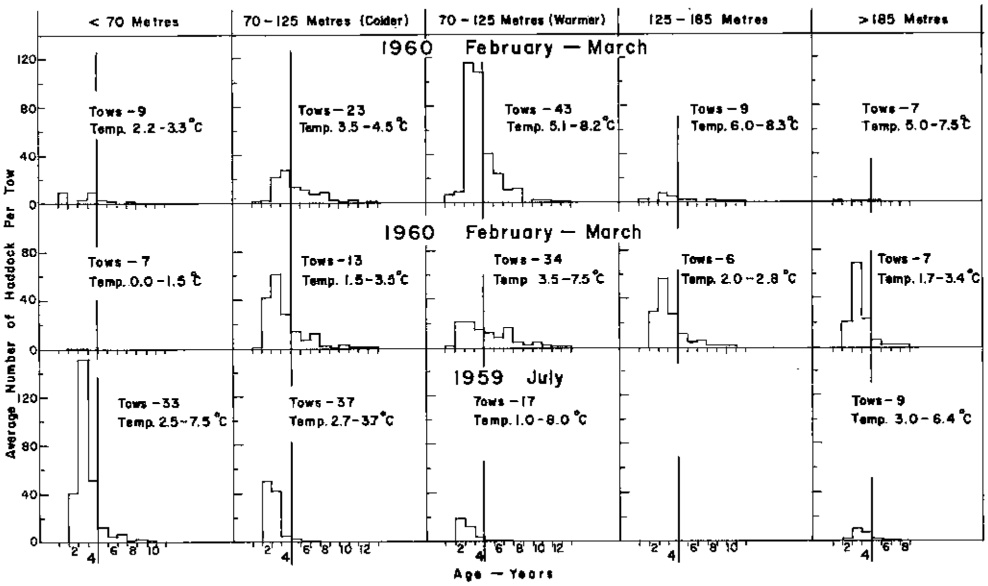

Fig. 20. Average catches and ages of haddock by depth zones in the Sable Island-Emerald Bank region in winters of 1959 and 1960 and summer of 1959.

temperatures were lower than 3.5°C, large numbers of small haddock (20-40 cm) of ages 2-4 were taken. In 1960, with temperatures all above 3.5°C in this depth range, large haddock, over 40 cm and ages 5-8, were taken throughout. Small haddock, under 40 cm, ages 2-4, were most numerous in the warmer waters (5° to 8°C) rather than in the colder water as in 1959. In the summer of 1959 haddock catches were light in this depth range and were mainly of small fish, 20-30 cm long and 2-3 yr of age. However, a few large fish (>40 cm) occurred in nearly every tow.

3.3 Depth zone 125-185 metres

In the winter of 1959 there were large numbers of small fish, 20-40 cm and ages 2-4, in this depth range along the seaward slope of the banks. Bottom temperatures were low (2° to 3°C). A few larger haddock (>40 cm) were also present. In the winter of 1960, when the water was warmer (6° to 8°C) at these depths, only small catches of mixed sizes were obtained. In the summer of 1959 a few hauls at this depth caught small numbers of small haddock, 20-30 cm and ages 2 and 3.

3.4 Depth zone >185 metres

In the winter of 1959, small haddock, 20-40 cm and 2-4 yr of age, were taken in fair quantities at depths greater than 185 m and at bottom temperatures of about 2° to 3.5°C. However, in 1960, haddock were virtually absent from these depths. In summer a few haddock about 30-40 cm in length were taken there at temperatures around 6°C.

In summary, we see that in the Sable Island-Emerald Bank region seasonal differences in haddock distribution are very clear. In summer, small and large haddock are most numerous in the shallow waters where they are virtually absent in winter; and, throughout the region, at all depths, larger haddock, over 40 cm and ages 5-7, are much less abundant than in winter.

The variation in haddock distribution at the same season for different years is less simple. In 1959, when bottom temperatures were colder on top of the banks and colder temperatures also extended further westward than in 1960, haddock were found in much deeper water. Principally these were small fish, under 40 cm and about 2-4 yr of age. In 1959 even fewer haddock were taken in the cold water on top of the bank than in 1960. In both years larger fish (>40 cm) were most numerous in middle depths (70-125 m) and at moderate temperatures (4° to 6°C). Small fish, 20-40 cm, were also numerous in the intermediate depth zone in both years. However, in 1959, they were found in colder parts of this depth zone, and in 1960 the warmer parts. In both instances, these small haddock were found to the eastward around Sable Island Bank close to where they had been most numerous in summer.

DISCUSSION

Considering haddock catches in the 4T-V-W region both by research vessels and commercial otter trawlers, it is clear that season, temperature, depth, and size are major factors determining haddock distribution and migrations.

Within this region, summer and winter distribution of both large and small haddock differs markedly. This can be accounted for only by migration. In May-June, large fish leave their centre of winter abundance around Sable Island and Emerald Banks. Indications are that many move to shallower inshore regions to the east and north, where they spend the summer. About the same time, small haddock leave the deep water at the edges of the banks and move into shallow water on top of the banks and spend the summer there.

In November-December, large haddock leave inshore regions for deeper offshore areas, moving south and west to reach these regions. About the same time, small haddock and those few large haddock which were found on tops of offshore banks in July-August, leave the shallows and move into deeper water on the edges.

What controls the timing of these migrations is not elucidated by this study. Both the spring and fall migrations occur while rapid seasonal changes are taking place. These movements of large fish out of the southern Gulf of St. Lawrence and movements of both large and small fish off the tops of the banks both begin before temperatures fall very low. Nevertheless, temperature appears to play an important part since the autumn and early winter migration is much more pronounced from the northeastern, cold-water areas than from the more westward. Georges Bank is an example where haddock never leave the shallows (< 100 m) in winter (Schuck, 1952). Browns Bank shows a similar situation. Haddock are found there in good quantities on top of the bank at depths less than 100 m in March (McCracken, unpublished). In both the Georges and Browns Banks regions, winter bottom temperatures on top of the banks are several degrees higher than those found on Banquereau and Sable Island Bank.

The depth and temperature at which haddock are found in winter grades from deeper, colder water to the north towards shallower, warmer water to the south. Off Cape Breton, haddock were most numerous around 200 m at temperatures around 3.4°C; around Banquereau the depth range was 100-150 m at temperatures around 4° to 5°C; and off Emerald Bank at depths of 70-100 m and temperatures of 4° to 8°C. Thus, the distribution of haddock in winter appears to be a combined function of temperature and depth. Where colder water extends deep they are forced to move deep, but where cold water is more shallow they tend only to move into intermediate depths. Templeman (1960) describes the marked concentration of haddock on Grand Bank in the winter of 1959, "in a narrow band at depths of 220 to 255 metres". Haddock were apparently avoiding the colder water above but were also resisting moving into deep water even though it was warmer and, as a result, they were very much concentrated. In the same year (1959) when cold water went much deeper in the Sable Island Bank region, haddock, particularly small fish (<40 cm), extended into deeper water, and more of the larger fish moved to the westward around Emerald Bank where the water was warmer. The fact that mainly small haddock remain in the eastern region during winter suggests that small fish may have a greater tolerance than large for greater depths and lower temperatures.

It is also apparent that the distribution of haddock plays an important part in the fishery. Concentration of haddock in the warmer-water region off western Sable Island Bank and Emerald Bank in the February-April period is the main basis of the Canadian late-winter fishery in Division 4W. When haddock spread into the shallows in spring and summer and migrate into inshore regions, they appear to be too dispersed for profitable fishing.

Variations in temperature from year to year and resulting differences in degree of concentration of haddock can produce pronounced changes in catch per effort without much change in either stock size or recruitment. This fact must be taken into account in estimating population sizes from catch-per-effort data in predicting fishing conditions and in devising management regulations.

ACKNOWLEDGEMENTS

The writer takes pleasure in acknowledging the assistance provided during the course of this study by various members of the technical staff at the St. Andrews Biological Station. Principal among these were N. J. McFarlane and R. J. Thurber. Advice and criticism of colleagues, Drs W. R. Martin, Yves Jean, and A. C. Kohler, during the course of the investigation have been received gratefully. Dr J. C. Medcof helped edit and Mrs Ruth Garnett assisted in preparing the manuscript. The figures were produced by W. McMullon and F. Cunningham.

REFERENCES

CLARK, J.R. and VADIM D. VLADYKOV. 1960. Definition of haddock stocks of the northwestern Atlantic. *U. S. Fish and Wildlife Serv., Fish. Bull.,* 60: 283-293. (Fish. Bull. No. 169).

JEAN, YVES. 1964. Seasonal distribution of cod (*Gadus morhua* L.) along the Canadian Atlantic coast in relation to water temperature. *J. Fish. Res. Bd. Canada,* 21(3): 429-460. *Also this symposium contribution No. A-2 (Abstract).*

MCCRACKEN, F.D. 1956. Cod and haddock tagging off Lockeport, N.S. *Fish. Res. Bd. Canada, Atlantic Prog. Rept.,* No. 64, pp. 10-15.

MCCRACKEN, F.D. 1960. Studies of haddock in the Passamaquoddy Bay region. *J. Fish. Res. Bd. Canada,* 17(2): 175-180.

MCCRACKEN, F.D. 1963. Migrations of haddock between the Gulf of St. Lawrence and offshore Nova Scotian Banks. *J. Fish. Res. Bd. Canada,* 20(3): 855-857.

MCKENZIE, R.A. 1946. The haddock fishery of grounds fished by Canadians. *Bull. Fish. Res. Bd. Canada,* No. 69, 30 pp.

NEEDLER, A.B. 1931. The haddock. *Bull. Biol. Bd. Canada,* No. 25, 28 pp.

NEEDLER, A.W.H. 1930. The migrations of haddock and the interrelationships of haddock populations in North American waters. *Contrib. Canadian Biol. Fish., N.S.,* 6(10): 243-313.

PALOHEIMO, J.E. and L.M. DICKIE. 1963. Sampling the catch of a research vessel. *J. Fish. Res. Bd. Canada,* 20(1): 13-25.

SCHUCK, H.A. 1952. Offshore grounds important to the United States haddock fishery. *U.S. Fish. and Wildlife Serv., Research Rept.,* No. 32, 20 pp.

TEMPLEMAN, W. 1960. Canadian research report. A. Subareas 2 and 3. *Annu. Proc. int. Comm. Northw. Atlant. Fish.,* 10: 19-25.

A-4

COD AND LOW TEMPERATURE IN ST. MARY'S BAY, NEWFOUNDLAND

By

Wilfred Templeman[1] and A. M. Fleming[1]

ABSTRACT

In St. Mary's Bay Newfoundland in 1957 bottom temperatures at 125 - 150 m in February were -1.4°C and in April -1.3°C. In February no large cod were present although there were many small cod mostly 14-21 cm in length.

Large cod were moderately numerous in January when the bottom temperature was 1.4°C. By April there were still large numbers of small cod of the same sizes and a few large cod had returned. The cod, especially the small ones were actively feeding at this time.

INTRODUCTION

There are enough apparently contradictory statements in the literature about the ability of cod, *Gadus morhua* L., to live at temperatures of -1.0°C and lower that additional evidence on this subject is desirable.

Cod are resistant to low temperatures. This is shown by the scarcity of reports of dead cod in the Newfoundland area, despite the fact that we have many reports of the death in winter to early spring of large numbers of capelin, haddock, dogfish and Greenland halibut. On the east coast of Newfoundland in late winter and early spring temperatures of the water down to 150 m or more often fall below -1.0°C and sometimes to -1.7 to -1.8°C. Usually the larger cod, at least evade these low temperatures by passing deeper. However, cod must be trapped in some east coast bays and coastal areas in deep holes where water temperatures fall to low levels, but which have no deep passage seaward through which the cod can escape.

For the few records of mass mortalities of cod in the Newfoundland Area, no direct observations of water temperatures are available. Collins (1884) mentions large quantities of cod floating at the surface over an area of at least 10-16 sq km (4-6 sq miles) at Cape Charles, Labrador on 1 August 1876. Local fishermen picked up and cured over 300 quintals (ca. 60 metric tons round fish). These deaths were attributed to the presence of numerous icebergs grounded in the vicinity. The Evening Telegram, St. John's, Newfoundland of 15 May 1934 (Thompson,1943) reported large quantities of dead cod seen floating at the surface for a distance of over 30 km in the northern part of the Gulf of St. Lawrence early in May 1934.

Simpson (1953) reports the presence of dead cod and other fishes in the North Sea during the cold winter-early spring of 1947, not only in areas where the bottom temperatures in March reached 0°C but also over a wide area where temperatures could not have fallen below 1.5°C. This author also says that small cod were caught at the piers in Lowestoft throughout late February and early March 1947, when the sea temperature was below 0.5°C for 18 days (including 7 days below 0°C) with a minimum of -0.4°C and there were no reports of dead cod or other species.

Dannevig (1930) records that cod and other fishes died on the Norwegian coast at temperatures probably from about -1.1 to -1.4°C, but that 2 cod which were impounded near the wharf for a month or more lived through temperatures as low as -1.4°C. Dannevig also conducted an experiment with cod 20-30 cm long which were taken from the sea, where the temperature was 3.5°C, and placed in a tank of water at 0.6 to 0.7°C but with the temperature being continually reduced. After 35 min when the temperature had reached -0.9°C, the cod were shivering and after 45 min with the temperature lowered to -1.1°C, all the cod were floating upside down with 4 dead and 1 showing some sign of life.

Nielsen (1893) reports the death of a cod in about 12 min after being transferred from the holding pound of the cod hatchery at Dildo, Trinity Bay, Newfoundland, at 32°F (0°C) to the spawning pound of the hatchery where the water was 31°F (-0.6°C). Also, on 6 and 7 February 1893 when temperatures at the holding pounds dropped to 29° and 30°F (-1.7 to -1.1°C) all the cod in pounds

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died.

Earll (1880) reports that all mature cod retained for hatchery purposes at Gloucester, Massachussetts, died in January 1879 when the temperature of the water fell to 30°F (-1.1°C).

Thompson (1943) says that, during the 1931 research cruise of the *Cape Agulhas* in the Newfoundland area, a few cod were captured at bottom temperatures as low as -1.6°C. No details of locality, depth or date are given and we have not been able to verify this statement from the yearly reports or the original records of the 1931 cruise.

Martin (1961) says that very small cod (0 and 1 age-groups) were still present in shallow water off Shippegan Island, New Brunswick in January, at a bottom temperature of -1.5°C.

ST. MARY'S BAY

Between 16 November and 29 May 1957 the research vessels *Marinus* and *Investigator II* made a series of half-hour bottom hauls with an otter trawl in St. Mary's Bay, Newfoundland, in the central area of the bay, mainly between 125 and 150 m (Table 1). The lower part of the codend was lined and the upper part covered with nylon shrimp netting so as to retain the small fish.

The sets in St. Mary's Bay were not planned as cod research but were part of sampling cruises to Hermitage Bay for redfish and to St. Mary's Bay for American plaice. Consequently information on the sizes of cod present in the earlier sets is not as complete as would be desirable.

TABLE 1. ABUNDANCE OF COD IN RELATION TO WATER TEMPERATURE IN ST. MARY'S BAY, NEWFOUNDLAND, 1956 AND 1957. (THE *Marinus* USED A NO. 35 TRAWL WITH A 15.3 M HEADLINE AND THE *Investigator II* A NO. 36 TRAWL WITH AN 18.3 M HEADLINE.)

Ship	Year	Date	Time† dragging	Depth	Bottom temp.	Cod per hour's dragging* Small (below ca. 44 cm)	Scrod (ca. 44-52 cm)	Market (ca. 53-85 cm)	Large (ca. 86 cm and over)
			hr	*m*	*°C*	*avg no.*	*avg no.*	*avg no.*	*avg no.*
Marinus	1956	Nov.16	1 (2)	128-146	0.29	135	...	40	...
Investigator II	1957	Jan.16	2.5(3)	132-146	1.37	1	...	(210)	
Marinus	1957	Feb.26	2 (4)	124-150	-1.40,-1.37, -1.40	(210)	...	...	...
Marinus	1957	Apr. 9	1 (2)	124-132	-1.33	687 (70)	...	3 (20)	3 (45)
Marinus	1957	Apr. 9	0.3(1)	198	-1.38	(45)	...	...	...
Marinus	1957	May 29	1 (2)	95-128	-0.48 to -0.67	770 (145)	...	6 (45)	8 (120)

† no. of sets in parentheses

* lb. per hr in parentheses

Bottom temperatures (usually at a few metres above the bottom) were taken with Negretti and Zambra deep-sea reversing thermometers attached to Nansen bottles and a 36 kg weight. Two reversing thermometers were always used at the same time. The thermometers were provided with National Physical Laboratory (Great Britain) certificates and all temperatures are corrected temperatures. It is possible to feel reasonably confident that actual temperatures in the bottom layers were as low as those recorded. On 9 April, for example, when cod were caught at 124-132 m, temperatures were -1.33 and -1.38°C at 110 and 188 m. On 26 February, with 4 sets giving essentially the same kind of catches in 124-132, 124-146, 139-150 and 146-150 m, temperatures of -1.37, -1.40 and -1.40° C were recorded in 3 different set locations in actual thermometer depths of 132, 123 and 142 m. Salinities at the 100-140 m depths were between 32.3 and 32.7 $o/_{oo}$.

Bottom temperatures were 0.29°C in November and some larger (1.1-4.5 kg) cod as well as greater numbers of small cod were present.

In January, with bottom temperature 1.37°C, modest amounts of the larger cod from 1.1 to over 4.5 kg were present, but very few small cod.

On 26 February the bottom temperature was -1.4°C. (Actually, 1957 was a cold winter in the Newfoundland area and by the end of February temperatures in St. Mary's Bay from surface to about 150 m would have been -1.4°C or lower. Two miles off Cape Spear near St. John's on 1 March 1957 temperatures were -1.7°C from surface to 100 m and -1.4°C at 150 m and on 5 April 1957 -1.6°C from surface to 100 m and -1.7°C from 150 m to bottom at 170 m). No cod of commercial size were present but small cod were numerous, one 35 cm with the remainder all below 30 cm in length and almost all 14-21 cm in length.

On 9 April, with bottom temperature -1.33°C, there were fewer small cod taken than in February and only a few larger cod had returned. In deeper water at 198 m where the temperature was -1.38°C there were, also, fairly large numbers of small cod but no large cod. The cod were almost all below 20 cm (616 out of 693) and only 6 were over 50 cm (Table 2). The cod were feeding at this time, and stomachs especially in the small cod, were quite full mainly of euphausiids and amphipods with an occasional polychaete worm. Stomachs of the larger cod contained relatively smaller amounts mainly of spider crabs, some amphipods and small fish remains.

TABLE 2. LENGTH FREQUENCIES OF COD (ENTIRE CATCHES),
ST. MARY'S BAY, NEWFOUNDLAND.

Total length snout-mid-fork	*Marinus* 2 sets 9 April 1957 124-132 m -1.33°C	*Marinus* 1 set 29 May 1957 95 m -0.48°C
cm	*no.*	*no.*
8-10	4	10
11-20	612	312
21-30	62	148
31-40	9	8
41-50	0	2
51-60	1	2
61-70	1	0
71-80	0	0
81-90	1	5
91-100	3	2
Total	693	489

By the end of May, in slightly shallower water with bottom temperatures -0.5 to -0.7°C, large numbers of small cod were present, almost all 15-23 cm in length, and small numbers of larger cod (Table 2).

DISCUSSION

Simpson (1908), for large cod caught near bottom by handline in about 90 m, and with the surface temperature of 11.1 to 11.6°C usually only 0.1 to 0.2°C higher than the bottom temperature, found rectal temperatures 0.40°C higher and muscle temperatures on a smaller number of specimens 0.46°C higher than the bottom temperature. Temperatures were measured immediately after capture so that the effect of struggle in increasing the temperature was included. Dogfish, flounders and haddock, however, allowed to remain alive in a tank of sea water for an hour after capture before taking their temperature, had body temperatures no higher than those of their tank water environment.

Britton (1924) using a thermometer and a rectal insertion found temperatures of living cod to average 0.7°C higher than the bottom temperatures of 7.9 to 10.0°C in 31 m from which they had just been lifted. Fish already dead on being landed showed rectal temperatures equal to those of the deep water from which they were taken. Thus, although the surface water was 1 to 4°C higher than the deep-water temperature, it apparently was not responsible for the increased temperatures of the fish. These cod would have done a good deal of struggling, with consequent increase in temperature, while the line was being hauled. In shallow water of 4 m, 13.8°C, temperatures of other bottom fishes were 0.4°C above their environmental temperatures and temperatures of bottom fishes taken from a shallow tank at 14.9 to 15.5°C were 0.1°C above those of their environment. Only larger specimens, generally 1.4-4.5 kg were used.

Clausen (1934) used thermocouples in the stomachs of 10 species of freshwater fish and found that although fish temperatures and water temperatures were approximately the same any stimulation resulted in an increase in temperature of the fish.

Morrow and Mauro (1950) mention many authors who, using thermo-electric methods and small fish, found only insignificant differences between fish temperature and water temperature, and also that several authors have shown that stimulation of fish from handling on being caught in a net results in an increase in their temperature.

Allowing for the increase in temperature resulting from violent struggling on capture of cod, such as those studied by Simpson and Britton there is little to encouraee the belief that cod living normally for a long period of time at low temperature have a body temperature more than 0.1°C higher than the surrounding water.

Scholander *et al.* (1957) using fish from Hebron Fjord, Labrador found that fishes such as the Arctic cod, *Boreogadus saida*, from the bottom water with temperatures of -1.73 to -1.75°C all year round, had plasma freezing points of -0.9 to -1.0°C in both summer and winter and thus, granting that the body temperatures of the fishes were the same as that of the environment, were supercooled by -0.7 to -0.8°C. These fish rapidly froze to death when brought to the surface at the same temperature as that at the bottom and put in contact with ice which seeded the fish with ice crystals. Fishes such as the Greenland cod, *Gadus ogac*, normally living under the ice in the shallow water where the temperature was -1.75°C in winter, had a plasma freezing point of -1.5°C in winter and -0.8°C in summer when the water temperatures were 4 to 7°C. These fish did not freeze in winter at -1.75°C even if they were touched by the ice but in summer turned belly up and ice masses filled their eyes at -1.0°C. It was repeatedly found that even large specimens of Greenland cod and sculpin had a body temperature within 0.1°C of the sea water.

Doudoroff (1945), for the hardy marine species *Fundulus parvipinnis*, inhaviting shallow bays and estuaries of California, found that death, at slowly lethal low temperatures in sea water of normal salinity, was preceded by dehydration of the tissues and delayed but not prevented by dilution of the sea water to 45% of its normal salinity. Osmoregulative failure was indicated as the cause of slow death at low temperatures but not of rapid death at still lower temperatures which may have been caused by respiratory disturbances.

Woodhead and Woodhead (1959) found a condition of osmotic imbalance in cod of the Barents Sea. Cod caught from October to June at bottom temperatures below 2°C had slightly higher amounts of blood salt (chlorides) than those caught at temperatures above 2°C. The fish taken below 2°C were caught at temperatures from 0 to below 2°C. In July and September, freezing point depressions and blood salts were at their normal values in cod from bottom water both above and below 2°C. These authors say that the cod lose their ability to survive in water below 2°C at the beginning of

October and that their results may explain the deaths of cod encountered in the North Sea (Simpson, 1953) at temperatures from 0 to 1.5°C.

Scholander *et al.* (1957) found in summer that chlorides (halides) made up about 80% of the osmotic pressure in both deep and shallow water fishes. In shallow water winter fishes living at -1.7°C or lower, and with a very large freezing point depression of about -1.5°C, the chlorides produced only half the freezing point depression. Thus the chlorides were increased relatively little in winter at these very low temperatures. Also, if fishes were transferred in summer from the warm surface water to bottom water at -1.73°C the total concentration of osmotic substances increased but the chlorides rose relatively less than the other substances.

The North Sea deaths of some of the cod population at temperatures of 0 to 1.5°C or over, were from a group of cod not normally encountering cold water and may have been due to chill or to osmoregulative failure in some of the cod, such as that found at low temperatures for *Fundulus* by Doudoroff (1945) and for cod by Woodhead and Woodhead (1959). The deaths of cod in coastal water and in shallow water or experimental tanks at temperatures of about -1.1°C were presumably due to quick chilling without time for gradual acclimatization, and in some cases to ice-seeding.

The St. Mary's Bay cod in moderately deep water could in many years encounter temperatures as low as -1.0°C or lower. Decrease of temperature in winter would be relatively slow, allowing for gradual acclimatization, and their ability to withstand temperatures of -1.4°C is very likely due to ability to maintain life when supercooled as were the Hebron Fjord deep water fishes. Small cod were probably more adapted than larger cod to these very low temperatures.

REFERENCES

BRITTON, S.W. 1924. The body temperature of fishes. *Contrib. Can. Biol. N.S.* 1: 413-418.

CLAUSEN, R.G. 1934. Body temperature of fresh water fishes. *Ecol.*, 15 (2): 139-144.

COLLINS, J.W. 1884. History of the tile fish. *Rep. U.S. Fish. Comm. for 1882*, pt. 10: 237-294a.

DANNEVIG, Alf. 1930. The propagation of our common fishes during the cold winter 1924. *Rep. Norweg. Fish. Mar. Invest.*, 3(10): 1-132.

DOUDOROFF, PETER. 1945. The resistance and acclimatization of marine fishes to temperature changes. II. Experiments with *Fundulus* and *Atherinops*. *Biol. Bull.*, 88: 194-206.

EARLL, R.E. 1880. A report on the history and present condition of the shore cod-fisheries of Cape Ann. Mass., together with notes on the natural history and artificial propagation of the species. *Rep. U.S. Fish. Comm. for 1878*, pt. 6: 685-740.

MARTIN, W.R. 1961. Canadian research report, 1960: B, Subareas 4 and 5. *Annu. Proc. int. Comm. Northw. Atlant. Fish.* 11: 31-37.

MORROW, JAMES E., and ALEXANDER MAURO. 1950. Body temperatures of some marine fishes. *Copeia, 1950*, No. 2: 108-116.

NIELSEN, A. 1893. Report for the year 1893 by A. Nielsen, superintendent of fisheries. *Ann. Rep. Nfld. Dept. Fish. for 1893*, App. No. 1: 20-86.

SCHOLANDER, P.F., L. VAN DAM, J.W. KANWISHER, H.T. HAMMEL and M.S. GORDON. 1957. Supercooling and osmoregulation in Arctic fish. *J. cell. comp. Physiol.*, 49 (1): 5-24.

SIMPSON, A.C. 1953. Some observations on the mortality of fish and the distribution of plankton in the southern North Sea during the cold winter, 1946-1947. *J. Cons.*, 19(2): 150-177.

SIMPSON, SUTHERLAND. 1908. The body-temperature of fishes and other marine animals. *Proc. Roy. soc. Edinb.*, 28: 66-84.

THOMPSON, HAROLD. 1943. A biological and economic study of cod (*Gadus callarias* L.) in the Newfoundland area. *Res. Bull. (Fish.) Nfld. Dept. Nat. Resources*, 14: 1-160.

WOODHEAD, P.M.J., and A.D. WOODHEAD. 1959. The effects of low temperature on the physiology and distribution of the cod *Gadus morhua L.*, in the Barents Sea. *Proc. zool. Soc. Lond.*, 133(2): 181-199.

A-5

MASS MORTALITIES OF MARINE FISHES IN THE NEWFOUNDLAND AREA PRESUMABLY DUE TO LOW TEMPERATURE

By

Wilfred Templeman[1]

ABSTRACT

Large numbers of cod have died off Labrador, in the northern part of the Gulf of St. Lawrence and smaller numbers in Trinity Bay probably due to cold. In proportion, however, to the great numbers of cod present in the Newfoundland area the reported deaths of cod are rare due to their ability to withstand cold, if time is available for acclimatization to it, and the tendency of the cod to retreat to deeper water in winter.

In proportion to the relative numbers of cod and haddock there are many more occurrences of haddock deaths in winter-spring in cold coastal surface waters. Haddock remaining overwinter in Newfoundland coastal areas apparently have less ability to withstand cold and a greater tendency than cod to enter shallow water too early in the year where they are destroyed by chilling or ice-seeding in the case of supercooled fish.

On two occasions in late March-early April, Greenland halibut died in large numbers in Trinity Bay. Although the deaths were most likely due to cold and related to the pelagic feeding on capelin well off the bottom in colder water, there is some doubt because there are no similar reports of Greenland halibut deaths from more northerly bays with Greenland halibut populations.

There are many occurrences of capelin deaths and most appear to be from ice-seeding of supercooled fish, at the surface. The pelagic life of these fish and their ability to live in the cold upper layer are responsible for their nearness to the surface in winter where they may enter the surface layer containing abundant ice crystals. It is possible that whales or more usually harp seal herds may at times drive capelin schools to the surface in winter and early spring.

Spiny dogfish in the Newfoundland area are migrants from southwards and with their higher temperature requirements than most native fishes have died in large numbers apparently from cold. The mechanism is presumably not supercooling and ice seeding but a disturbance of the nervous mechanism with loss of balance and great reduction of muscular and respiratory activities at low temperatures.

Mackerel were reported to have driven ashore on two occasions and at least one of these occurrences was probably due to cold.

INTRODUCTION

Well authenticated reports of mass mortalities of sea fishes in the North Atlantic due to low temperature have been reported by many authors especially by Dannevig (1930*a*, 1930*b*) and Johansen (1929) for cod and other fishes of southern Norway and Denmark, and by Lumby and Atkinson (1929) and Simpson (1953) for cod and other fishes of the North Sea. Although temperatures causing death on the Norwegian Coast were below 0°C, in the North Sea most of the deaths occurred in areas where the bottom temperatures probably did not fall below 1.5°C.

In many other instances of deaths of cod by cold at temperatures below 0°C in semi-natural situations (Nielsen, 1892, 1893, for the cod spawning pounds at Dildo, Newfoundland; and Earll, 1880 and Carswell, 1889, for the hatchery retaining pounds at Gloucester and at Woods Hole, Massachusetts), conditions were unnatural. The cod held in shallow pounds near the surface were

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killed by rapid lowering of water temperature and had no opportunity to respond naturally to falling temperatures by going deeper to warmer water.

Mass mortalities in Greenland in winter and spring of redfish (Jensen, 1922) and of redfish, cod, wolffish and lumpfish (Jensen, 1939) have been ascribed to unusually cold water. Collins (1884) reports the deaths of immense quantities of haddock in early December 1789 from the Arcto-Norwegian area. These dead haddock were seen floating in the sea off the coasts of Lapland and Norway on a voyage from Archangel to Leith. The subject of mass mortalities in the sea, from various causes, has been the subject of an excellent review by Brongersma-Sanders (1957).

In the Newfoundland-Labrador area, the coastal shelf area of Labrador and most of the west and east coasts of Newfoundland, including the bays, are covered by ice each winter. Also, sea temperatures over these parts of the coast have fallen by February-March to below 0°C to a depth of over 170 m and often to -1.5°C and even to -1.7°C, or slightly lower, over a great part of this depth. (See Fig. 1 for average temperatures off St. John's in the southern part of the area under discussion, and Fig. 2 for a section from St. John's to the Grand Bank in March after a cold winter).

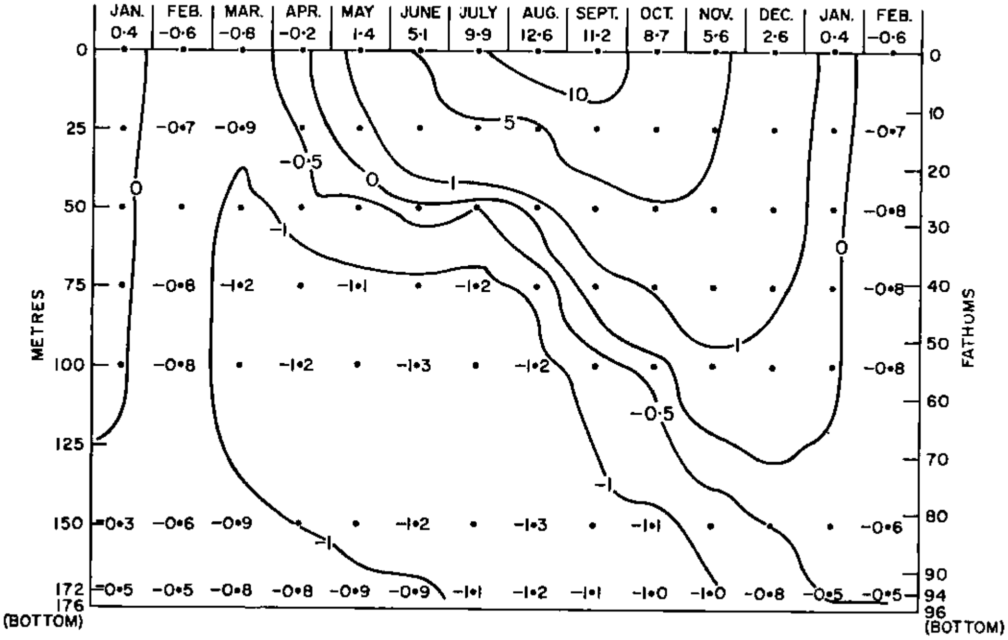

Fig. 1. Average sea temperatures (°C) at Station 27, 3.2 km (2 nautical miles) off Cape Spear, near St. John's, Nfld. (Average mid-monthly temperatures at the depths indicated, for 1950-62. Position of station, 47°31'50"N, 52°35'10"W, 176 m).

At Station 27, 3.2 km off Cape Spear near St. John's, (Fig. 1) average temperatures in February, March, April in °C (taken at each 25 m level surface to bottom in 176 m) were:

1950, -1.1, -1.6, -1.3; 1951, -0.5, -0.7, -0.2; 1952, -0.5, -0.8, -0.6;

1953, -0.1, -0.4, -0.5; 1954, -0.9, -1.0, -1.0; 1955, -0.2, -1.1, -1.2;

1956, -0.1, -0.5, -0.7; 1957, -1.4, -1.6, -1.3; 1958, -0.2, -0.4, -0.3;

1959, -1.4, -1.6, -1.2; 1960, -0.7, -0.7, -0.7; 1961, -1.5, -1.5, -1.3;

1962, -0.4, -1.3, -1.0; 1963, -0.3, -1.1, -1.0.

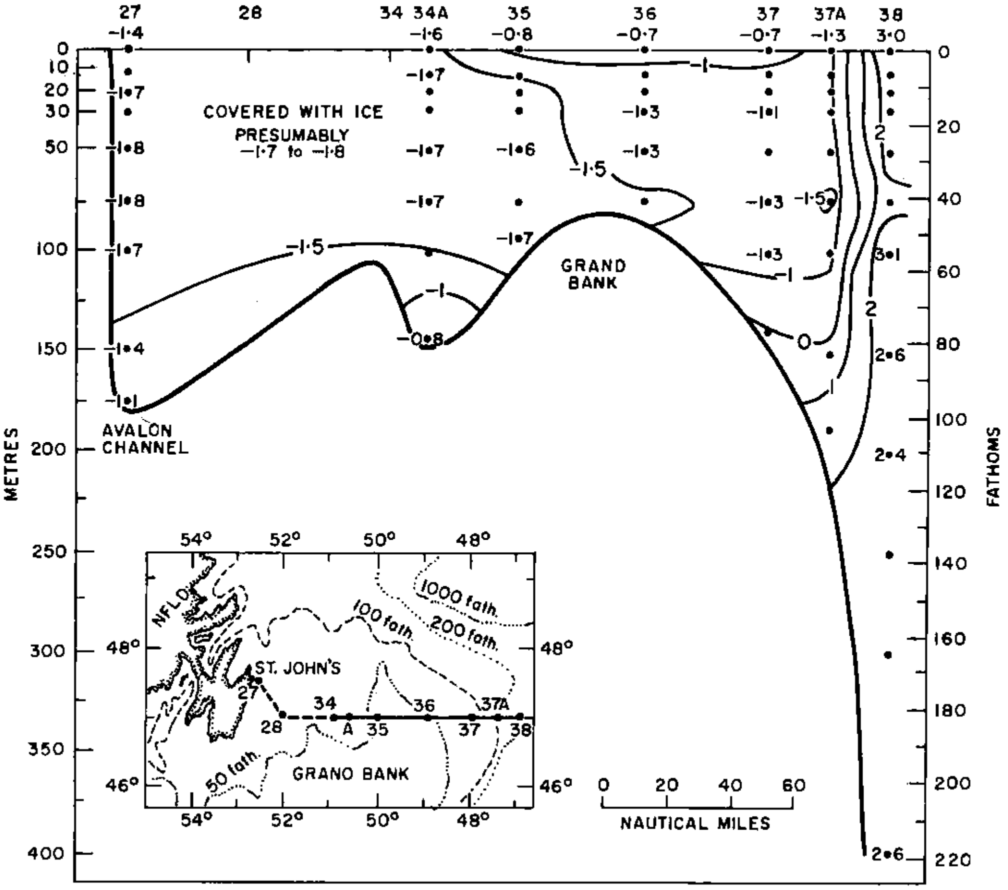

Fig. 2. Temperature section (°C) from Station 27 off Cape Spear across the Avalon Channel and the Northern Grand Bank, March 25–27, 1961.

In this period the coldest years judging from these southerly east coast records were 1950, 1957, 1959 and 1961. In all other years temperatures were low enough in the upper layers or could have been low enough at the surface in the more northerly bays to produce the recorded deaths.

It is not surprising, therefore, that there are winter-spring deaths of fish which can clearly be attributed to cold. There are other mass deaths in winter-spring where the evidence is not quite so clear. We have, over the years, collected many of these records from the Newfoundland area of mass or individual mortalities of fish in nature, examined some of the fish and come to conclusions on the cause of death. It is unfortunate that water temperatures are not available at the time of death but in many cases the evidence is clear and the accounts of the deaths may stimulate future investigation.

Cod and capelin are normal residents of the whole Newfoundland and Labrador continental shelf area. Greenland halibut, haddock, dogfish and mackerel are more restricted in distribution, the main populations of the latter three retreating southward in winter.

The location of the many Newfoundland place names mentioned in this paper is shown in Fig. 3.

COD *Gadus morhua* L.

Collins (1884) says that Captain Kirby, at Cape Charles, on the coast of Labrador on 1 August, 1876 saw an immense number of cod floating at the surface over an area of at least 10–16 sq km (4–6 sq miles). More than 300 quintals (ca. 60 metric tons round fish) were picked up and cured by local fishermen. At the time of this occurrence an unusual number of icebergs were grounded in the vicinity.

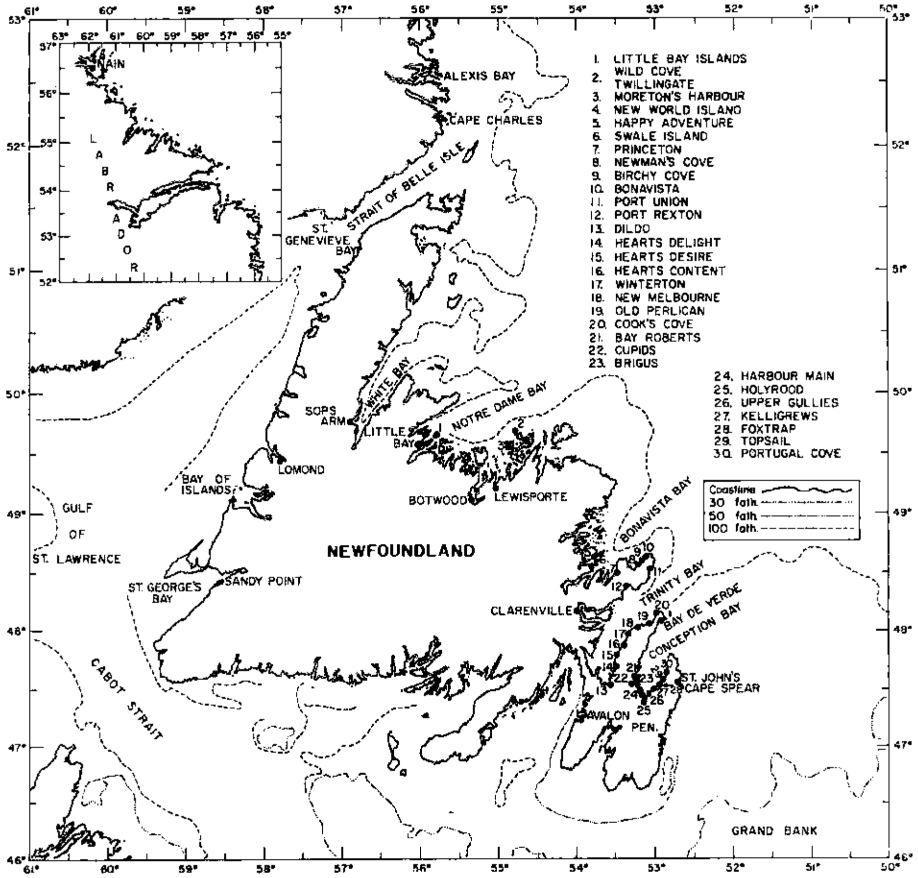

Fig. 3. Place names, Newfoundland area.

As many as 7 or 8 large bergs were within an area of 6-8 km (4-5 miles) and 40 bergs were in sight from the hills of Cape Charles. The local fishermen were of the opinion that the excessive coldness of the water, caused by the proximity of so much ice had killed the fish.

The St. John's Evening Telegram, 15 May, 1934, reported that Captain Tremblay, Master of the S.S. *North Voyageur*, stated that he steamed through over 32 km (20 miles) of dead codfish early in May 1934. This occurred in the northern part of the Gulf of St. Lawrence from 49°49'N, 59°10'W to 49°04'N, 58°40'W.

Mr P.J. Bannister, fishery officer, reported that off Port Rexton, Trinity Bay on 22 March 1960, numerous dead baby cod were floating on top of the water. There was a thin layer of white ice on the fish and they could not get to the bottom. The same observer in February 1948 coming from Swale Island to Happy Adventure, Bonavista Bay noticed a large cod floating on the surface. The fish was covered with a layer of ice. He says that the fish was taken, put in a pan and when the ice had melted it jumped out of the pan, very much alive. The fish was eaten with no ill effects.

HADDOCK *Melanogrammus aeglefinus* (L)

The St. John's Daily News, on 22 February 1957 reports (from their old files) that in May 1906 a shoal of haddock came in from Trinity Bay and hundreds of them went ashore on the beach at Clarenville.

The St. John's Evening Telegram of 16 March 1912 records that at Portugal Cove, Conception Bay, on 15 March thousands of haddock swam into the cove through a lake of water in the ice. These fish died and floated on the surface. The people of the village who went out in small boats each obtained 500 - 1,000 lbs. Such a happening had never before occurred in Portugal Cove.

A letter from Mr J. Strong of Little Bay Islands on 11 April 1957 informed us that 2 haddock, 15 and 35 cm long, were found dead near the shore. At this time the whole sea area out to about 160 km was covered with ice. Another haddock 28 cm long in good condition was found dead near Twillingate on 28 March 1960, by Mr E. Drover. Again on 7 May 1961, Mr Strong reported finding, at Little Bay, 5 dead haddock about 25-45 cm long. The bay was at the time covered with ice.

On 5 June 1959, fishery officer Nichols reported that thousands of small haddock were floating and being washed ashore in the Sops Arm area of White Bay.

Fishery officer P.J. Bannister, reported that off Port Rexton, Trinity Bay, on 22 March 1960, numerous dead haddock were floating on the surface of the water. There was a thin layer of white ice on the fish.

GREENLAND HALIBUT *Reinhardtius hippoglossoides* (Walbaum)

On 8 April 1943, Greenland halibut (called turbot in Newfoundland) came to the surface and died in large numbers on the eastern side of Trinity Bay.

During the week of 26 March-2 April 1959, mass deaths of Greenland halibut occurred again in Trinity Bay. The following account of this occurrence is mainly from the report of a survey by Mr A.G. Kelland, technician at the St. John's Station. At Old Perlican it is estimated that large numbers of Greenland halibut were killed. Slob ice was present and most of the Greenland halibut were seen dead but in good condition in shallow water on the bottom. One man salted a barrel of these fish and they were reported to be of average size and in good condition. In the same period at Winterton, about a dozen dead Greenland halibut were picked up floating at the surface in fresh condition and not frozen. Mr Kelland ate some of these and the taste was excellent. There were reports of similar numbers of dead Greenland halibut washed on shore at Hearts Delight and Hearts Desire.

CAPELIN *Mallotus villosus* (Müller)

Templeman (1948) notes mortalities of capelin during winter in Labrador. In the deep fjords of northern Labrador near Nain great cracks appear in the surface ice in winter and these run across the fjord every few miles throughout its length. Capelin rise into the open water in these cracks and apparently freeze when they reach the cold surface water. As much as two barrels of capelin have been obtained from one crack in an hour or two. Also in southern Labrador in March and April 1941 capelin were obtained in open cracks in the ice of Alexis Bay. These fish were plentiful and were used as dogfood.

On 8 April 1943, when, as we have reported, large numbers of dead Greenland halibut were washed ashore in Trinity Bay large numbers of dead capelin were noted in the same area. Similarly, in Mr Kelland's report of the deaths of Greenland halibut in Trinity Bay, 26 March - 2 April 1959, small quantities of fresh dead capelin were washed ashore at the same time.

Seven of these were examined at the St. John's Station by Mr T.K. Pitt and were adult capelin 14-17 cm long which would spawn in 1959. The normal amount of fat was present and the condition of the internal organs gave no indication of the cause of death. Four stomachs were empty, two had remains of euphausiids or mysids and one contained digested material. The male capelin did not possess spawning ridges. Capelin in this condition are usually called "whitefish" by Newfoundland fishermen.

On 13 April 1950, a fisherman, Mr Walter Baggs, noted fair quantities of dead capelin floating on the surface of the sea just north of St. John's. These capelin were in good condition, *i.e.* recently killed. Some were brought in and eaten. They were of the size which would spawn in the same year.

On 19 March 1960, Mr E. Drover of Twillingate saw hundreds of newly dead capelin floating near the beach on the western side of Twillingate. Over a stretch of 50 m of beach he picked up several gallons. These capelin were in excellent condition and were eaten.

Mr P.J. Bannister, fishery officer, reported that, on 22 March 1960, numerous capelin were floating at the surface off Port Rexton, Trinity Bay. There was a thin layer of white ice on the bodies of these fish and although when they were being collected a few were alive enough that they flicked away, the ice prevented them from escaping toward the bottom.

On 1 March 1963, very large numbers of floating dead capelin appeared among the slob ice in the Newman's Cove and Birchy Cove area Bonavista Bay. The Bay was full of slob ice pressed closely to shore. Thousands of capelin could be seen on the ice and intermingled with and below the slob ice. Local people collected large numbers for food. Probably at least several millions of capelin were killed here. Two men secured two barrels of capelin in one hole in the ice. These capelin were excellently fresh and were eaten in large numbers in the Newman's Cove and Bonavista area.

The author examined 6 of these capelin at Bonavista several weeks later. They were about 16-20 cm long, a bright silvery colour on the belly and bluish grey on the back. The bellies were more silvery and the back and the whole fish not as dark in colour as later, in late June-early July, when the fish are in shallow water near the beaches to spawn. The spawning ridges had not appeared on the males but the males could be separated externally from the females by the greater size of the anal fin. Eggs in the ovaries of the females could barely be seen with the naked eye.

SPINY DOGFISH *Squalus acanthias* L.

Templeman (1944) reports that, in the week preceeding 11 January 1939, at Sandy Point, St. George's Bay, a large number of spiny dogfish (called dogfish in remainder of paper) were washed ashore after heavy northwest gales which lasted for 3 days and produced a heavy sea in this area.

Mainly from 20-26 February 1951, large numbers of dogfish were driven ashore at many places in Conception Bay. At Cupids on 20 February 1951, they were observed by a technician of the St. John's Station, Mr B.W. Andrews, who was stationed in the area and who reported as follows: I first noticed these dogfish in Cupids harbour early morning 20 February. There was no wind or sea and new slob ice was forming in the harbour. The dogfish were noticed in the water near the beach - some alive, all belly-up and waving their tails, and others dead but all afloat on the surface. All died eventually. They could be seen all along 3 km of beach about 1 every 20 m. All the dogfish were small and lean, much different from the usual run in size and stoutness.

Also from the local branch of the Department of Fisheries of Canada information was obtained that numbers of small dogfish drove ashore and were found on the beach at Harbour Main on Sunday 25 February 1951.

Fishery officer Badcock of Bay Roberts reported that hundreds of small dogfish were ashore there on 5 March, or earlier, 1951 and many dead and dying dogfish were also reported from Brigus on 20 February from Kelligrews and Harbour Main.

Additionally Mr Donald Andrews reported large numbers of dying dogfish driving onshore at Foxtrap in Conception Bay on 5 April 1951. These were all small dogfish, alive but stupid and without sense of direction. They could be thrown off the beaches but would come in again.

Twelve of these dogfish selected at random from Cupids on 20 February and 3 from Bay Roberts on 5 March were examined by the author. Nine were immature males 57-65 cm in greatest total length and 6 were immature females, 5 being 58-66 cm and one 70 cm in greatest total length. All stomachs were empty.

In the winter of 1952 large numbers of dogfish died in Notre Dame Bay. The following information of this occurrence was supplied by Mr S.A. Knight of Moreton's Harbour: During the month of January 1952 large numbers of dogfish drifted ashore on the southern side of Notre Dame Bay in the area from Twillingate to Lewisporte and Mr Knight believes that conditions were generally the same all around the bay. Large numbers of small to medium sized dogfish drifted in at Wild Cove on New World Island early in January. The fish were in a stunned condition usually belly-up with only slight movement of the fins. A gale of northeast wind was blowing at the time and the fish drifted onto the beaches. The St. John's Daily News of 8 February 1952, reported from its Botwood correspondent that every hole of water in the ice near beaches and wharves was filled with dead and dying dogfish.

In the winter of 1954 large numbers of dogfish were noticed dead or dying at the surface and washed ashore on the beaches of Trinity and Conception Bays. The Federal Department of Fisheries (Newfoundland area) reported on 11 February 1954, that dogfish had been driving ashore at Old Perlican in Trinity Bay since January. There were scores around the beach and some came in on 10 February. There was a little life in them when they came in but not enough to keep them from being washed up on the beaches. Mr Earl Frost, technician at the St. John's Station, reported on 23 February 1954, that numbers of dogfish were washed ashore early in February at Old Perlican, Cook's Cove and New Melbourne, Trinity Bay, with the greatest number at Cook's Cove. Also at these places large numbers were seen on the surface in a stunned condition. Dogfish also washed ashore at Bay de Verde, Conception Bay on 15-18 February among the slob ice. They appeared half-dead and floated on the surface of the water before being driven ashore.

On 25 February 1954 Mr A.G. Kelland, technician at the St. John's Station, investigated reports of dogfish washing ashore in Conception Bay. On Topsail Beach 35 dogfish were noted and 5 on the beach at Upper Gullies. At Holyrood several hundred dogfish were on the beach. On these beaches most had been washed ashore on 23-24 February and these were in good condition but some were beginning to decay and had been washed ashore earlier. A local resident of Holyrood said that the first dogfish he noted on and near the beach was on 24 February. Some were floating on the surface barely alive and others were washed ashore dead. At Holyrood 203 dogfish were measured and 110 females 56-75 cm in greatest total length were all immature whereas of 93 males 56-78 cm long many of the larger males were mature. All 9 males and 7 females examined had empty stomachs.

The St. John's Daily News on 15 March 1954, reported that on the west coast of Newfoundland thousands of dead dogfish were being drifted ashore on the coastline between Lomond and St. Genevieve Bay.

Also the Fisherman's Advocate of Port Union, reported on 26 March 1954, that at Princeton, Bonavista Bay, in common with other places around the coast, dogfish had been plentiful and found dead on the beaches during the early winter.

MACKEREL *Scomber scombrus* L.

In the St. John's Daily News of 2 February 1952, it was reported that thousands of mackerel, *Scomber scombrus* L., had driven ashore in Notre Dame Bay beginning about 20 December 1951.

Mr B.W. Andrews, technician of the St. John's Station, reported that on the night of 27 December 1951, small numbers of mackerel with an average weight of 1 kg came ashore on the beach at Cupids, Conception Bay.

DISCUSSION

1. Cod

The deaths described are in situations and times when they could most likely be ascribed to cold water although the occurrence reported for August on the Labrador Coast must be very unusual. In view of the large numbers of cod in the Newfoundland area there are few records of mass deaths. Small cod in this area, when acclimatized slowly, can live in water at least as low as -1.4°C and larger cod commonly to -0.5°C and in small numbers to -1.3°C or lower (Templeman and Fleming, this symposium). In winter, in the Newfoundland area, cod of mature and large immature sizes tend to seek deeper water below the influence of the winter chilling and hence are usually in water above 0°C and often between 2 and 3.5°C. In late winter-early spring (Fig. 1, 2) water temperatures may be the same or almost the same, -1.0 to about -1.7°C, from surface to bottom down to 150 m or more and as low as -1.8°C on the surface where ice crystals are then forming. Occasional cod caught in this cold layer might come to the surface and being seeded by contact with ice crystals, their body fluids would change from their supercooled liquid condition to a frozen condition (Scholander *et al.*,1957). Also, although mature cod may live in deep water at above 0°C in winter after spawning, in the Labrador area mainly on the seaward slope of the continental shelf, many of them become pelagic in late spring-early summer and enter shallow water of the coastal region. In the Gulf of St. Lawrence, cod, which winter in the deep water near the Newfoundland side of Cabot Strait, move rapidly northward in late spring and enter shallow water as far northward as the Strait of Belle Isle. It is probable that a rapid change from deep warm to shallow cold water in the latter situation resulted in the mass mortalities recorded for the Gulf of St. Lawrence. The mortalities of Labrador cod in August have been ascribed to cold water due to the presence of icebergs. Although again death from cold water is a likely cause there is some doubt because icebergs are common on the Labrador Coast and no other mass deaths have been reported from iceberg melting.

2. Haddock

Haddock are accustomed to living at a temperature one to several degrees higher than cod. Consequently, it is to be expected that their resistance to low temperatures will be correspondingly less than that of cod.

The most northerly large spawning population of haddock on the continental shelf east of Newfoundland and Labrador lives mainly on the southern Grand Bank, returning to the southwestern slope in winter and mainly spawning there, and in summer spreading northeastward over the Grand Bank but still mainly over the southern half of this bank. Some of these Grand Bank haddock and occasionally large numbers in their northward passage reach the coast of Newfoundland, especially the Avalon Peninsula, in late June and early July, and in July and August work northward along the east coast of Newfoundland. A few migrate as far as Notre Dame Bay and occasional individuals, either by way of the east coast of Newfoundland or from another small population along the west coast of Newfoundland, reach southern Labrador. Presumably most of these haddock retreat southward in autumn, but at least some remain and spend the winter with the cod in the deep warmer water below the cold layer. From their natural winter abode in the deeper water on the southwestern slope of the Grand Bank haddock move northeastward into shallower water from April to June as water temperatures rise in the shallow water of the bank. There is, however, a tendency at this time to move northward even if water remains fairly cold but in these months the bottom water of the southern shallow-water part of the Grand Bank is usually 1 to 4°C and occasionally 0 to 2°C (Templeman and Hodder, this symposium). The surface temperatures on the southern Grand Bank at this time are slightly higher than the bottom temperatures and there are no records of mass mortalities from cold. Northward, however, along the coasts of Newfoundland where some haddock which migrated northward from the Grand Bank in previous years spend the winter in deep water, the haddock apparently have the same instinct to move into shallower water fairly early in spring and may be killed by cold water especially in presence of ice crystals. It is likely that some of the winter kills are of haddock caught in bays of only moderate depth and in passing to the surface when the water becomes chilled below -1°C are killed by ice-seeding in the surface layer. Also many of the haddock, instead of passing into the deeper water to the east, may be trying during the winter to retreat southward pelagically in shallow water which becomes too cold for survival.

Only a very small number of haddock winter off the Newfoundland east coast (probably not more than 1 haddock to at least 10,000 cod). In spite of this disparity in numbers present there are more records from this area of haddock than of cod mortalities which can definitely be attributed to cold water. It is probable that the natural behaviour of the haddock is not suited to over-winter survival in numbers on the east coast of Newfoundland and thus no coastal spawning populations have developed here.

3. Greenland Halibut

Although Greenland halibut are abundant in many other deep bays of the Newfoundland area all the accounts of deaths of Greenland halibut are from Trinity Bay. This is not the coldest bay and in the more northerly White Bay and the bays and arms of Notre Dame Bay the cold water should extend more deeply and on the average be colder.

Trinity Bay is a deep water bay with a threshold depth at its mouth of about 230-265 m and water as deep as 330 m off Old Perlican and over 370 m off Winterton and Hearts Desire. The Greenland halibut in Trinity Bay in summer and autumn are almost all below 180 m and the larger ones and the greater numbers below 280 m. In an otter-trawl survey of this bay by the *Investigator II* in late November-early December 1953 the largest quantities of Greenland halibut, 350-1,180 kg per hour's towing, were between 300 and 400 m and bottom temperatures of 0.4 to 0.8°C. Greater depths were not investigated due to lack of towing warp. In this bay at the depths inhabited by the larger Greenland halibut temperatures should not fall below 0°C in winter and spring. The upper layer of water down to 150 m or deeper should in almost all winters fall below 0°C by February-March and in very cold winters reach -1.5 to -1.8°C for at least a considerable part of this depth with as low as -1.75°C and ice crystals and ice at the surface. (At the usual winter salinity near St. John's of slightly over 32 o/oo the freezing point of sea water and formation of ice crystals is at -1.75° C). The depth of the entrance to the bay is also great enough that there should not be oxygen depletion.

The pelagic capelin which can inhabit water below 0°C is one of the chief foods of the Greenland halibut and is a favoured bait for them. Jensen (1935) records that in the West Greenland fjords the Greenland halibut often move into the intermediate layer in numbers and feed on capelin as much as 100 m off the bottom in a depth of 300 m. Here they are often caught pelagically and abundantly by the Greenlanders using handlines only 200 m long. It is very likely, therefore, that in Trinity Bay schools of Greenland halibut carry out similar vertical migrations moving up from the deeper water of above 0°C temperatures into colder water above. Thus, in years when water temperatures are low and the cold water extends deeper than usual they may move suddenly into water so cold that they may be stunned and lose control of their movements and finally be killed by the cold water or by ice-seeding at the surface. This might especially occur when strong northerly winds send the colder water deeper than usual on the southern side of the narrow bay.

There remains the problem why Greenland halibut, lacking an air bladder, should float at the surface. These are rather fat fish and (in summer at least) have about 10-12% fat in their flesh which helps to lighten them. Passage toward the surface should cause a good deal of gas to come out of the blood and be retained in the tissues and the very cold surface water is fairly dense in spite of the approximately 32 o/oo coastal salinity. Any formation of surface ice on the fish, which has not been reported for the Greenland halibut, but has been reported for some of the other fishes, would also help to float the fish. After a while at the surface the sea-birds pick away the guts and liver and the fish then apparently sinks unless it has meanwhile become frozen into the ice.

There must, however, remain an element of doubt that low temperatures were the cause of the mortalities of Greenland halibut because of the absence of information on such deaths from more northerly bays where temperatures should be lower and low temperatures extend deeper. In favour of cold being the cause of death is the record that on both occasions when Greenland halibut died, capelin died also, and many of our instances of capelin dying have certainly been due to cold, most likely to ice-seeding of supercooled fish.

4. Capelin

That capelin can live in very low temperatures is apparent from the fact that they occur in numbers as far north as Hudson Bay. They are pelagic, cold water fish commonly found in the Newfoundland area in winter, near and in the cold upper layer. It is not surprising, therefore, that at times during late winter and early spring when temperatures are approximately the same and often below -1.0°C in the upper 150 m near the coast that some schools of capelin may come into the immediate shallow water near the shore or at the surface where temperatures of -1.7 to -1.8°C and great quantities of ice crystals are available to seed them with ice and kill them. The general occurrence of capelin deaths described seems to suit this kind of situation. The ice which often covers the fish keeps the capelin floating and even if some life remains prevents them from passing deeper.

In the surface kills of capelin (also of some haddock and baby cod) reported by Mr Bannister from Trinity Bay, 22 March 1960, 6 large baleen whales were at the surface in the vicinity and it was thought that these whales which, off Newfoundland, feed partly on capelin might have driven the capelin and other fishes to the surface where they iced up and died. It is possible that in spring the numerous harp seals may occasionally also drive some capelin into the icy surface layer or the inshore shallow water area. Many of the occurrences, however, are very likely mass movements of the capelin into the shallow water and surface environment at a time when these situations are fatal due to the presence of ice crystals.

5. Spiny Dogfish

These are rather warm water fish not liberating their young in the Newfoundland area. In summer they migrate northward along the Newfoundland coast as far as southern Labrador. In their migrations northward around the east coast of Newfoundland dogfish move in the warmer surface layer rather than in the deeper and colder water occupied by cod. In the autumn the mature females pass southward out of the Newfoundland area to produce young on the continental shelf of the United States (Templeman, 1944). Large numbers of dogfish of intermediate size — immature females, immature males and mature males — sometimes remain in the bays. Here they often find themselves in shallow holes or harbours when too low temperatures develop. Being a warmer water fish than cod and capelin they probably cannot survive at as low a temperature as these fish. Conception Bay, from which many of our reports of dogfish deaths in winter have come, has a deep central hole below 170 m but the threshold at the entrance of the bay is shallower than 170 m. Thus all the water of the bay can fall below 0°C during the winter, the first 170 m, at least, below -1.0°C and the surface to -1.7 to -1.8°C. In early December 1953 the bottom water in the deep hole of this bay was at a uniform -0.9°C in all depths from 180-265 m. The deaths of dogfish cannot be attributed to ice-seeding at the surface of supercooled fish since the body fluids of elasmobranchs are isotonic with sea water and these dogfish before dying have presumably risen from deeper waters of higher salinity. The surface floatation and deaths are very likely produced by loss of muscular and respiratory control and possibly from other causes such as osmoregulative failure (Doudoroff, 1945; Pitkow, 1960).

Although in the dogfish there is no air bladder and the flesh not fatty the oily liver would often assist in floatation once the animal has lost its power to swim more deeply.

These overwinter deaths from cold may be an important factor in preventing the establishment of native populations of dogfish in the Newfoundland area.

6. Mackerel

The two accounts of mackerel going ashore on the beaches in December are not detailed enough to indicate whether or not they were killed before going ashore. The Notre Dame Bay occurrence, however, was accompanied by massive deaths of dogfish at the same time and was presumably the effect of cold. Mackerel are rather warm-water fish and only occur in the eastern Newfoundland area in quantity in the warmer periods of years. They are apparently migrants into this area rather than regular inhabitants and might be expected to be affected detrimentally by low temperatures.

7. Other Fishes

Redfish, *Sebastes mentella* Travin are present in moderate numbers in some deep Newfoundland bays, such as Trinity Bay and Notre Dame Bay, and are relatively abundant in the Gulf of St. Lawrence. It is surprising that no mortalities of redfish in winter-spring are reported from these or other Newfoundland Areas although winter deaths of large numbers of redfish probably from cold are reported from the fjords of West Greenland (Jensen, 1922, 1939; Templeman, 1959). Redfish are normally below 180 m in the east coast Newfoundland bays, even in summer, and tend to go deeper in winter. The bays are deep and very low temperatures probably do not reach deeply enough to kill redfish which, although most prevalent in the Newfoundland area at temperatures above 3°C, are sometimes caught in small numbers in water of 1°C or less.

Herring, *Clupea harengus* L. are present in great quantities in winter in ice-covered bays such as Bay of Islands and Trinity Bay and yet we have no report of herring deaths which are likely to have been caused by cold.

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REFERENCES

BRONGERSMA-SANDERS, MARGARETHA. 1957. Mass mortality in the sea. *Geol. Soc. Amer.*, 67 (1): 941-1010.

CARSWELL, JAMES. 1889. Report on the artificial propagation of the codfish at Woods Hole, Mass., for the season of 1885-86. *Rep. U.S. Fish. Comm. for 1886*, pt. 14: 779-782.

COLLINS, J.W. 1884. History of the tile-fish. *Rep. U.S. Fish. Comm. for 1882*, pt. 10: 237-294*a*.

DANNEVIG, ALF. 1930*a*. The propagation of our common fishes during the cold winter 1924. *Rep. Norweg. Fish. Mar. Invest.*, 3(10): 1-133.

1930*b*. The death of fish in very cold winters. *J. Cons.*, 5(2): 194-196.

DOUDOROFF, PETER. 1945. The resistance and acclimatization of marine fishes to temperature changes. II. Experiments with *Fundulus* and *Atherinops*. *Biol. Bull.*, 88(2): 194-206.

EARLL, R.E. 1880. A report on the history and present condition of the shore cod fisheries of Cape Ann, Mass., together with notes on the natural history and artificial propagation of the species. *Rep. U.S. Fish. Comm. for 1878*, pt. 6: 685-740.

JENSEN, AD. S. 1922. *Sebastes marinus*. Researches on the distribution, biology, and systematics of Greenland fishes. I. *Videns. Medd. Naturh. Foren. Kjöbenhavn*, 74: 89-109.

1935. The Greenland halibut (*Reinhardtius hippoglossoides* (Walb.)) its development and migrations. *D. Kgl. Danske Vidensk. Selsk. Skr.*, 9. Raekke, 6(4): 1-32.

1939. Concerning a change of climate during recent decades in the arctic and subarctic regions, from Greenland in the west to Eurasia in the east, and contemporary biological and geophysical changes. *K. Danske Videns. Selsk., Biol. Medd.*, 14(8): 1-75.

JOHANSEN, A.C. 1929. Mortality among porpoises, fish, and the larger crustaceans in the waters around Denmark in severe winters. *Rep. Dan. Biol. Sta.*, 35: 63-97.

LUMBY, J.R. and G.T. ATKINSON. 1929. On the unusual mortality amongst fish during March and April, 1929, in the North Sea. *J. Cons.*, 4: 309-332.

NIELSEN, A. 1892. Report for the year 1892 by A. Nielsen, superintendent of fisheries. *Ann. Rep. Nfld. Dept. Fish. for 1892*, App. No. 1: 27-80.

1893. Report for the year 1893 by A. Nielsen, superintendent of fisheries. *Ibid. for 1893*, App. No. 1: 20-86.

PITKOW, RONALD B. 1960. Cold death in the guppy. *Biol. Bull.*, 119 (2): 231-245.

SCHOLANDER, P.F., L. VAN DAM, J.W. KANWISHER, H.T. HAMMEL, and M.S. GORDON. 1957. Supercooling and osmoregulation in Arctic fish. *J. Cell. Comp. Physiol.*, 49(1): 5-24.

SIMPSON, A.C. 1953. Some observations on the mortality of fish and the distribution of plankton in the southern North Sea during the cold winter, 1946-1947. *J. Cons.*, 19(2): 150-177.

TEMPLEMAN, WILFRED. 1944. The life-history of the spiny dogfish (*Squalus acanthias*) and the Vitamin A values of dogfish liver oil. *Res. Bull. (Fish.) Nfld. Dept. Nat. Resources*, 15: 1-102.

1948. The life history of the capelin (*Mallotus villosus* O.F. Müller) in Newfoundland waters. *Res. Bull. Nfld. Govt. Lab.*, 17: 1-151.

1959. Redfish distribution in the North Atlantic. *Bull. Fish. Res. Bd.Canada*, 120: 1-173.

TEMPLEMAN, WILFRED and A.M. FLEMING, 1964. Cod and low temperature in St. Mary's Bay, Newfoundland. This symposium, Contribution No. A-4.

TEMPLEMAN, WILFRED and V. M. HODDER, 1964. Distribution of haddock on the Grand Bank in relation to season, depth and temperature. This symposium, Contribution No. A-8.

A-6

RESEARCH VESSEL CATCHES OF COD IN THE HAMILTON INLET BANK AREA IN RELATION TO DEPTH AND TEMPERATURE [1]

By

Wilfred Templeman and A. W. May [2]

ABSTRACT

The interrelationships of distribution and abundance of cod in the Hamilton Inlet Bank area ith depth and temperature have been studied by analysis of catch, depth and temperature data from esearch vessels, generally fishing at pre-determined positions and depths.

Surveys in April and May of 1963 revealed large concentrations of spawning and post-spawning od on the extreme eastern slope of the bank in depths of 225 - 330 m at temperatures mainly be- ween 2.5 and 3.1°C. The larger, mature fish were most abundant in deeper warm water, while the maller, immature fish generally inhabited shallower and cooler water. It is apparent that in winter ost mature cod of this area move as far away from the coast as possible and accumulate on the eastrn continental slope for spawning, since they are not found in abundance closer to shore in similar epths and otherwise suitable temperatures.

Following, but not immediately after spawning, these concentrations begin to break up, and by ate June many of these cod have found their way inshore, and are fished throughout the summer at ariable temperatures with a range of at least -0.8 to 8.7°C. Those remaining offshore are found ainly in shallower (165-250 m) cooler (-1.0 to 2.0°C) water close to and on the central part of he bank, occasionally concentrating to feed, and by late summer may be restricted in movement due o temperature barriers or to feeding.

Concentrations found in late autumn on the southwestern slope of the bank may be gathering or movement eastward to the spawning area.

INTRODUCTION

Between 1950 and 1963 the Fisheries Research Board of Canada research vessels *Investigator 11* nd *A.T. Cameron* carried out bottom trawling surveys on Hamilton Inlet Bank and on the eastern and outheastern slopes of this bank. The *Investigator 11* a 25-m, 250-h.p. vessel used a No. 36 otter-trawl with an 18.3-m headline. The *A.T. Cameron* a 54-m, 1000-h.p. vessel used a No. 41 otter-trawl ith a 24.1-m headline. The codend in each case was lined or covered with small-meshed netting. his was of 29- or 35-mm external stretched mesh size, except for an *A.T. Cameron* cruise in August 962, when 2-inch mesh courlene was used as a cover. Both ships trawled at about the same speed f 3½ knots. Except where otherwise indicated the period of towing on bottom for each set was 30 in. On the slope of the bank the vessels always towed along a depth contour, attempting to keep he same depth in any one set. A bottom temperature was taken at the end of each set, usually bout 4 m from the bottom, using 2 reversing thermometers on a Nansen or Knudsen water bottle, and 36-kg weight. In all the more recent work temperatures have been corrected for thermometer and uxiliary error but, in these waters of low temperature, corrections are as a rule small—in the econd decimal place. Also, in all the work by the *A.T. Cameron* in depths to 275 m, an additional heck was made by a bathythermograph cast, at each station, to bottom or about 1 m above bottom. emperatures from the thermometers and bathythermograph slide were compared and adjustments made o the bottom temperatures where necessary. Below 275 m temperatures are usually rising slowly nd the effect of the thermometers being several metres off bottom is not significant in relation o the wide temperature scales used in this contribution. Unless otherwise noted all temperatures eferred to in this contribution are bottom temperatures.

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Fisheries Research Board of Canada Biological Station, St. John's, Nfld.

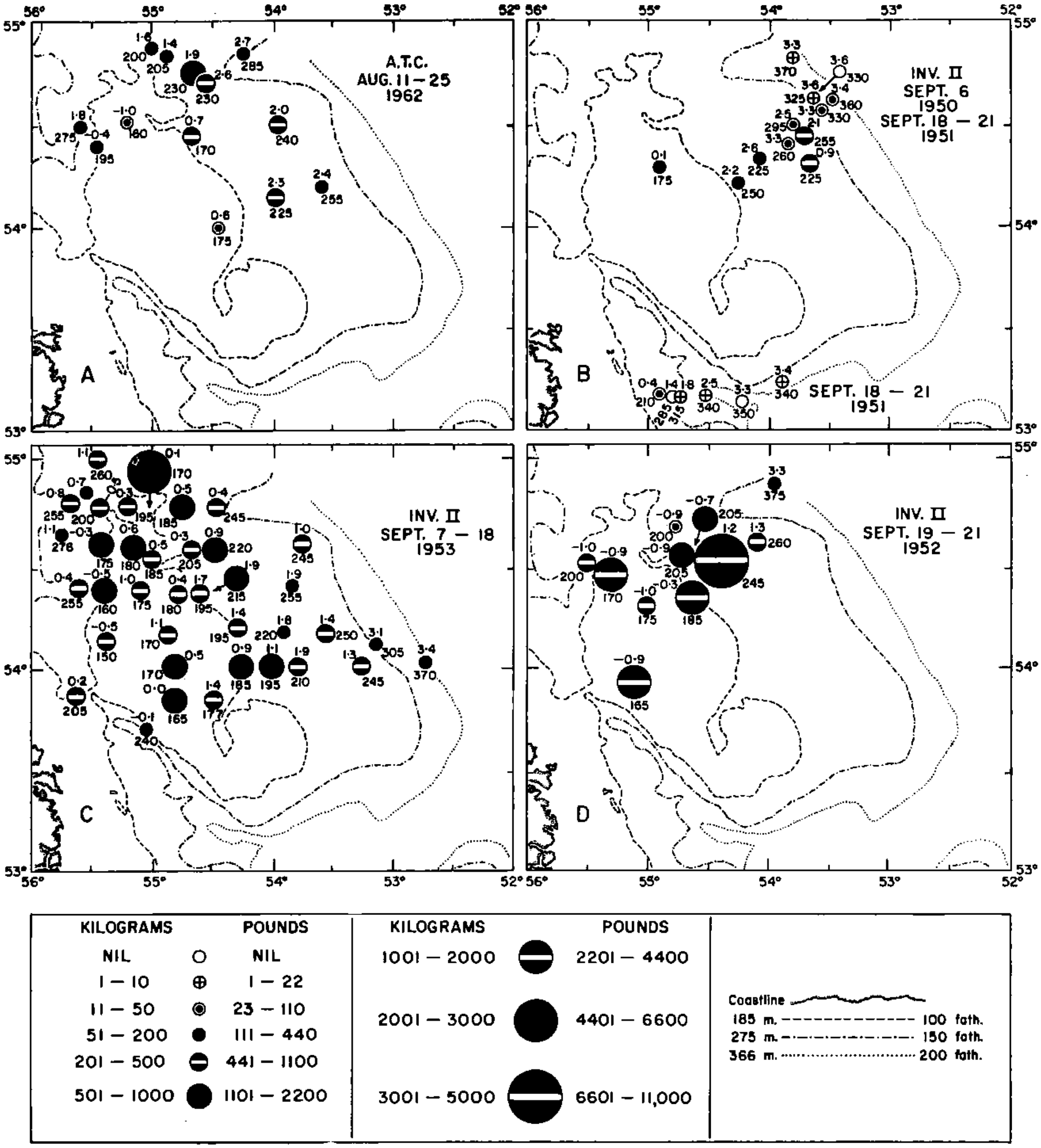


Fig. 1. Cod catches per half-hour tow by the *A.T. Cameron* and the *Investigator 11* on Hamilton Inlet Bank and its slopes, 9 April-11 August, 1958, 1960 and 1963. (Bottom temperatures in °C and depths in m are inserted near the catch symbols which are for whole cod.)

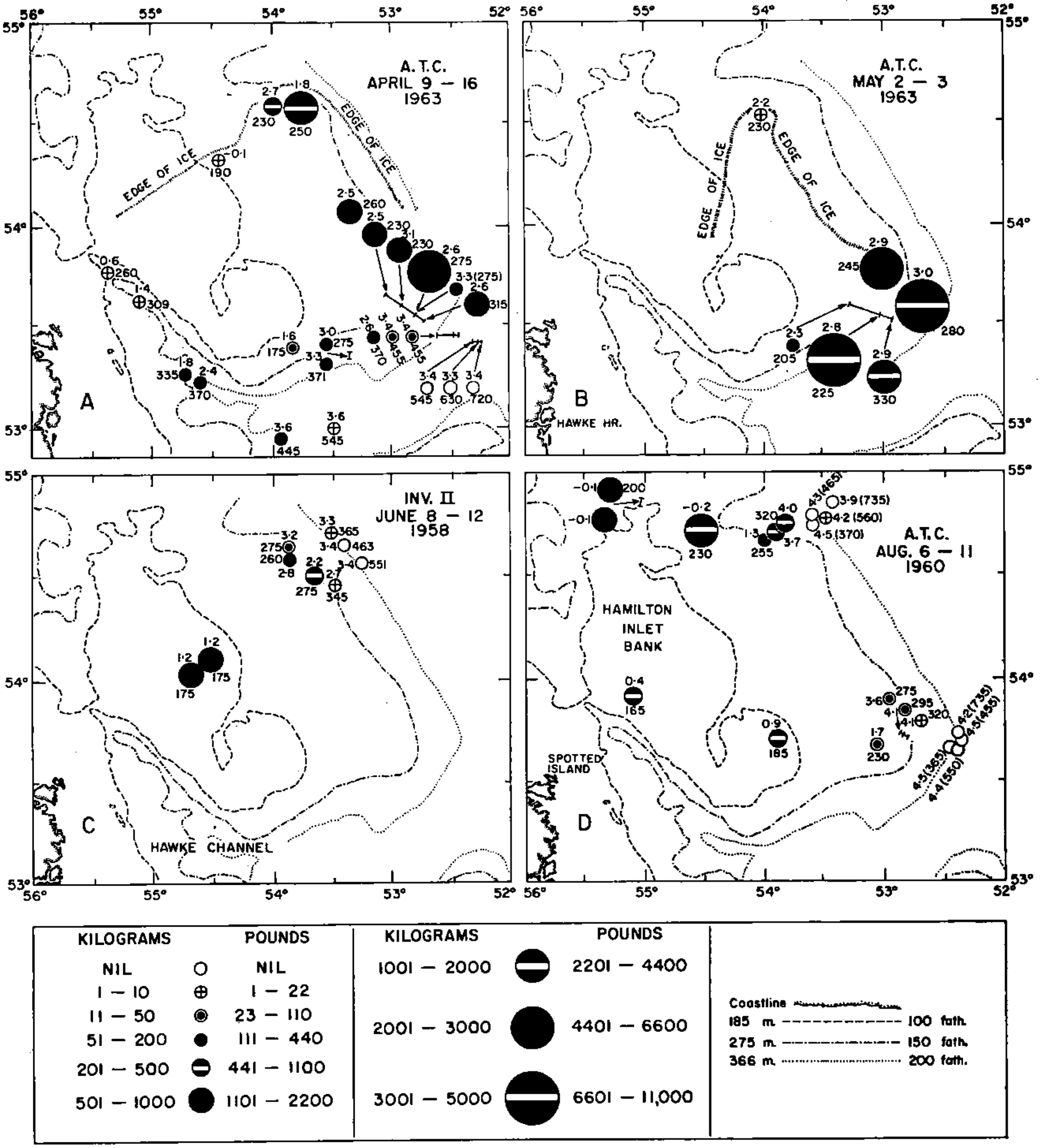


Fig. 2. Cod catches per half-hour tow by the *A.T. Cameron* and the *Investigator 11* on Hamilton Inlet Bank and its slopes, 11 August-21 September, 1951, 1952, 1953, and 1962. (Bottom temperatures in °C and depths in m are inserted near the catch symbols which are for whole cod.)

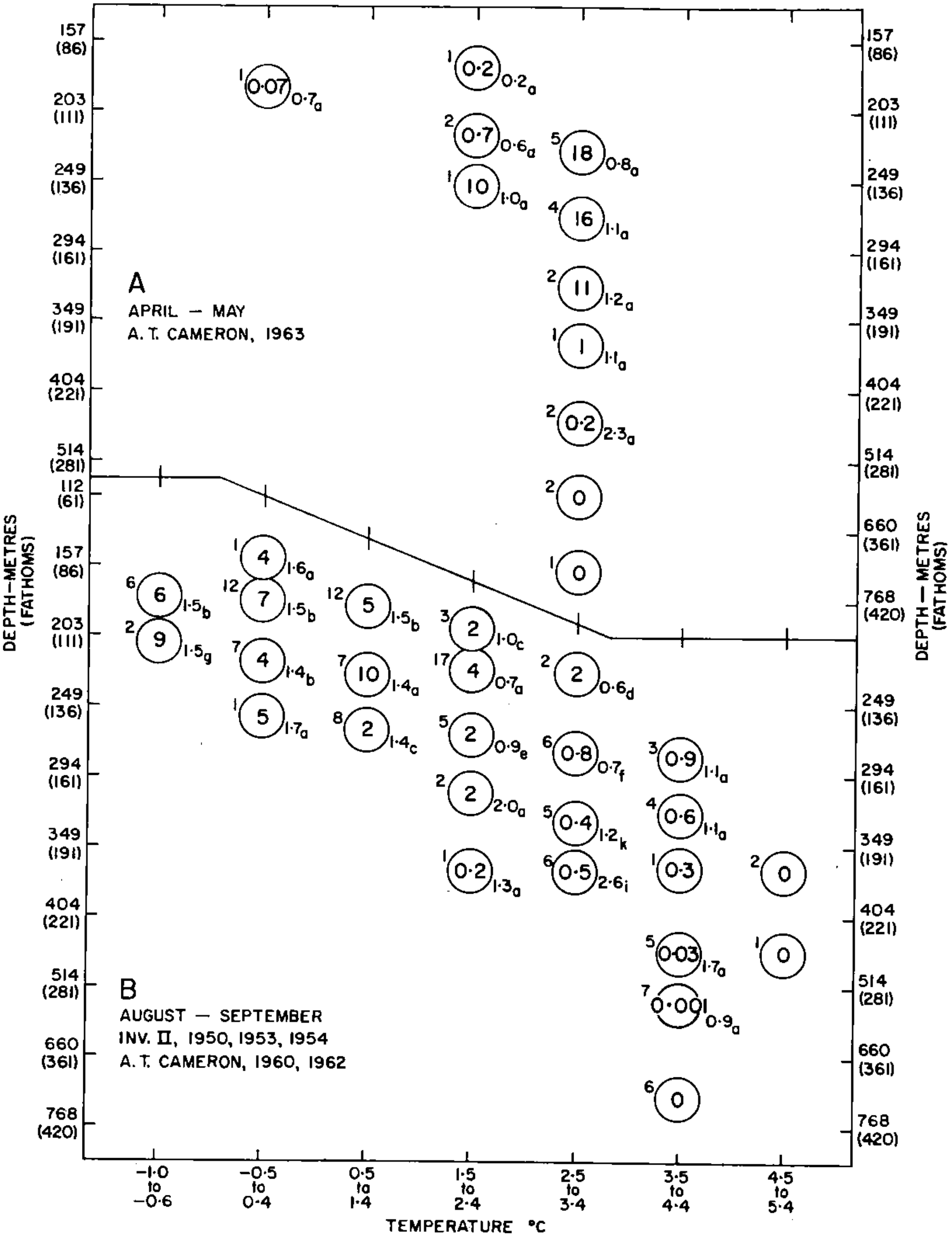


Fig. 3. Average catches of whole cod in the Hamilton Inlet Bank area in relation to depth and bottom temperature. (The figure in the circle is the average catch in hundreds of kg. At the upper left of the circle is the number of sets included in the average. At the lower right is the average weight of the whole cod in kg. The letter index to the lower right of the weight, indicates the percentage of the cod catch represented in the averages for average weight: a, 100; b, 90–99; c, 80–89; d, 70–79; e, 60–69; f, 50–59; g, 40–49; h, 30–39; i, 20–29; j, 10–19; k, 1–9.)

In paired haul comparisons of the *A.T. Cameron* and *Investigator 11* during 4 cruises involving a total of 101 sets the *Investigator 11* caught 80% as much cod as the *A.T. Cameron* although the *A.T. Cameron* caught over twice as much haddock as the smaller ship. Assuming that on Hamilton Inlet Bank the August and September concentrations and distributions are similar, and allowing for the additional catching power of the *A.T. Cameron*, it appears likely that the *Investigator 11* catches in September 1952 and 1953 (Fig. 2C, 2D) and even the *A.T. Cameron* catches of August 1960 (Fig. 1D) indicate a greater cod population on Hamilton Inlet Bank than in August 1962, judging by the *A.T. Cameron* catches at the later period (Fig. 2A). Because the *Investigator 11* surveys were in the earlier part of the period under consideration when cod were more plentiful, and the *A.T. Cameron's* surveys in the latter period when a large fishery was developing in this area, it has not been found necessary to separate the *Investigator 11* and the *A.T. Cameron* catches in Fig. 3.

The sets were made at pre-determined positions without reference to abundance of fish as indicated by echo-sounder. However, most of the larger catches of the *A.T. Cameron* in April-May 1963 (Fig. 1A, 1B) and the two 200-m catches of the *A.T. Cameron* in August 1960 (Fig. 1D) were made in areas where commercial trawlers were fishing. All sets were made in daylight.

A.T. CAMERON AND *INVESTIGATOR 11* SURVEYS

1. Spring

In early April 1963 (Fig. 1A) the *A.T. Cameron* found heavy concentrations of cod on the eastern and southeastern slopes of Hamilton Inlet Bank. The heaviest concentrations on the southeastern slope during 9-12 April were in 275 m at 2.6°C, and on the northern part of the eastern slope at 250 m and 1.8°C. On the southeastern slope trawling was extended to 720 m, but only a few cod were found deeper than 370 m (2.6 to 3.4°C), and none between 545 - 720 m (3.3 to 3.4°C). On the northern part of the slope the fishing was at the edge of the ice and it was not possible to trawl deeper. Sets in shallower water (175-190 m) and at lower temperatures (-0.1 to 1.6°C) on the eastern edge of the bank produced only a few small cod. Sets in deeper water in the western part of Hawke Channel at low temperatures (0.6 to 1.8°C) also produced few cod.

On 2-3 May, 1963, very large catches of post-spawning cod were obtained on the southeastern slope (Fig. 1B) just south of the ice edge at 225-280 m (2.8 to 3.0°C). These spawning and post-spawning concentrations in April-early May appear to be on the extreme eastern edge of the slope, and in 1963 were chiefly at depths between 225 - 330 m at temperatures from 2.5 to 3.1°C (Fig.1-5). The larger mature fish were in the deeper water and higher temperatures, and smaller immature fish predominated in shallower water and lower temperatures (Fig. 3-5).

2. Summer to early Autumn

From August to early September (Fig. 1-3) and probably also in June (Fig. 1C), the cod were concentrated on and near Hamilton Inlet Bank rather than on the seaward border of the eastern slope, and in shallower water and lower temperatures than in the spawning and immediate post-spawning period in April-May. The larger catches were generally in depth ranges of 165 - 250 m and at temperatures from -1.0 to 2.0°C and cod were usually scarce below 300 m. At the higher temperature ranges (Fig. 3B) there was a tendency for cod to be more plentiful at the shallower depths. At similar depths they were more abundant in the lower temperature ranges, most large mean catches occurring below 1.5°C and almost all below 2.5°C. At locations with significant numbers of cod in the same depth range, there was usually a decrease in fish size with increase in temperature. There was, however, little difference in size at any depths within the -1.0 to 1.4°C range. At the higher temperature ranges the scarce fish from the deep water were often on the average larger than those from the greater populations of the shallower water in the same temperature range (Fig. 3B).

3. Cod Catches in Relation to Temperature Sections

3.1 Spring. For some recent surveys temperature sections are available with the catch data (Fig. 4,5) and it is worthwhile to consider these data in detail. In the 9 April-3 May period (Fig. 4, 5A) all the large catches of 501-1000 kg and over per half hour were in temperatures of 1.8 to 3.1°C, and all the very large catches of 2001-3000 kg and over in temperatures of 2.6 to 3.0°C. Bottom temperatures adjacent in a shoreward and shallower direction to the positions of these large catches were 2 and 1°C and these would not be a barrier to cod during the feeding season. Temperatures of the water layers immediately above the large catches, however, were usually changing

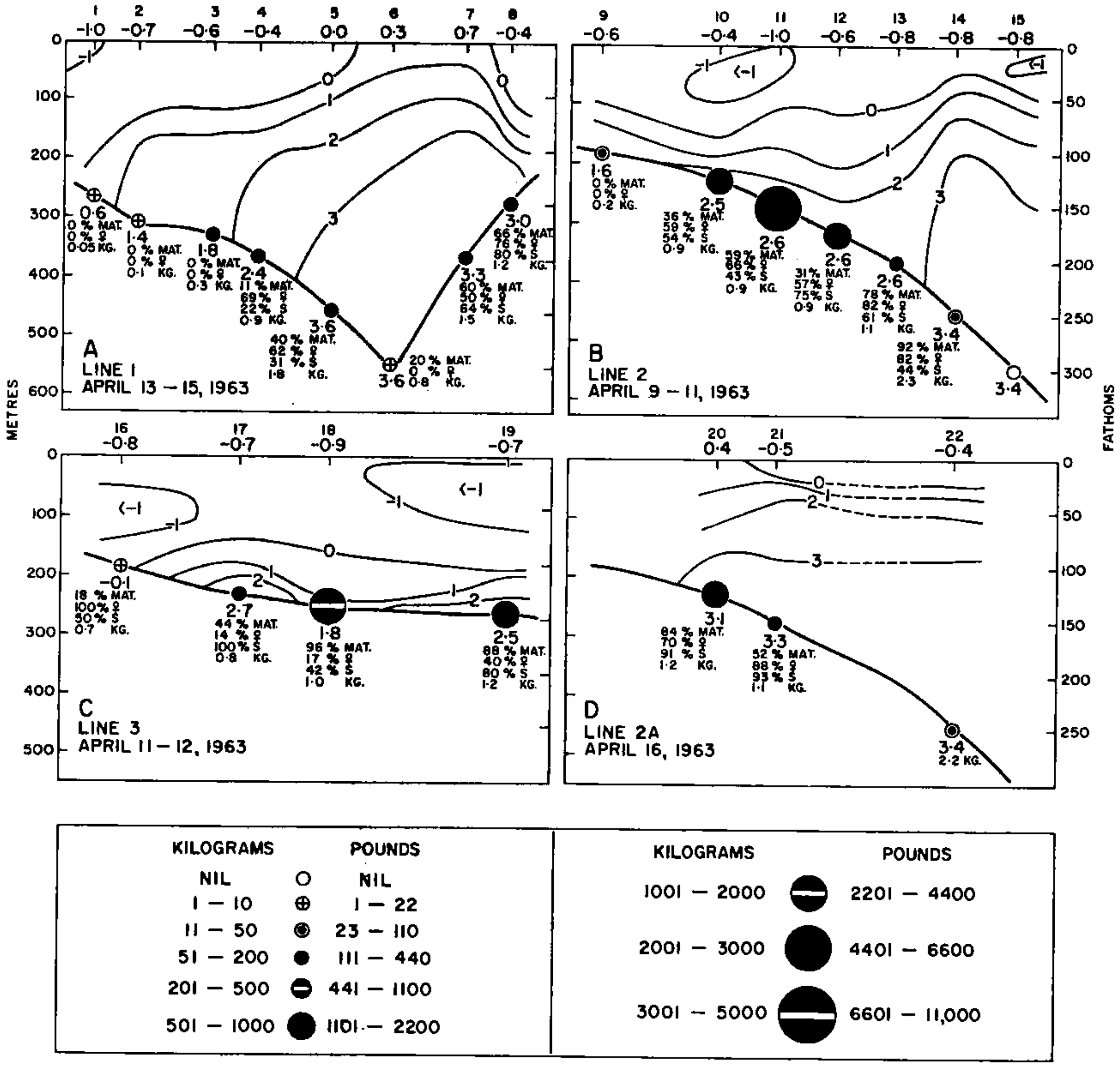
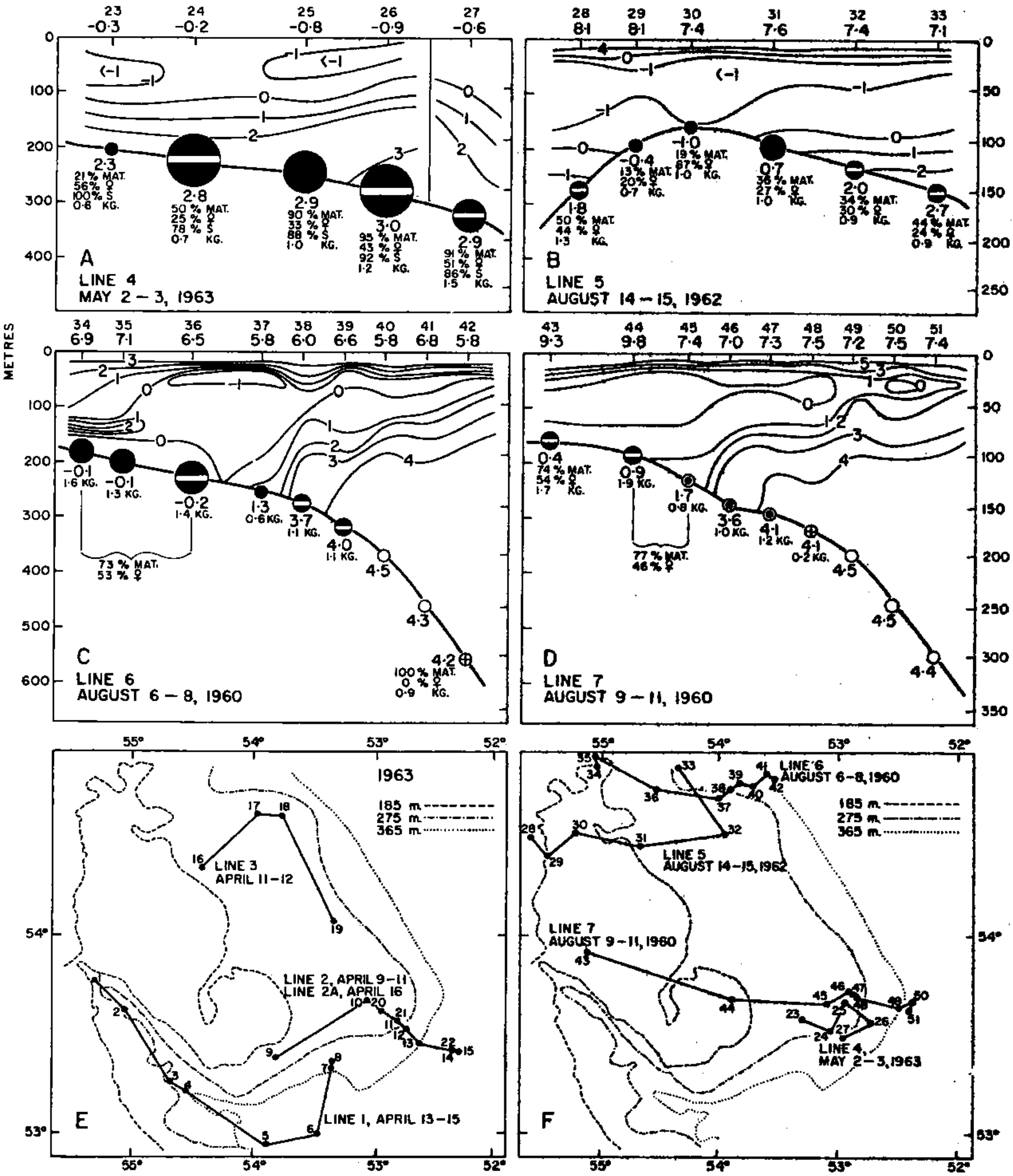


Fig. 4. Cod catches by the *A.T. Cameron* per half-hour tow on bottom in relation to temperature sections, bottom temperature °C, percentage of cod sexually mature (Mat.), percentage of females among the mature cod, percent spent (S), and average weight of the whole cod in kg. (The positions of the various lines and sets are shown in Fig. 5.)

quickly enough to 2, 1 and 0°C that movement upward may have been temporarily restricted and thus have made the cod more available near bottom. It must be remembered here that the vertical scale is greatly exaggerated and if drawn in the same proportion as the horizontal scale would only have a depth of a fraction of a millimetre. Hence the overlying isotherms were relatively very much closer together than appear in these figures. In this period the cod were feeding very little except on viscera, heads and backbones of cod being discarded by trawlers. There was no evidence from the net catches that any other food was abundant on or near bottom (Templeman, this symposium).

On 9-11 April 1963, (Fig. 4B) a large catch of cod (2,450 kg) was obtained on Line 2 in Set 11 at 275 m and 2.6°C, and a smaller catch (530 kg) at 230 m and 2.5°C. On 16 April (Fig. 4D) and in



ig. 5. Cod catches by the *A.T. Cameron* per half-hour tow on bottom in relation to temperature sections, bottom temperature °C, percentage of cod sexually mature (Mat.), percentage of females among the mature cod, percent spent (S), and average weight of the whole cod in kg. (The values of the catch symbols are shown in Fig. 4).

Set 21 at the same depth and position as Set 11, but at a higher temperature (3.3°C), only 160 kg of cod were caught. At 225 m in Set 20 at approximately the same position as Set 10 but at a higher temperature, the catch was approximately the same as in Set 10 (860 kg). In the intervening period there had been a 3-day storm of northeast wind, 35-80 km per hour, which had apparently caused upwelling of deep warm water from Hawke Channel over the shallower rim of the channel toward the north and probably caused cod to move shallower. Many European trawlers were fishing cod at and near the 275 m depth in this area on 9-11 April but by 16 April they had disappeared toward the northward apparently because of the lack of cod at the usual depths. On 2-3 May 1963, 90-100 trawlers were observed fishing the seaward tip of the southeastern slope of Hamilton Inlet Bank within a radar range of 10 nautical miles in the vicinity of the large catches shown in Fig. 1B and 5A and the large concentrations seen in the echo-sounder records (Fig. 6-8).

In the regions of heavy concentration on the southeastern slope during 9-11 April, 43-75% of the females had completed spawning, and 42-80% had completed spawning on the more northerly line on the eastern slope during 11-12 April. Spawning was proceeding rapidly since by 16 April returning to the same line southeast of the bank, 91% of the females in the only large catch were spent. In Hawke Channel to the west of Hamilton Inlet Bank only 22-31% were spent in the 2 small catches which contained mature females. On 2-3 May, on Line 4, on the southeastern part of the slope (Fig. 5A), in the same area as the fishing on 11-12 April and 16 April, 78-92% of the females were spent. In the Hamilton Inlet Bank area generally in April and May the pre-spawning mature cod were usually the largest fish. On all lines cod sizes and the percentages of mature cod, and in the areas of concentration the percentage of females among the mature cod, usually increased with depth and increasing temperatures.

3.2 August. At this time (Fig. 5B, 5C and 5D) all catches of 501-1000 kg and over per half hour were at lower temperatures (0.7 to -0.2°C) than in the spring, but smaller catches of 201-500 kg of cod were still made in deeper water at temperatures up to 3.7 to 4.0°C.

In August most cod tend to occupy shallower situations than in winter and the reasons for the concentrations are likely to be food abundance and temperature barriers. In Fig. 5B the concentration at 0.7°C at Set 31 on the eastern slope may be hindered from moving west to the shallowest water of the bank by the 0 to -1°C temperatures along the bottom. At the same time the 0 to -1°C temperatures overhead, together with the tendency at this time for the cod to move shallower, may act to trap the fish in this position and restrict their vertical movements.

In Fig. 5C the cod concentrations in Sets 34-36 at -0.2 to -0.1°C could not be restricted in position by the temperatures in the vicinity of 0°C immediately overhead. They were, however, feeding heavily on capelin which presumably caused the concentrations to accumulate and be retained in position. Similarly the smaller concentrations at 3.7 to 4.0°C in deeper water at Sets 38 and 39 were not restricted by the overhead ceiling, but may have been restricted by the rapidly declining temperatures to the west. Dispersion was restricted here also by heavy feeding on scaled lancet fish, *Paralepis coregonoides borealis* Reinhardt (Templeman, this symposium).

The largest cod in August 1960 (Fig. 5C and 5D) on the eastern slope of Hamilton Inlet Bank were in the shallowest (but still deep) water at the lowest temperatures. In August 1962 (Fig. 5B) this was also true in a limited degree for the portion of the section on the eastern slope of the bank but not for that on the western slope.

4 Echo-sounder Observations, May 2-3, 1963.

Simrad echo-sounder records were obtained during and between most of the sets shown in Fig. 1B and 5A and these reveal the distribution of fish in relation to the bottom. Figure 6 shows echo recordings made during the set at 245 m (Set 25), and afterward while steaming at 8 knots in a southeasterly direction until a depth of 300 m was recorded. In each case there are scattered recordings well off bottom with occasional heavy concentrations showing near bottom. Figure 7 gives the picture between 200 and 230 m, or between Sets 23 and 24 of Fig. 5A. Here fish are observed to be very close to bottom all along the recording to a depth of approximately 220 m. At this point the fish appear to be moving off bottom, and for the remainder of the trace are seen to hold this depth, although the bottom drops away to 230 m. A set was made at this point (Set 24 in Fig. 5A) and the resulting echo recording shown in Fig. 8. Some heavy patches are seen close to bottom, with concentrations off bottom also in about 220 m. Figure 8 also shows the echo recording made while steaming between Sets 24 and 27, *i.e.* from about 230 to 310 m. Here we see that fish are beginning to leave bottom between 260 and 280 m, remaining mainly in this depth range as the bottom falls away.

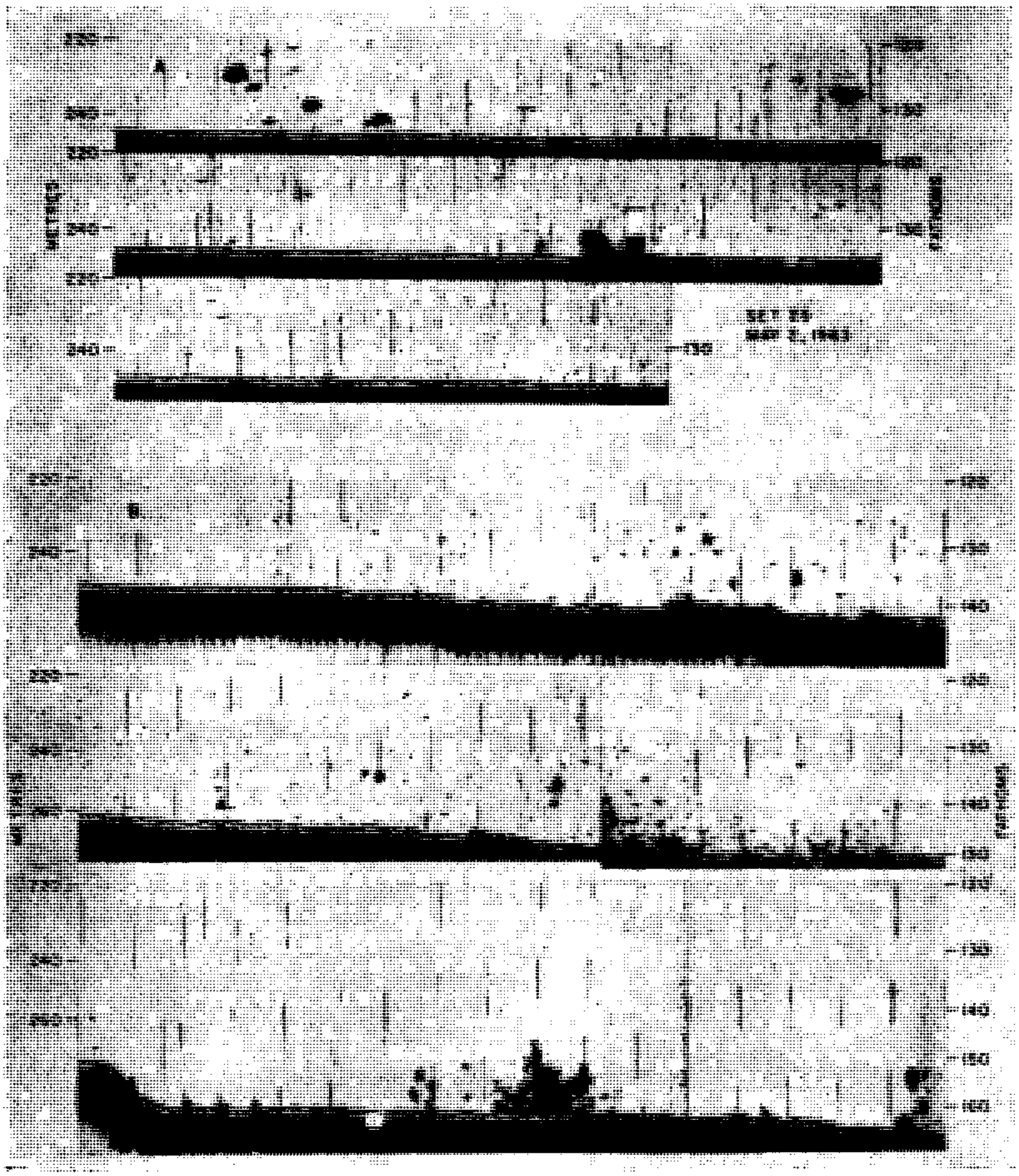


Fig. 6. Simrad echo-sounder records (A) during Set 25 (Fig. 5A, 5F) at 3.5 knots and (B) while steaming to the southeast at 8 knots from the end position of Set 25 to the 300 m contour, 2 May, 1963. The cod catch in Set 25 was 2560 kg per half-hour tow at a depth of 245 m.

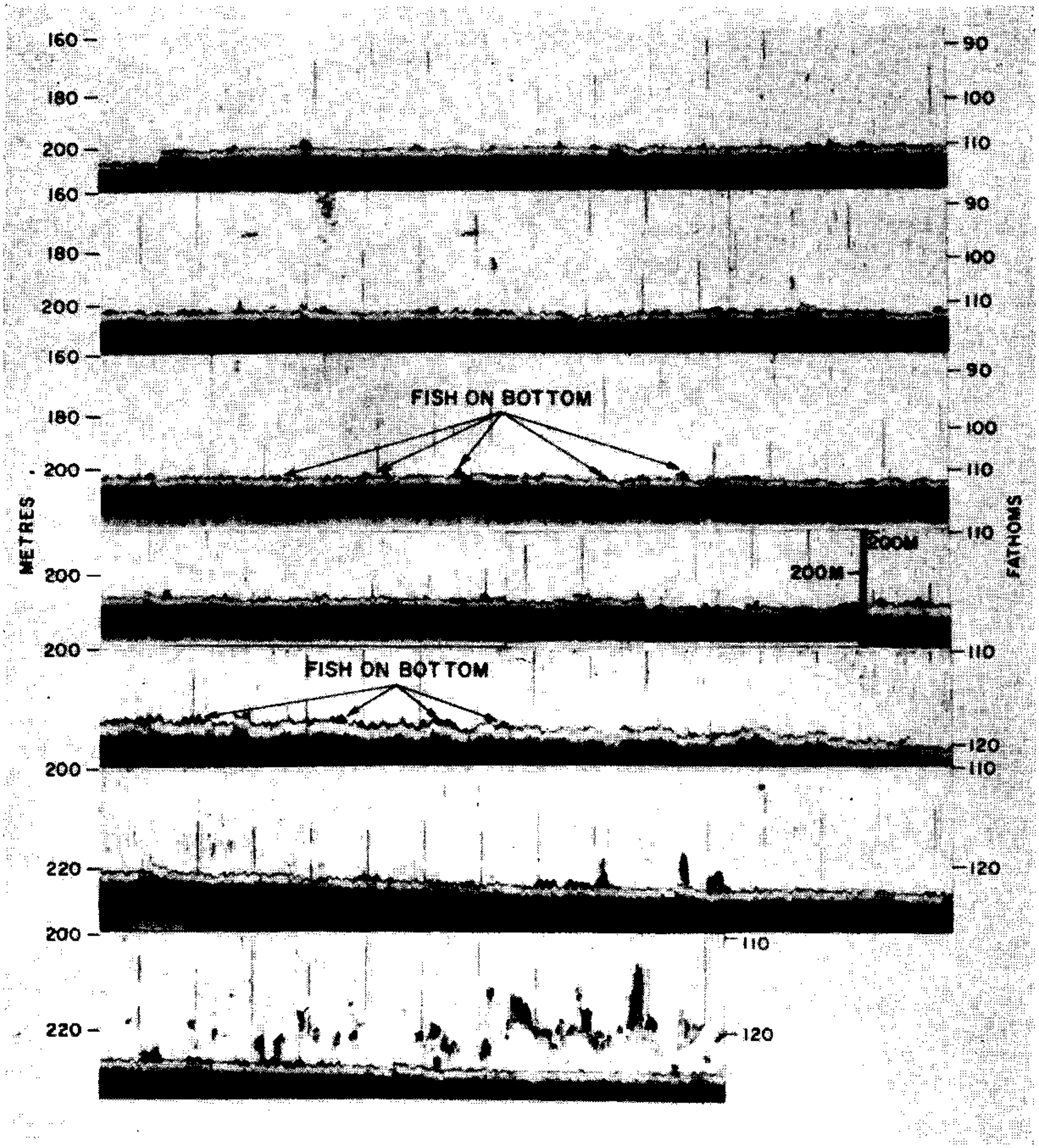


Fig. 7. Simrad echo-sounder record made while steaming at 10 knots between Sets 23 and 24 (Fig. 5A, 5F), 3 May, 1963. The cod catches per half-hour tow in Sets 23 and 24 were 140 kg and 4830 kg respectively at depths of 205 and 225 m.

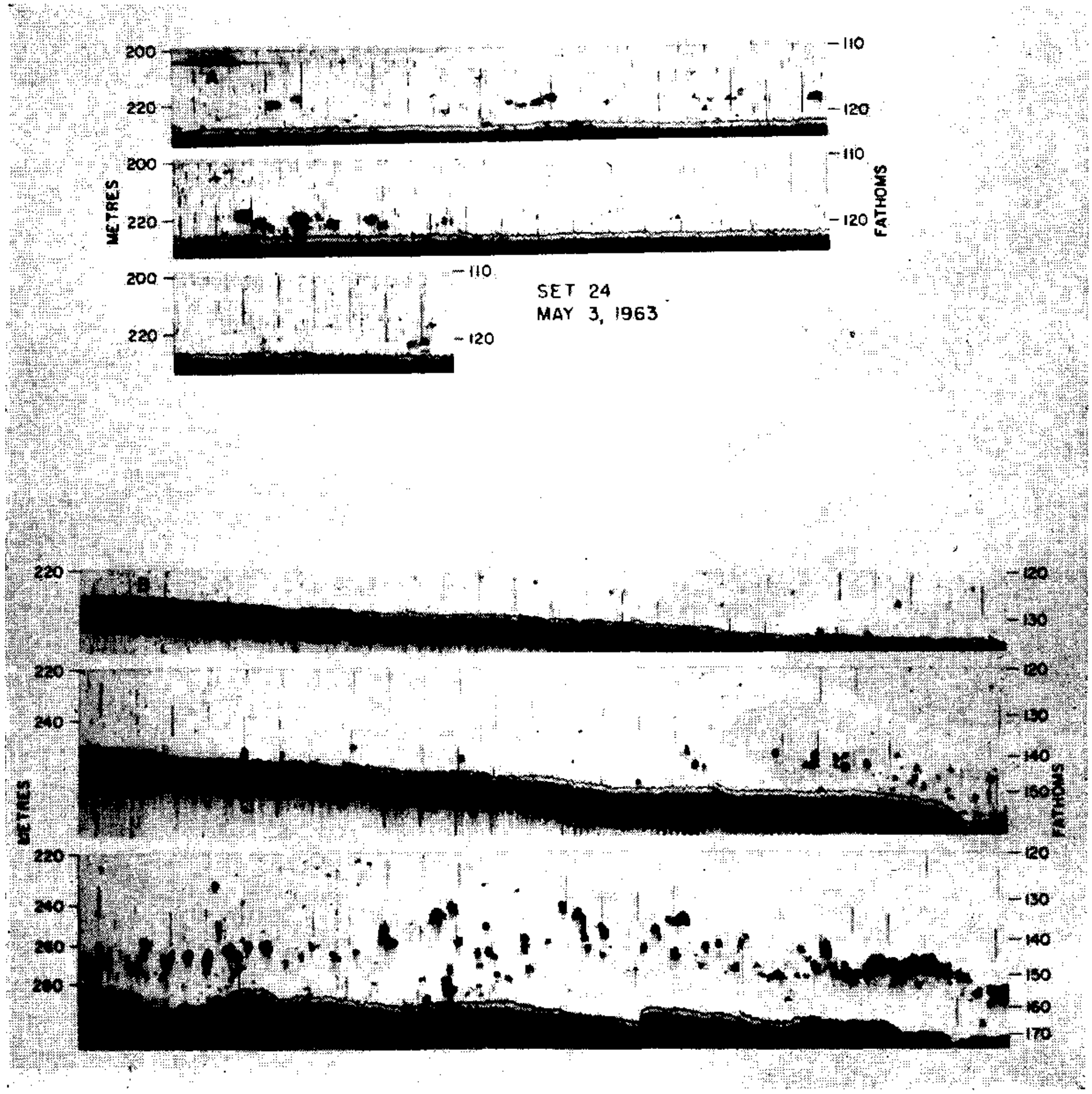


Fig. 8. Simrad echo-sounder records (A) during Set 24 (Fig. 5A, 5F) at 3.5 knots and (B) while steaming at 10 knots between Sets 24 and 27, 3 May, 1963. The cod catches per half-hour tow in Sets 24 and 27 were 4830 kg and 1590 kg respectively at depths of 225 and 330 m.

Fish can also be seen close to bottom as a thickening of the bottom line, as well as scattered between 220 and 260 m. The echo sounder was also used to search for cod in the surface layers, but none were found. Several attempts to jig cod at various depths in the upper 50 m were likewise unsuccessful.

There would thus appear to be two centres of abundance among the cod distributed along the edge of the bank, one represented by Set 24 (223 m) and the other by Set 26 (278 m). In each case there is a tendency for the fish to be distributed off bottom, beginning at about 220 m for the former group and 260-280 m for the latter. The reason for these two centres of abundance is illustrated in Fig. 9, which shows a marked correlation between depth and size of fish in the catch. In fact the fish can be separated on the basis of size into two distinct groups, one consisting mainly of fish less than 40 cm long (Sets 23 and 24) and the other of fish greater than 40 cm long (Sets 25-27). From the echo-sounder recordings it is apparent that both these groups are beginning to move off bottom at about the same time.

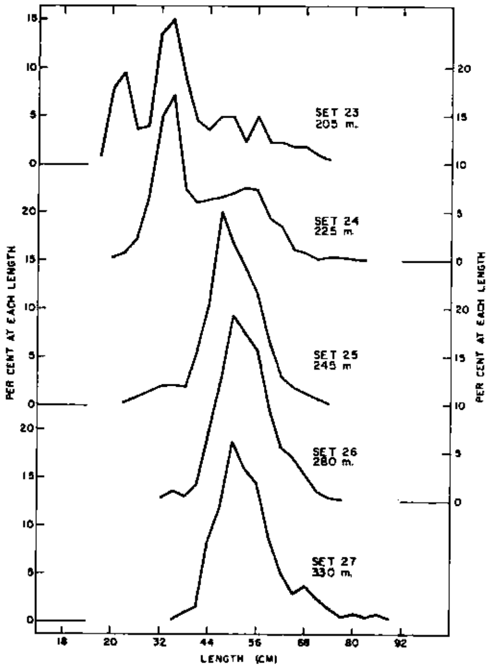


Fig. 9. Length frequencies by depth of cod taken on the southeastern slope of Hamilton Inlet Bank, 2-3 May,1963. Set positions are shown in Fig. 1B and 5F.

The off-bottom movement is probably related to a subsequent migration inshore as described by Templeman and Fleming (1956) for the Bonavista area. Since these are post-spawning concentrations (though many immature fish are also present at the shallower depths) this upward movement probably begins as a search for food, the bulk of the mature fish having completed spawning. In this area however, natural food appeared very scarce, and occasional examination of stomachs showed that the only significant food item was cod offal. More than 90 vessels were fishing in this area at the time and these of course were the source of the offal. It is possible that without this source of food the cod might have already dispersed and the very fact that trawlers were fishing in the area helped to keep the concentration intact. Certainly there were no temperature barriers to prevent horizontal dispersion. Eventually, many or most of these cod would presumably find their way inshore in time for the inshore fishery which in southern Labrador begins toward the end of June.

On 29 July, 1951 a large pelagic cod school was found by the *Investigator II* close to shore near Seal Islands, Labrador (Fig. 10). Temperatures were 7.3°C at the surface, 5.5°C at 25 m where the fish were located and -1.10°C near bottom at 50 m. These mid-water cod at 25 m, probably just above the thermocline, were jigged from the *Investigator II* as fast as they could be pulled in.

5. Notes on the Inshore Labrador Cod Fishery

In the Strait of Belle Isle the fishery is carried out by trap, linetrawl, and jigger (although a few gillnets are also in use) and begins about mid-June. The fishery in southern Labrador is carried on almost entirely by trap and jigger, beginning during the last week of June and the first week of July. The fishery in northern Labrador is almost entirely an Eskimo handline fishery, with some traps in the Nain area, and begins about mid-July. In former years fishing was carried on in the far north beginning late July to early August. The fishery goes on to about October in most areas, generally by means of handline.

Traps are set in depths of 10-30 m. Recorded bottom temperatures at these depths during 1959-62 ranged from 6.3 to -0.8°C. Surface temperatures at the same time ranged from 4.2 to 14.5°C. Temperatures recorded in July and August while jigging fish in depths of 7-70 m, ranged from 8.7°C at the former depth to -1.1°C at the latter. Fish seem to jig best in fairly high temperatures (about 4 to 9°C). The cold intermediate layer is close to the surface in inshore Labrador in early and mid-July, temperatures below 0°C being encountered at about 15-18 m.

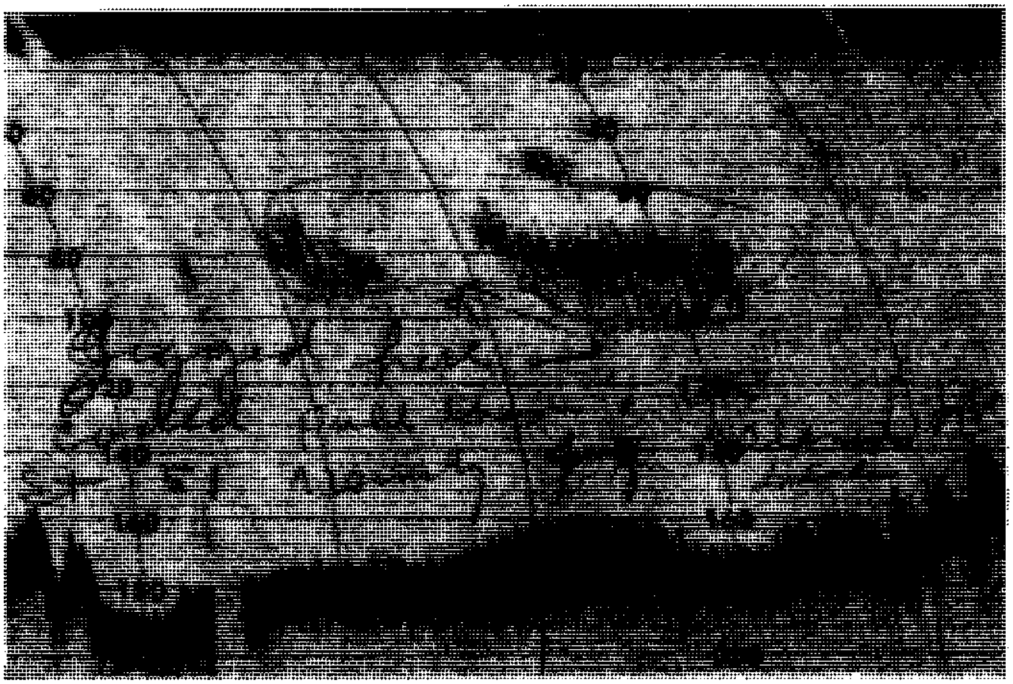


Fig. 10. Echo-sounder record of a pelagic school of cod (circled area) close to shore at 53°14'N, 55°39'W near Seal Islands, Labrador on 29 July 1951. (The echo-sounder record is in feet. 1 ft = 0.3 m. The handwritten comments were entered on the record at sea).

. Additional Autumn Data

In April our small catches and the absence of the fishing fleet indicate no concentrations of od in Hawke Channel and on the northern border of this channel west and southwest of Hamilton nlet Bank. However, in the autumn there is some evidence of cod concentrations here although not early as great as the winter-spring concentrations on the eastern slopes of this Corlett nd Ramster (MS,1963) report that in a cruise of the *Ernest Holt* to Labrador from 22 November to December 1962, a good catch of 1,510 kg of cod was obtained in the channel northwest of Hamilton nlet Bank at about 55°20'N 56°30'W in 210-220 m at 2.5°C. In this same cruise on the southwestern lope of Hamilton Inlet Bank (the northern slope of Hawke Channel) at about 53°27'N (reported as 5°27'N in the MS), 54°40'W the best catch of cod was over 1,540 kg per hour in 310-365 m with verage catches of 1,040 kg per hour in 300-375 m. Bottom temperatures were about 3°C. Eight arge trawlers were fishing in this area. Most of the cod were feeding on the pelagic amphipod, *hemisto*, with some shrimp, *Pandalus*, and spider crabs, *Chionoecetes*.

In a cruise of the *A.T. Cameron* on the southern Labrador Shelf in September 1963 (too late to e included in detail in the figures and text of this paper) covering depths where available from ess than 180-730 m, the best catch of cod (1,420 kg per half hour) was obtained on 15 September t 295 m, 1.4°C at 53°20'N, 54°29'W. This position is close to the area of Hawke Channel south-est of Hamilton Inlet Bank where the *Ernest Holt* obtained similar catches in late November,1962.

On the southeastern slope of Hawke Channel in the same general area as in April (Fig. 4E, ine 2) the only significant catches of cod were 480 kg and 690 kg at 220 and 271 m, 3.1° and 3.7° . Also in this cruise on 11-12 September on the northeastern slope of Hamilton Inlet Bank, in a ine from 54°51'N,55°04'W to 54°51'N,53°22'W and depths ranging from 192 to 805 m the best catch of od (690 kg) was in the shallowest set at 192 m and 0.6°C.

Also in October in a brief survey along a line from 53°58'N,55°04'W to 53°19'N,54°22'W from 54 m (-0.5°C) to 284 m (0.9°C) and extending from the top of the southern half of Hamilton Inlet ank to Hawke Channel the best catches of cod (1,600, 2,325 and 1,770 kg per hour) were on top of the bank in the southern quarter at 161, 168 and 165 m at 1.3, 1.1 and 0.4°C. At 53°32'N, 54° 40'W on 6 October in 146 m, where the *A.T. Cameron* obtained 1,720 kg of cod in an hour's dragging (0.5°C), 40-50 European trawlers were fishing in the neighbourhood. Again on 8 October in the general area of 53°25'N, 54°15'W at 152-174 m, with catches by the *A.T. Cameron* of 710, 210 and 1,340 kg of cod per hour (1.0 to 1.7°C), 22 European trawlers were observed in a radius of 6 nautical miles on the radar. Most of the cod on the plateau of the bank, at moderately low temperatures in this October cruise, were feeding heavily on capelin.

DISCUSSION AND CONCLUSIONS

Lee (1952), for the Bear Island area, found that in May and June the greatest otter-trawl catches were at bottom temperatures between 3 and 5°C, in August-November between 3.5 and 4°C and in winter between 1.75 and 3°C. The lower limit of 1.75°C for good catches applied to the area west of 21°E, and east of this meridian paying catches were taken in the summer months at temperatures as low as -0.3°C. No cod were taken at bottom temperatures below -0.6°C. These fish were feeding heavily on capelin and krill whereas those concentrated at higher temperatures west of this meridian were either feeding lightly to moderately or not feeding.

Thompson (1943) obtained the greatest otter-trawl catches of cod on the southern Grand Bank, February-May, 1934-36, between 0 and 6°C. In early autumn, 1935, large catches of cod were obtained on the eastern and northeastern Grand Bank at temperatures from -0.5 to 0.2°C. In the 1931 research cruise a few cod were captured at as low a temperature as -1.6°C. Whiteley *et al.* (1932) in otter-trawl hauls in the coastal area of Newfoundland and Labrador, August-September 1931, found cod most plentiful at temperatures above 3°C.

Martin (1961) found January otter-trawl research vessel catches of commercial-sized cod in the southwestern Gulf of St. Lawrence and in the Laurentian Channel off Cape Breton concentrated between 180-230 m at bottom temperatures of 2 to 4°C. In the same month very small cod (0 and 1 age-groups) were still present in their summer locations in the shallow water in the Gulf of St. Lawrence at a bottom temperature of -1.5°C. Medium-sized cod of about 40-70 cm were caught in approximately equal quantities at depths from 27 to 230 m and temperatures from 0 to 4°C in May, and in 27 and 110 m at 3 to -1°C in June. In autumn these medium-sized cod were mainly in 90-130 m at 0 to 1°C while smaller cod at this time were mainly in shallow water at 6 to 8°C. Again Martin (1963) in the winter and early spring of 1962 found cod of commercial size in the southwestern Gulf of St. Lawrence in deep water, 145-230 m, along the western edge of the Laurentian Channel with the largest catches off Cape Breton at 1 to 3°C.

Pechenik and Noskov (1962) say that in the early part of 1961 cod occurred in stable concentrations and were fished successfully on the southeastern slopes of Hamilton Inlet Bank at depths of 285-360 m and temperatures of 3 to 3.75°C. Noskov *et al.* (1963) report dense shoals of post-spawning cod in April 1962 with catches of 4-6 tons per hour's trawling between 59° and 58°N on the northern Labrador Shelf at 400-500 m. In Division 2J in the spring of 1962 day-time catches were smaller than at night, the cod being off the bottom in the day-time feeding on planktonic organisms and near bottom feeding on benthic forms at night.

McKenzie (MS, 1951) found good cod catches with line gear over a wide range of bottom temperatures in the Nova Scotian and New Brunswick coastal areas: at Shelburne, 2 to 9°C; at Cape Breton, 0 to 6°C with a good catch also at 16°C; and at Halifax Harbour (in reported fishing) 0.25 to 11°C with two fairly good catches at 13.5 and 15.0°C. In this area the largest cod were taken at intermediate temperatures with smaller cod at the highest or lowest temperatures. The jig was much more effective than baited hooks at the high temperatures. Also in experimental line trawling off Halifax good catches were made in 1932 between 0.5 and 4°C with decreases above 4°C, and in 1932 good catches at 1 to 6°C with a decline in catch and more catch failures after 5°C but with a good catch also at 10 and at 12°C. A sudden influx of warm water (a sudden rise from 7 to 15°C at Halifax and 5 to 14°C at Shelburne) reduced successful line fishing in the shallower water to a near zero catch, but good fishing could be obtained in deeper and cooler water beyond the over-warmed area.

Rasmussen (1950, 1952) described fishing at Spitzbergen, Bear Island and West Greenland as profitable for Norwegian longliners only where bottom temperatures were 2°C or higher. Rasmussen (1954, 1955) for the pelagic longline fishery in Holsteinsborg Deep in West Greenland found the greatest catches of cod below the thermocline. In 1953 the greatest catches were between 100 -

35 m at a temperature of 2.2 to 2.3°C and in 1954 at 120-140 m at temperatures of 0.8 to 0.9°C.

Templeman and Fleming (1956, 1963) found that good bottom longline catches, in deep water of 00 m and deeper off the east coast of Newfoundland and Labrador in May-November, generally occured when there was a temperature of at least 0.1 to 0.5°C at one end of the longline. Catches were till of commercial quantity when the longline was in the range of temperatures from 0.6 to 1.0°C t one end to 2.1 to 2.5°C at the other. In the cold water layer at intermediate depths cod catches ere usually low when the bottom temperature was below -0.5 and extremely low at -1.5°C. In the inhore shallow water layer commercial catches were obtained at temperatures from 0 to 4°C.

Tremblay (1942) in experiments with a lognline set at different bottom temperatures from 1 to °C in Bay Chaleur of the Gulf of St. Lawrence found the greatest catches at 8°C. Catches rose at irst gradually and then rapidly from 2 to 8°C and declined rapdily from 8 to 9°C. Catches at 4 nd 9°C were only about one-fifth those at 8°C.

In the Newfoundland and Labrador inshore area large quantities of cod are caught in cod traps et close to the shore in depths usually of 18-37 m but sometimes less, especially in Labrador. leggs (1931) at Raleigh, at the northern tip of Newfoundland, found the best catches in cod traps o occur in July at temperatures between 8 and 10°C.

Thompson (1943) says that in 1934, owing to the prevailing high-water temperatures of 8 to °C in the coastal region from Trinity Bay to Cape Race, the inshore trap fishery yielded poor reults but that farther north—*e.g.* at Fogo—the water was colder (2 to 3°C at a depth of 25 m) nd an excellent trap fishery resulted. On the east side of the Strait of Belle Isle the water as of the usual high temperature (8 to 9°C) and the trap fishery was the best for many years. At ay Bulls, near St. John's, a group using 4 deep cod traps obtained 2,000 quintals of cod in 1932, ,000 in 1933 and 500 in 1934, with July and August temperatures in these years of 1.5 and 2.0°C, .3 and 4.7°C and 6.5 and 6.2°C. These temperatures were at 25 m (approximately the mid-depth of he trap) and bottom temperatures would have been lower. Apparently, as mentioned by Thompson, in n area with temperatures usually high in summer, such as the eastern side of the Strait of Belle sle, trap catches are successful at high temperatures. Where temperatures in 18-37 m are usually ow in summer, as on the east coast of Newfoundland, a rise of several degrees beyond the usually ow temperature may greatly reduce the trap catch.

Rasmussen (1955), in recording the largest catches of Norwegian longlines in pelagic fishing n Holsteinsborg Deep at 2.2 to 2.3°C in 1953 and at 0.8 to 0.9°C in 1954, says that the cod are pparently not attracted by the temperature but by the large quantities of food organisms such as apelin and sandeels existing below the thermocline.

Our Labrador data add to the evidence that cod in winter go deeper to higher temperatures and ccumulate in large pre-spawning, spawning and post-spawning masses not necessarily in areas with a lentiful food supply. In our sets these temperatures were 1.8 to 3.1°C and for very large catches .6 to 3.0°C. The Labrador area does not have very high temperatures in the slope water, the highst in most years being below 4°C. The offshore movement of these cod seems to be instinctive and e great mass of these mature fish appear to move for spawning as far away from the coast as posible to the seaward slope of the continental shelf. To the west, in an area of Hawke Channel west f Hamilton Inlet Bank and closer to the coast where there are often abundant cod in the autumn, ery few cod were found in depths and temperatures which would have been suitable in summer and the ew cod present were small and mainly immature.

The cod which proceed inshore to the shallow waters near the coast are found in late June-July t varying temperatures, usually above 0°C, and are often plentiful at temperatures considerably igher than any to be found in the deep slope water where they spend the winter and spring. In the ummer and early autumn the greatest masses of offshore cod are on or close to Hamilton Inlet Bank t shallower depths and lower temperatures than in winter, and when great concentrations are enountered they are usually feeding on capelin. Other smaller concentrations in deeper water of igher temperature on the eastern slope are feeding on fish inhabiting these warmer waters. In the e year investigated this was chiefly the scaled lancet fish *Paralepis coregonoides borealis*.

The late autumn concentrations in Hawke Channel and on the southwestern slope of Hamilton Inlet ank, at higher temperatures similar to those at which the spawning cod are found in spring, may be ginning to gather for movement eastward to form pre-spawning concentrations along the northern lope of Hawke Channel and the eastern slope of Hamilton Inlet Bank.

Many of these cod of the offshore spawning area are known from tagging results (Sidorenko and Postolaky, MS, 1963, and unpublished data of the St. John's Station) to be, in summer, coastal (inshore) cod of Labrador and the northeast coast of Newfoundland. On the Labrador coast these cod arrive in quantity in the shallow water near the southern coast of Labrador in late June to early July and progressively northward along the coast to late July and early August in northern Labrador.

The echo-sounder records and the failure to jig cod in the surface layers in early May indicate that the fish at this time are not in the shallow water surface layer, in which they live while inshore, but there is a great amount of vertical migration which may be preliminary to presumably pelagic coastward movement.

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REFERENCES

CORLETT, J. and J. RAMSTER. MS, 1963. United Kingdom investigations in Subareas 2 and 3, November-December 1962. *Annu. Meet. int. Comm. Northw. Atlant. Fish.* 1963, Doc. No. 30, Ser. No. 1101: 1-7.

LEE, A.J. 1952. The influence of hydrography on the Bear Island cod fishery. *Rapp. Cons. Explor. Mer*, 131: 73-102.

MARTIN, W.R. 1961. Canadian research report, 1960. B. Subareas 4 and 5. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 11: 31-37.

1963. Canadian research report, 1962. B. Subareas 4 and 5, biology. *Int. Comm. Northw. Atlant. Fish. Redbook* 1963, Part II: 14-21.

MCKENZIE, R.A., MS, 1951. Cod and water temperature. *Fish. Res. Bd. Canada, MS. Rep. Biol.Sta.*, No. 435: 1-23.

NOSKOV, A.S., G.P. ZAKHAROV and I.N. SIDORENKO. 1963. USSR research report, *Int. Comm. Northw. Atlant. Fish. Redbook* 1963, Part II: 79-101.

PECHENIK, L.N. and A.S. NOSKOV. 1962. USSR research report, 1961. *Int. Comm. Northw. Atlant. Fish. Redbook 1962*, Part II: 128-139.

RASMUSSEN, BIRGER. 1950. Notes on the fishery and bottom temperature in the Barents Sea. *Ann. Biol. Cons. Explor. Mer*, 6: 9-11.

1952. Sea temperatures and the cod fishery. *Ibid.*, 8: 30-32.

1954. On the Norwegian pelagic long-line fishery in the Holsteinsborg Deep -1953. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 4: 40-45.

1955. Norwegian research report for 1954. Notes on the composition of the catch by Norwegian long-liners off West Greenland, 1954. *Ibid.*, 5: 43-49.

SIDORENKO, I.N. and A.I. POSTOLAKY., MS, 1963. First results of cod migration studying obtained by means of tagging by the Polar Research Institute of Marine Fisheries and Oceanography (USSR). *Annu. Meet. int. Comm. Northw. Atlant. Fish.*, 1963, Doc. No. 60, Ser. No. 1131: 1-10.

SLEGGS, G.F. 1931. A study of the relation of cod-fishery to water temperature at Raleigh, Newfoundland, 1929. *Ann. Rep. Nfld. Fish. Res. Comm.*, 1(4), App. C: 1-8.

TEMPLEMAN, WILFRED. Some Instances of Cod and Haddock Behaviour and Concentrations in the Newfoundland and Labrador Areas in Relation to Food. *This symposium Contribution No. C-3.*

TEMPLEMAN, WILFRED and A.M. FLEMING, 1956. The Bonavista Long-lining Experiment, 1950-1953. *Bull. Fish. Res. Bd. Canada*, 109: 1-55.

1963. Longlining Experiments for Cod off the East Coast of Newfoundland and Southern Labrador, 1950-1955. *Ibid.*, 141: 1-65.

THOMPSON, HAROLD. 1943. A biological and economic study of cod (*Gadus callarias* L.) in the Newfoundland area. *Res. Bull. (Fish.) Nfld. Dept. Nat. Resources*, 14: 1-160.

TREMBLAY, JEAN-LOUIS. 1942. La pêche de la morue et la temperature d'eau de mer. *Fish. Res. Bd. Canada, Prog. Rep. Atl.*, 33: 7-9.

WHITELEY, G., S.T. LINDSAY, and H. THOMPSON. 1932. Cod Investigations. *Ann. Rep. Nfld. Fish. Res. Comm.*, 1 (4): 47-61.

A-7

ABOUT POSSIBLE FISHING/TEMPERATURE OF WATER RELATIONSHIP[1]

By

Orestes Cendrero[2]

ABSTRACT

A note on a possible fishing/temperature of water relationship in the Grand Bank area was submitted to the Thirteenth Annual Meeting of ICNAF as part of the Spanish Research Report. This paper gives a more detailed description of the observations used in that report. They were made from a Spanish pair trawler in February-April 1963 and it is argued that these preliminary observations indicate that a satisfactory relationship might not be found.

MATERIAL AND METHODS

Temperatures were recorded by the means of a Negretti & Zambra reversing thermometer fixed on a Nansen bottle. Water samples were not collected for salinity.

The thermometer was cast immediately after the haul, as the fish were being taken on board the ship and the latter was standing still, provided weather and other conditions allowed.

All observations took place aboard the commercial pair trawler *Playa de Ondarreta* throughout February, March and the first half of April 1963. Weather made it impossible to make observations every day, and on many days only once a day.

RESULTS

Table 1 summarizes all the temperatures recorded, the fish caught in each haul in kg per hour, and the dates and zones where the observations were made. The quantities of fish include both stored and discarded fish and are those of cod only.

The table shows that temperatures ranged from 1° to 5° C, except for the 8.5°C recorded on 26 March. Probably the temperature was not that high on that day, and maybe a wrong working of the thermometer gave an incorrect reading, but it could not be checked.

Although it may be a little premature to say so, a relationship between the temperature at the bottom and the quantity of fish caught is not likely to exist, or at least does not seem to exist from the observations carried out.

The following fact, which happened fairly often, makes us think so. When the trawl was dragging no fish were detected, either by the loop or by the echosounder. Nevertheless, after a normal tow (about 4·hr) a catch of 50 or 60 baskets was hauled in, *i.e.*, some 8-10 metric tons. Since this catch was a good catch the skipper had the net shot again to drag along the same place, steaming the other way about. After three or four more hours towing, just 2 or 3 baskets were caught. No fish were detected in either case. The gap between the two hauls had not been longer than 2 hr, not enough for the temperature to change significantly, and in fact it had not (*e.g.*, 9 March).

Why was there no good catch in the second haul? Why was there a good catch on one day and not on the following day at the same place, the temperatures being about the same? In our opinion, there are many other and more significant factors which determine the occurrence of cod.

No doubt cod like other animals have a range of temperatures in which they are at ease. But this range must be rather wide and we do not think that cod would move even a little distance from a place because of being subjected to a wide variation of temperature within the range if there were other reasons such as spawning zone, occurrence of food to make them stay. On the other hand, a preferred temperature would not mean necessarily the presence of cod if other

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preferred conditions were lacking.

TABLE 1. COD CATCH AND BOTTOM TEMPERATURE.

Date	Position	ICNAF Division	Bottom temperature (°C)	Total catch (kg)	Catch (kg/hr)
Feb.					
4	46°05'N-57°05'W	3Ps	1.2	9,760	1,956
5	46°21'N-57°11'W	3Ps	1.5	3,667	1,048
9	46°05'N-57°10'W	3Ps	2.0	2,445	652
14	43°45'N-59°15'W	4W	2.5	12,388	2,751
17	43°55'N-59°04'W	4W	3.0	10,269	2,738
23	43°35'N-60°47'W	4W	3.0	35,448	6,445
27	43°25'N-60°45'W	4W	2.8	1,630	466
28	43°21'N-61°12'W	4W	3.2	7,335	2,256
Mar.					
3	43°18'N-61°15'W	4W	1.8	5,705	1,630
5	43°19'N-61°17'W	4W	0.8	163	50
6	43°25'N-61°20'W	4W	5.0	31,296	13,765
9	43°27'N-61°37'W	4W	2.3	35,406	10,894
9	43°27'N-61°37'W	4W	2.3	6,601	2,031
10	43°31'N-61°34'W	4W	2.4	978	326
10	43°09'N-61°42'W	4W	5.8	25,917	7,405
11	43°30'N-61°95'W	4W	0.8	3,952	1,317
12	43°25'N-61°40'W	4W	2.2	5,868	1,805
12	43°25'N-61°40'W	4W	3.2	20	13
16	43°37'N-60°50'W	4W	2.1	2,445	611
18	43°28'N-61°40'W	4W	3.2	1,956	434
19	43°28'N-61°40'W	4W	3.6	4,025	1,254
19	43°28'N-61°40'W	4W	2.2	6,520	1,373
20	43°28'N-61°40'W	4W	4.0	5,216	1,159
21	43°27'N-61°48'W	4W	2.2	10,595	2,119
26	43°05'N-61°52'W	4W	8.5	1,304	348
28	44°29'N-59°40'W	4Vs	1.6	5,064	2,532
30	44°03'N-58°50'W	4Vs	1.0	4,890	931
31	44°27'N-59°16'W	4Vs	1.0	3,260	1,630
Apr.					
3	44°00'N-59°03'W	4Vs	3.4	9,880	2,821
4	43°40'N-60°10'W	4W	3.6	2,758	788
5	43°44'N-59°28'W	4W	2.7	5,705	1,426
6	44°00'N-59°09'W	4W	2.1	40,750	13,583
6	44°00'N-59°09'W	4W	1.8	8,350	1,965
7	44°01'N-59°07'W	4W	2.7	3,260	1,087
8	44°05'N-59°12'W	4W	1.8	2,445	611
8	44°03'N-58°53'W	4Vs	0.9	47,825	27,368
8	44°03'N-58°53'W	4Vs	1.2	3,260	1,304
12	43°57'N-58°49'W	4Vs	2.0	3,260	815
13	43°59'N-59°06'W	4W	2.0	2,495	998
16	43°26'N-61°30'W	4W	3.7	16,855	9,631
17	43°21'N-61°35'W	4W	4.8	27,710	7,389
18	43°25'N-61°35'W	4W	4.2	14,355	3,854
18	43°31'N-61°33'W	4W	4.2	5,379	1,289

Vertical migrations of cod support this theory. Cod rise to near the surface at night, and also when there is capelin *(Mallotus villosus)* about despite the fact that temperatures at the surface are quite often 2° or 3°C higher than those at the bottom.

A final reason for having obtained a poor catch where just a few hours before 8 or 10 tons were caught, may be that the trawl frightened the fish and they swam away to a safer place.

Other Spanish workers (Rodriguez Martin & Lopez Costa, 1954; Rodriguez Martin & Rojo Lucio, 1953; Rodriguez Martin, 1956) have given a very small range of temperatures for cod, defining practically what could be called a "cod temperature". We believe the latter cannot be defined so exactly and that, if it exists, it ranges from 1° to perhaps 8° or 10°C. Further observations will be made to assess this point.

REFERENCES

RODRIGUEZ MARTIN, O., R. LOPEZ COSTA. 1954. Report on the cruise carried out by the Spanish vessel *Vendaval* in the waters off Newfoundland, February-April 1953. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 4 : 49-54.

RODRIGUEZ MARTIN, O., A. ROJO LUCIO. 1955. Report on the cruise by the Spanish trawler *Mistral* in the waters off Newfoundland, June-July 1954. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 5 : 51-57.

RODRIGUEZ MARTIN, O. 1956. Report on the cruise by the Spanish vessel *Cierzo* in the waters off Newfoundland, June-July 1955. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 6 : 55-57.

A-8

DISTRIBUTION OF HADDOCK ON THE GRAND BANK IN RELATION TO SEASON, DEPTH AND TEMPERATURE[1]

By

Wilfred Templeman and V.M. Hodder[2]

CONTENTS

ABSTRACT

Haddock on the southwest Grand Bank spend late winter and early spring in the deep water of the southwest slope, usually between 120-275 m (65-150 fathoms) and at temperatures mainly between 2.5 and 9°C in the more central rather than the northern and southern extremes of the slope. By April the haddock tend to move shallower toward the plateau of the bank. This movement continues in May and in summer, the rate of progression onto the bank depending on the presence of temperatures usually approaching or beyond the 2°C level. Apparently the winter and early spring movement of haddock to warm deep water is necessary to escape the low temperatures of the water over the plateau of the bank but, also, must be partly due to a natural tendency to go deeper at this time because they usually descend deeper than is necessary to escape the low temperatures of the shallower water. Similarly the April-June movement to shallower water at first usually places the haddock in colder water than that in which they spent the winter. This, also, is therefore a natural movement not necessitated by changes in deep water temperatures.

The movement toward shallow water begins before spawning which occurs chiefly in May and June, and the direction of movement to summering areas on the bank is generally northeastward and eastward, agreeing with the distribution of the warmer water.

There is doubtless some pelagic movement over cold water which seems to account for the occasional large early-summer northwestward migration to the east coast of Newfoundland.

The greatest concentrations in summer are in the shallowest area of the southern part of the bank, the Southeast Shoal. When the haddock population is large very great quantities are concentrated on this shoal in the vicinity of capelin spawning grounds where they feed on capelin eggs and capelin.

The movement to shallower water which occurs in April-June is also usually a movement to colder water but with occasional exceptions the larger quantities are in temperatures of close to 2°C and

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over. Later in the year and in warm years, temperatures are higher and haddock concentrations are at higher temperatures.

The cold tongue of water from the eastern branch of the Labrador Current extends as a bottom or intermediate layer, strongly in some months and years and weakly in others, westward along the southwest slope of the bank. The area of bottom occupied by the cold tongue may be shallower or deeper than that occupied by the main haddock population and sometimes the cold tongue separates the haddock population into 2 parts with usually only a few individual haddock or no haddock in the colder parts of the tongue below 1 and especially below 0°C. Sometimes it seems partly to separate and partly to engulf and on other occasions to engulf haddock concentrations.

On the Grand Bank temperatures low enough to restrict haddock movement are common but usually bottom temperatures are not high enough to form more than a temporary restraint to movement. The best otter-trawl catches on the Grand Bank between February-June are usually made at temperatures between 2 and 8°C but within this range the most favourable temperatures for haddock concentrations vary in different years, months and depths.

INTRODUCTION

For many years, mostly from April to June but occasionally earlier, the research vessels *Investigator II* and *A.T. Cameron* have carried out otter-trawl surveys of the haddock (*Melanogrammus aeglefinus* (L.)) population on the southern Grand Bank. The *Investigator II* used a No. 36 trawl with an 18.3 m headline and the *A.T. Cameron* a No. 41-5 trawl with a 24.1 m headline. The towing speed of both ships is 3 1/2 knots. A number of comparisons of relative catches of haddock by the *Investigator II* and the *A.T. Cameron* have been made but the results are varying enough that conversions of the catches by the *Investigator II* to the *A.T. Cameron* level have not been made in the data presented. The *A.T. Cameron* catches approximately 2 1/4 - 3 times as much haddock per set as the *Investigator II* and the latter ship has been relatively ineffective for haddock at depths of 185 m (100 fathoms) and greater. Before 1951 a small mesh codend with meshes averaging about 70 mm internal stretched diameter was used. From 1951 onward either a codend liner or cover of 35 or 29 mm external stretched mesb was used for survey sets. For mesh selection cruises, also, only data from otter trawls with codend meshes about 70 mm internal stretched diameter have been included. All catches used in this paper are per 30-min drag on bottom.

Bottom temperatures and in recent years surface to bottom temperatures have always been taken at each tow. On the slope of the bank the tows were made along the contour maintaining the required depth as far as possible. Bottom temperatures were taken at actual thermometer depths about 4 m above the bottom using 2 reversing thermometers attached to Nansen bottles and a 36 kg weight. All temperatures are corrected for thermometer and auxiliary thermometer variation. Temperatures for 1958 and later are adjusted to bathythermograph temperatures either at the bottom or about 1 m from the bottom, the bottom thermometers still being used to check the bathythermograph readings. In this paper unless otherwise indicated all temperatures are bottom temperatures.

Since 1952 surveys have been along the same lines extending southwest-northeast and at the same depths and stations approximately in the same locations on the line (Fig. 1). Stations on lines B, D, F and H were always occupied, and those on lines A, C, E and G were sometimes omitted or not fully completed.

DISTRIBUTION OF HADDOCK ON THE GRAND BANK

1: Survey Cruises

On the southern Grand Bank during the late winter and early spring months (with occasional exceptions in and after warm winters) and in some years to early May, bottom temperatures over the plateau of the bank in depths less than 90 m (50 fathoms) usually range from about 0 to 1.5°C toward the north to 2°C and often below this temperature at many stations as far south as the 90-m (50-fathom) contour. At this time haddock concentrations do not occur on the bank but on the southwest slope usually at temperatures higher than 2°C (Fig. 2A, 2B, 2C). The greatest concentrations are usually in the more central rather than the extreme northern and southern parts of the southwest slope.

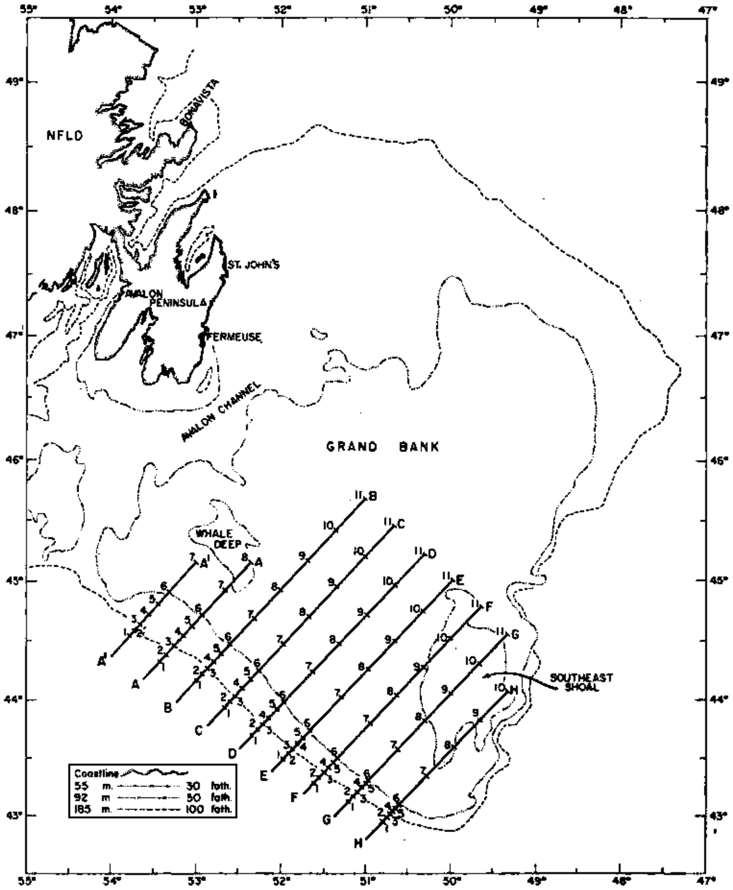

Fig. 1. Survey lines and stations on the southern Grand Bank (ICNAF Subarea 3).

Later in April and May, with rising temperatures on the bank, haddock pass onto the surface or plateau of the bank including the shallow Southeast Shoal. Concentrations on the bank are not great unless the bottom water is approaching 2°C and higher (Fig. 2C, 2D). The large concentrations are usually at temperatures greater than 2°C (Fig. 3). With the passage of haddock onto the plateau of the bank only occasional concentrations remain deeper than the 90-m (50-fathom) contour (Fig. 3), whereas in the earlier part of the year (Fig. 2A, 2B) almost all the haddock were deeper than this contour.

With increasing temperatures on the bank the haddock move still further away from the deep water of the southwest slope northeastward across the southern part of the bank (Fig. 4A, 4D).

When in April to June temperatures below 3°C occupy most of the southern part of the bank, there may be some haddock concentrations on the plateau of the bank at temperatures as low as or slightly lower than 2°C, but good concentrations may still remain on or near the southwest slope (Fig. 3A, 3B, 4C). When, however, in May and June still higher temperatures are present on the bank plateau most of the concentrations follow the tongue of high-temperature water from the central part of the southwest slope toward the Southeast Shoal. At this time most but not all haddock concentrations on the plateau of the bank are in water of higher temperature, usually between 3 and 6°C, but occasionally good catches are obtained in water where the temperature is as low as 2°C or slightly lower and as high as 8°C (Fig. 4). When these developments or incursions of higher-temperature water and the accompanying incursions of haddock are well underway over the bank plateau the haddock populations of the southwest slope are reduced to very low levels (Fig. 4A, 4D).

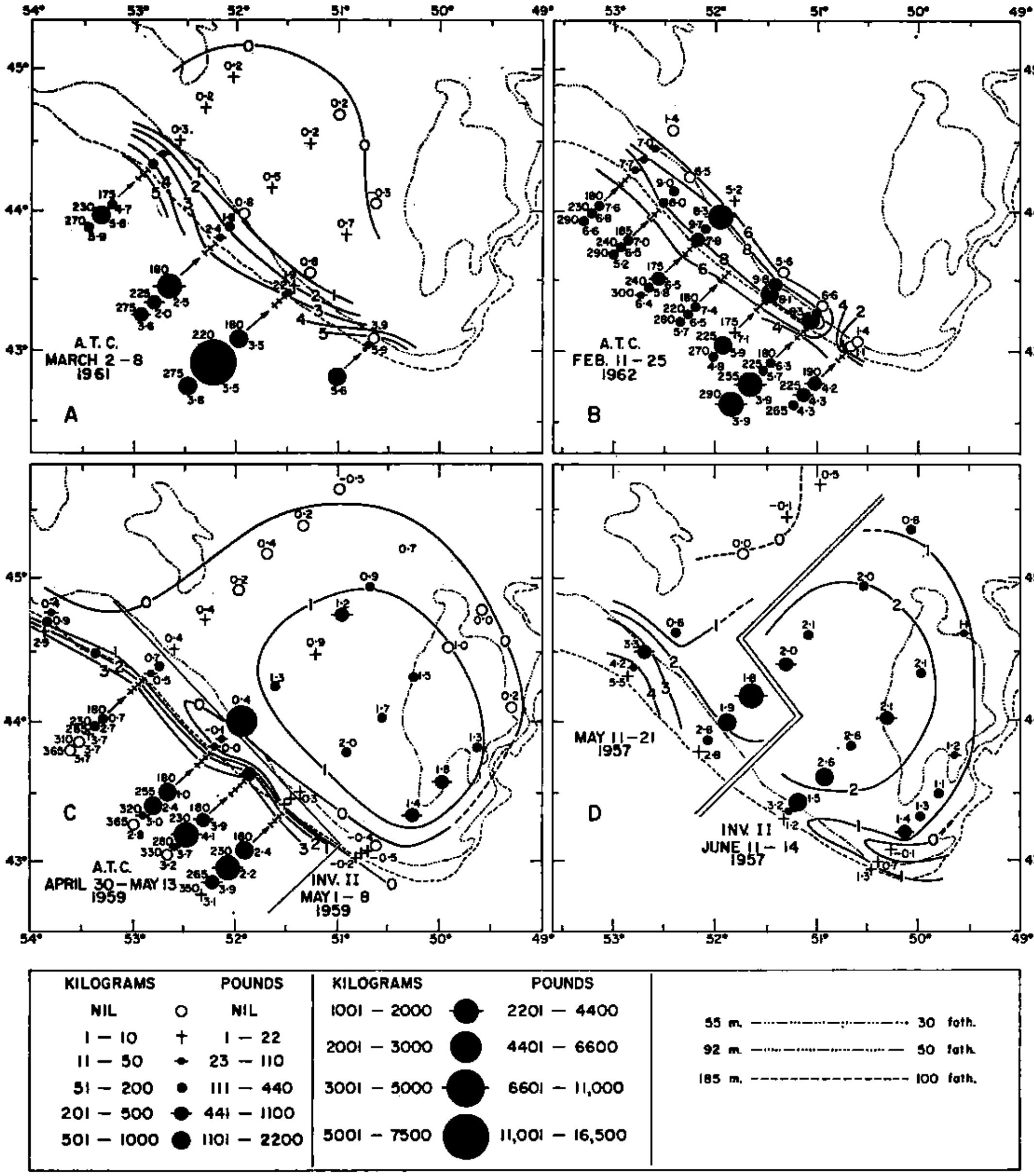

Fig. 2. Distribution of haddock on the southern Grand Bank in relation to bottom temperature. (On the slope depths in metres are given to the left of the catch symbols. In this and in all subsequent figures catches are in kilograms per half-hour tow on bottom, temperatures are in °C).

Figures 5 and 6 show in more detail some of the depth, temperature and catch relationships along individual lines (of Fig. 1) from February to June. On Line B, the most western of the 4 lines illustrated (Fig. 5), because of the influence of the cold western branch of the Labrador Current passing through the Avalon Channel, temperatures usually remain below 2°C and often below 1°C on the bank plateau. However, by April-June haddock have moved from the deeper water and the concentrations are usually located at the 90-m (50-fathom) contour (Station 6) or slightly shallower at Station 7 and in one case at Station 8. The movement occurs earlier and progresses farther when temperatures in the shallow water are higher (in the vicinity of 2°C or higher). The

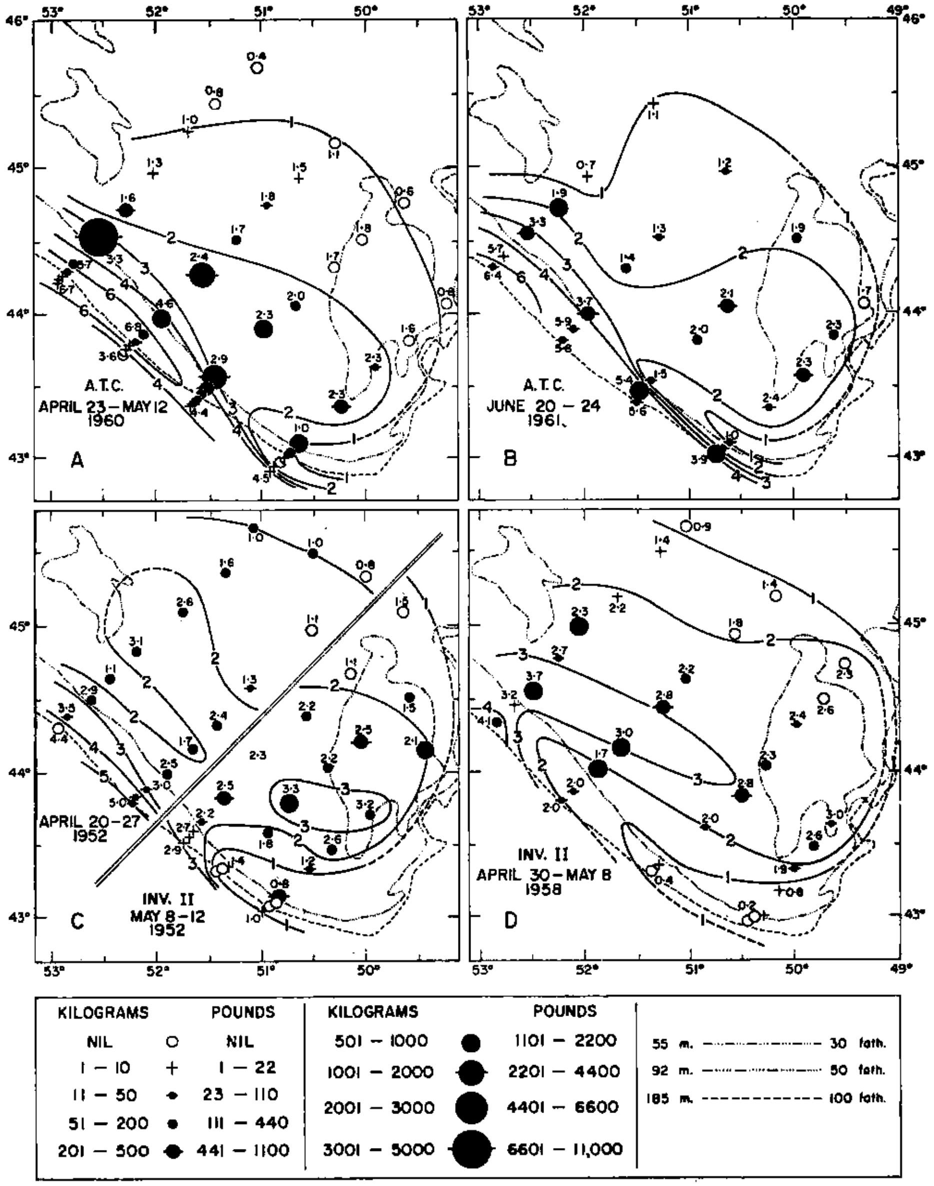

Fig. 3. Distribution of haddock on the southern Grand Bank in relation to bottom temperature.

largest catch on the plateau of the bank shallower than 90 m (50 fathoms) occurred in June 1955 when a temperature of 4.5°C was present at Station 7. Occasionally, when temperatures during this time of year are higher than 1°C over that part of the bank covered by the 3 northern stations (9-11), small quantities of haddock are caught at these stations, but when temperatures are below 1°C few or no haddock are usually present.

Somewhat eastward on Line D (Fig. 5) the progression of the haddock from the southwest slope to the plateau of the bank can be noted from March to June, the larger catches being usually associated with temperatures of about 2°C and over. The largest catch in the shallower water at Station 9 in June 1955 was at the highest temperature for this station (5.4°C). There was, however, a large catch at Station 6 in May 1959 at only 0.4°C just above the cold tongue of water from the eastern branch of the Labrador Current (see Fig. 8 and later section). Temperatures were very high in February 1962 and in consequence the haddock concentration was probably shallower than usual for this month.

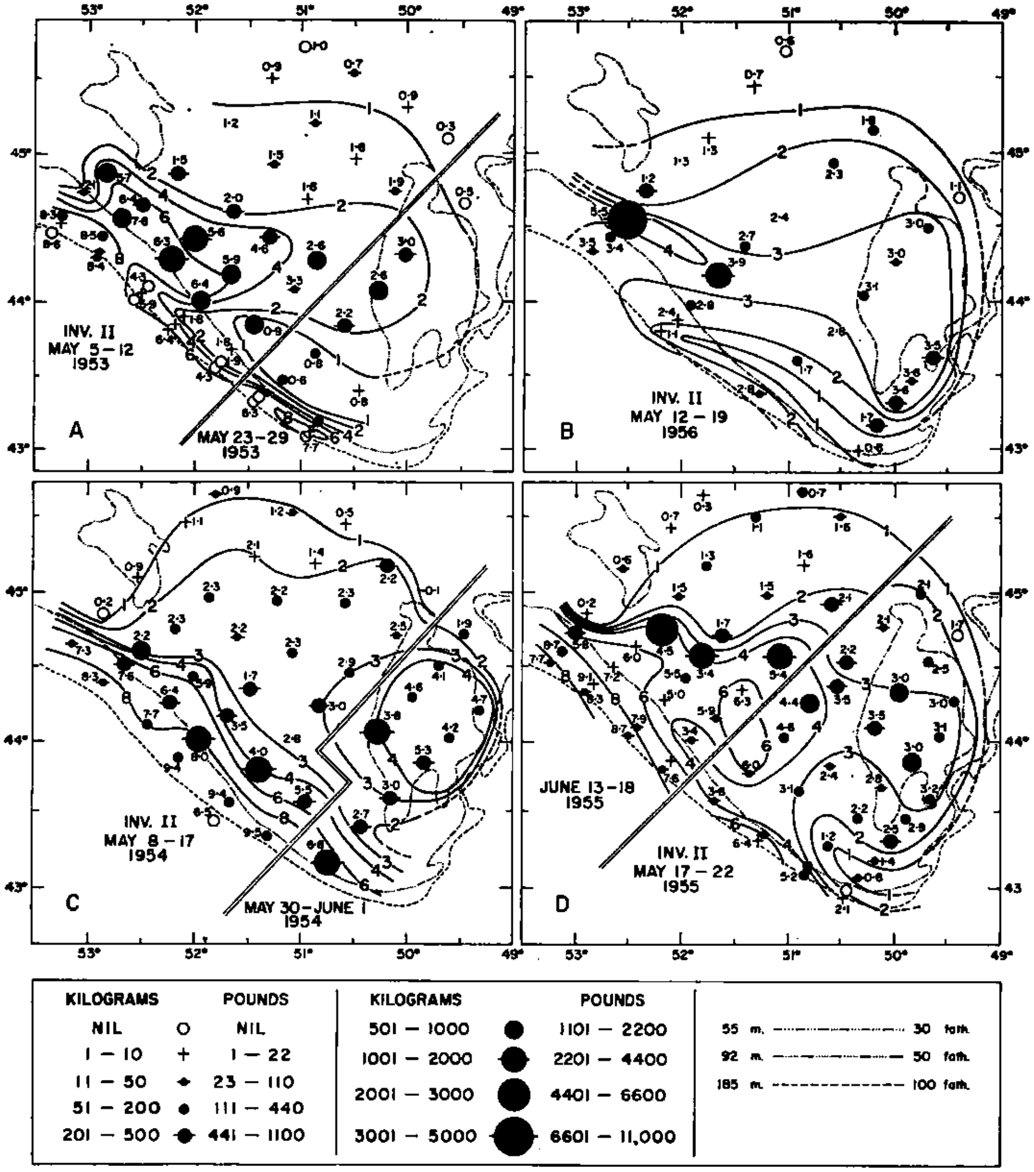

Fig. 4. Distribution of haddock on the southern Grand Bank in relation to bottom temperature.

Still further east on Lines F and H (Fig. 6) the location of the haddock in deep warmer water of the slope in the early part of the year can be noted, as well as the movement of the haddock northward over the plateau of the bank as the water temperatures increase. Good catches in the shallow water are again usually associated with temperatures above 2°C. On Line F the very high temperatures of February 1962 allowed haddock to occur in quantity shallower on the slope than in March 1961 when the water on the bank was much colder.

2: Haddock Concentrations in Relation to Temperatures of the Water Mass

For some recent years it is possible to show haddock distribution over the southern Grand Bank not only in relation to bottom temperatures as in Fig. 5 and 6 but also in relation to the temperature of water masses as determined from bathythermograph traces (Fig. 7, 8).

In February 1962 (Fig. 7) high temperatures were present on the southwest slope of the Grand

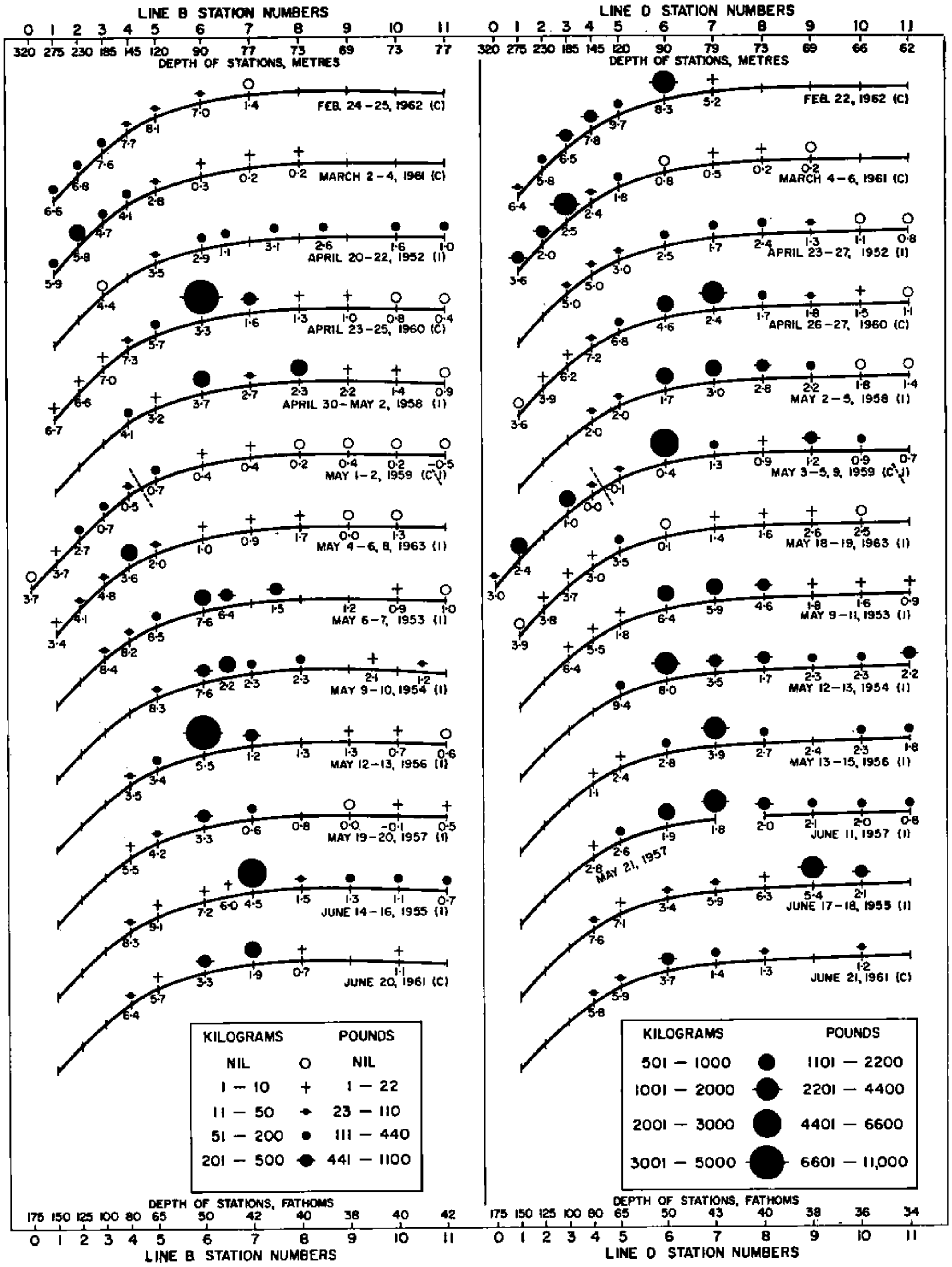

Fig. 5. Haddock catches per half-hour tow on bottom on survey lines B and D, February-June 1952-63, by the *A.T. Cameron* (C) and the *Investigator II* (I). (The location of the lines and stations is shown in Fig. 1.)

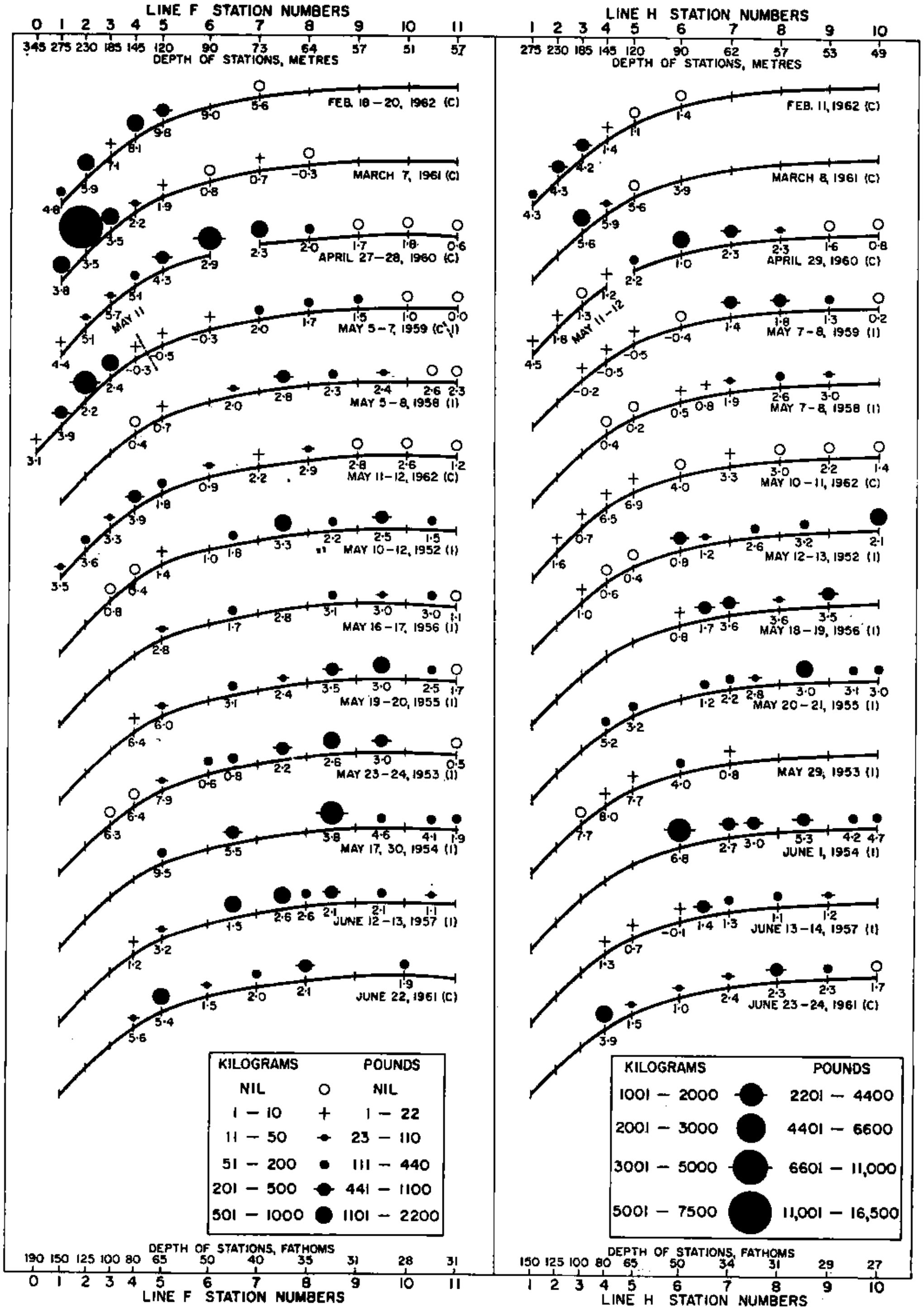

Fig. 6. Haddock catches per half-hour tow on bottom on survey lines F and H, February-June 1952-62 by the *A.T. Cameron* (C) and the *Investigator II* (I). (The location of the lines and stations is shown in Fig. 1.)

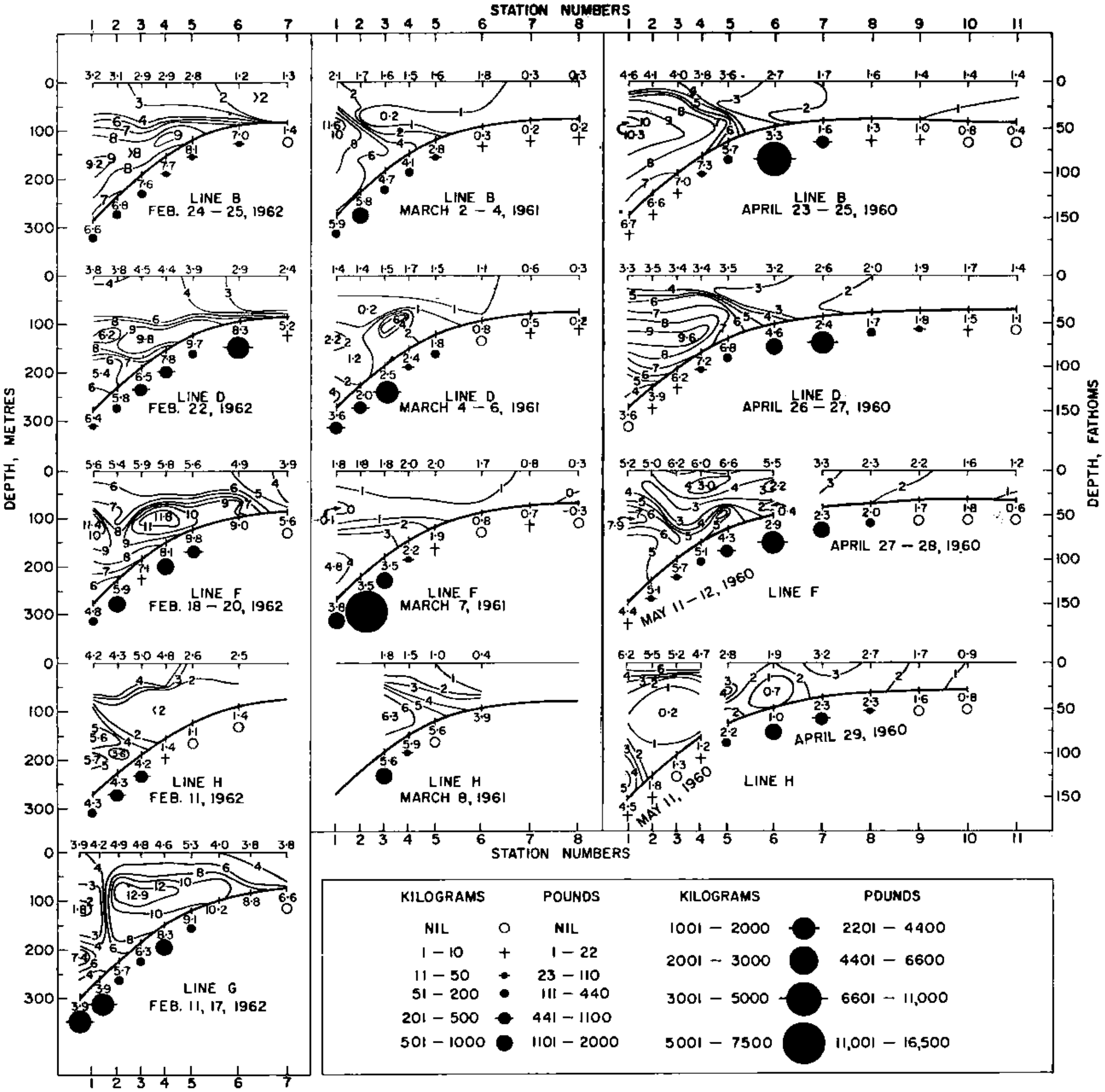

Fig. 7. Haddock catches per half-hour tow on bottom on survey lines B,D,F,G and H, February 1962, March 1961 and April 1960, by the *A.T. Cameron* in relation to temperature sections constructed from bathythermograph records taken at the fishing stations. (The location of these lines and stations is shown in Fig. 1.)

Bank and the haddock were in water with these high temperatures. The largest catches were obtained on Lines D, F and G, in water from 3.9 to 8.3°C. In general the haddock were located below the 90-m (50-fathom) contour, but in one case (Line D) a concentration was found as shallow as 90 m (50 fathoms) at a high temperature of 8.3°C. On Line H where temperatures were lower the best but not large catches were taken in 185 m (100 fathoms) at 4.2°C and in 230 m (125 fathoms) at 4.3°C. Even where suitably high temperatures of 5.1 to 7.0°C existed in water shallower than 120 m (65 fathoms) on Lines B-G, few haddock were taken, except for the 1 large catch on Line D, Station 6.

In March 1961 (Fig. 7) only a few individual haddock or none were present at stations in depths shallower than m (65 fathoms) and at temperatures between 0.8 and -0.3°C. All catches of significant size were obtained in 185-275 m (100-150 fathoms) at 2.5 to 5.8°C. Shallower sets between

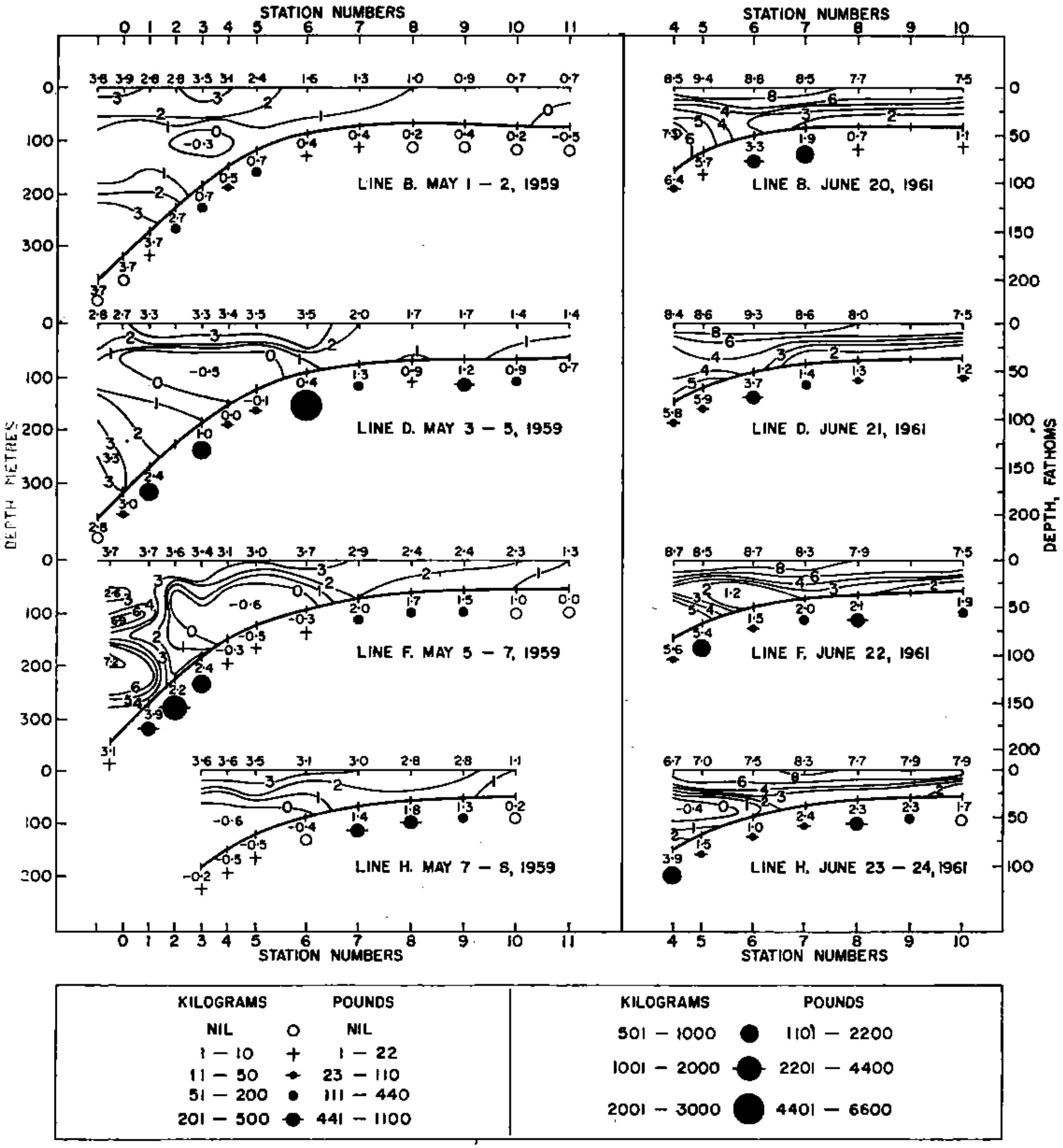

Fig. 8. Haddock catches per half-hour tow on bottom on survey lines B,D,F and H, May 1959 and June 1961, in relation to temperature sections constructed from bathythermograph records taken at the fishing stations. (The location of these lines and stations is shown in Fig. 1. Stations 5 to 11 on all lines in 1959 were occupied by the *Investigator II*; all others were by the *A.T. Cameron*.

120-145 m (65-80 fathoms) within this temperature range (5 sets between 2.8 and 5.9°C) and also 2 other sets between 2.2 and 2.4°C produced few haddock.

Thus in March and probably in February haddock were on the southwest slope rather than on the plateau of the bank, and they were lying deeper than was necessary to evade low temperatures. At this time there is evidently a tendency for the haddock to lie in deeper water where on the average temperatures are higher, rather than to seek the shallowest limits of favourable temperatures.

In April-May 1960 (Fig. 7) the haddock were definitely shallower than in February and particularly March and all good catches were obtained at Stations 6 and 7 in 90 and 77-m (50 and 42 fathoms),

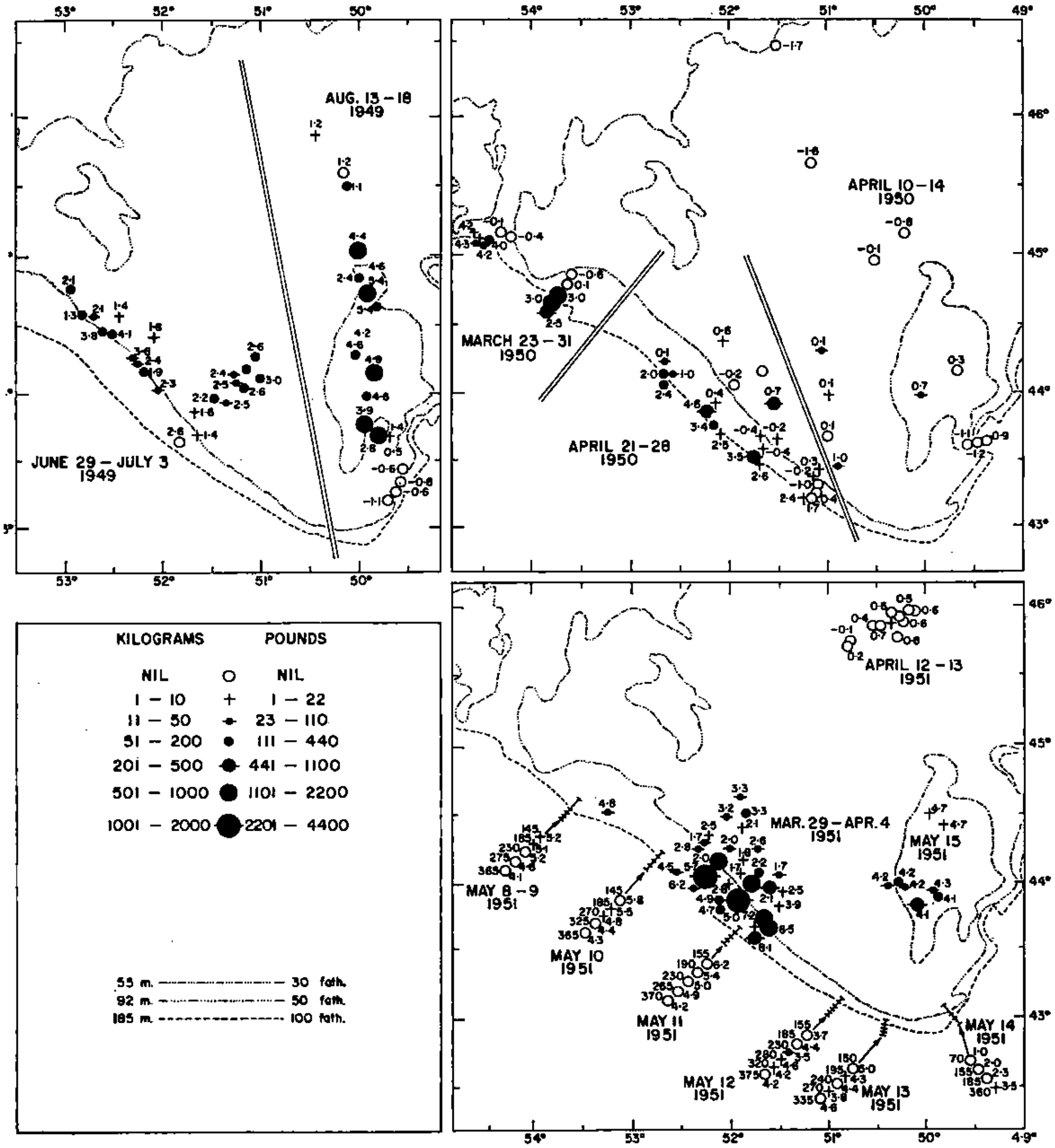

Fig. 9. Distribution of haddock on the Grand Bank in survey cruises of the *Investigator II*, March-August, 1949-51.

3 large catches at 2.4 to 3.3°C and 3 moderate catches at 1.0, 2.3, and 4.6°C. Two of the largest catches were taken at locations where there was a rapid change in water temperature of at least 1°C immediately above the bottom. (See also several instances of this kind in Fig. 7, 1962 D, F and G). These ceilings of water with a different temperature could have restricted the vertical range of the haddock and made them more readily available to a bottom trawl. The haddock concentrations were approaching but not penetrating the 2°C isotherm.

In May 1959 (Fig. 8) in all sections there was a mass of cold water, with temperatures between -0.6 and 0°C at intermediate depths, covering a wide area of the southwest slope in the 3 eastern sections (Lines D, F and H). This cold layer (or tongue), an extension of the eastern branch of the Labrador Current, projects westward around the tail of the bank and penetrates for varying distances along the southwest slope (Fig. 2, 3, and 4). The concentrations of haddock occurred on the slope below and on the shallower plateau of the bank above the cold layer but only a few individuals were found in sets in the cold layer at temperatures below 0°C. Most of the good catches in the deeper water were at temperatures from 2.2 to 4.1°C (see also Fig. 2C), but on Line D there was a good catch at 1.0°C immediately deeper than the cold tongue and an excellent catch at 0.4°C immediately shallower than the cold tongue. The good catches deeper than the cold layer sometimes had very cold water immediately overhead (Fig. 8, 1959, Lines D and F, Station 3). The deep-water concentrations of haddock at this time were engaged in their northward migration to shallower water and had moved northward close to the cold layer but had not entered it. On Line H the survey sets were not made deeply enough to sample the haddock of the warm water deeper than the cold tongue. (This is unfortunately true also for the more easterly lines in a number of situations and occasions in Fig. 5-8).

In June 1961 (Fig. 8) the cold tongue was neither as extensive nor as cold as in May 1959. Its effect, however, where it is well developed on the most easterly sections (Lines F and H), is again to separate the haddock into deep and shallow concentrations at higher temperatures (2.1 to 5.4°C) with only small quantities in the cold tongue at 1.0 to 2.0°C. On Lines B and D the haddock had moved partially but not wholly onto the plateau of the bank at temperatures of 1.9 to 3.7°C, their movement onto the bank being restricted by temperatures below 2°C.

There were several instances where haddock concentrations were found at moderately high temperatures along the slope immediately deeper than water masses, in which several degree isotherms of lower temperatures were crowded closely together (Fig. 8, 1961, Line D, Station 6; Line F, Station 5 and Line H, Station 4; Fig. 7, 1962, Line D, Station 6). There are many other examples in Fig. 5-8 where great changes from larger to smaller catches occur in the vicinity of sharp temperature changes. In some cases the abrupt catch and temperature changes occur above and below the cold tongue of water extending westward along the southwest slope from the eastern branch of the Labrador Current, this unfavourable environment separating shallow and deep-water concentrations both at more favourable temperatures.

The barrier effect of an impinging abrupt rise or fall in temperature needs to be interpreted also in relation to the most likely natural direction of movement of the haddock, deeper in winter-early spring and shallower in April-July. In winter-early spring (February-March in our figures), when haddock are moving deeper, the barriers should be at greater depths than the haddock concentrations. Deep-water temperatures below the winter-early spring haddock concentrations on the slope of the southwest Grand Bank are not extremely high or low and are within the favourable range for haddock at shallower depths on the slope. Consequently the barrier in the deep water is usually depth rather than temperature. The haddock upon reaching a certain depth presumably become concentrated due to a resistance to going deeper.

When the sharply differing temperature, serving as a temporary barrier, is within the favourable temperature range, such a barrier can only be temporary, functioning while the fish are becoming adjusted to the impinging higher or lower temperature.

3: Supplementary Results from Early Cruises

Before the repetitive surveys at approximately the same stations on the southern half of the Grand Bank were begun in 1952 there were some less extensive surveys by the *Investigator II* (Fig. 9) which help to fill some of the time and space gaps in the data from the survey cruises of recent years.

In March and April 1950 (Fig. 9) cold water below 1°C and much even below 0°C extended deeper than usual along the southwest slope. Haddock catches at these lower temperatures along the slope and in shallower water were usually zero or negligible, except for one modest catch just north of the 90-m (50-fathom) contour at 0.7°C. The best catches, although small, were obtained on the southwest slope below the cold water at temperatures between 2.5 and 4.6°C in depths from 145 to 240 m (80 to 130 fathoms), the latter being the lower limit of fishing.

In late March-early April 1951 (Fig. 9), when temperatures on the plateau and on the southwestern slope of the bank were considerably higher than in 1950, the largest catches of haddock were obtained in shallower water than in 1950 on and above the upper part of the slope in depths of 80-100 m (45-55 fathoms) at temperatures between 2.0 and 7.2°C. In early April no haddock were caught in many sets on the northern central area of the bank at -0.1 to 0.7°C, and in May no haddock or negligible quantities of haddock were found in the deep water of the southwestern slope in depths of 155-375 m (80-205 fathoms) at 3.5 to 6.2°C. By May 15, although temperatures were much higher than

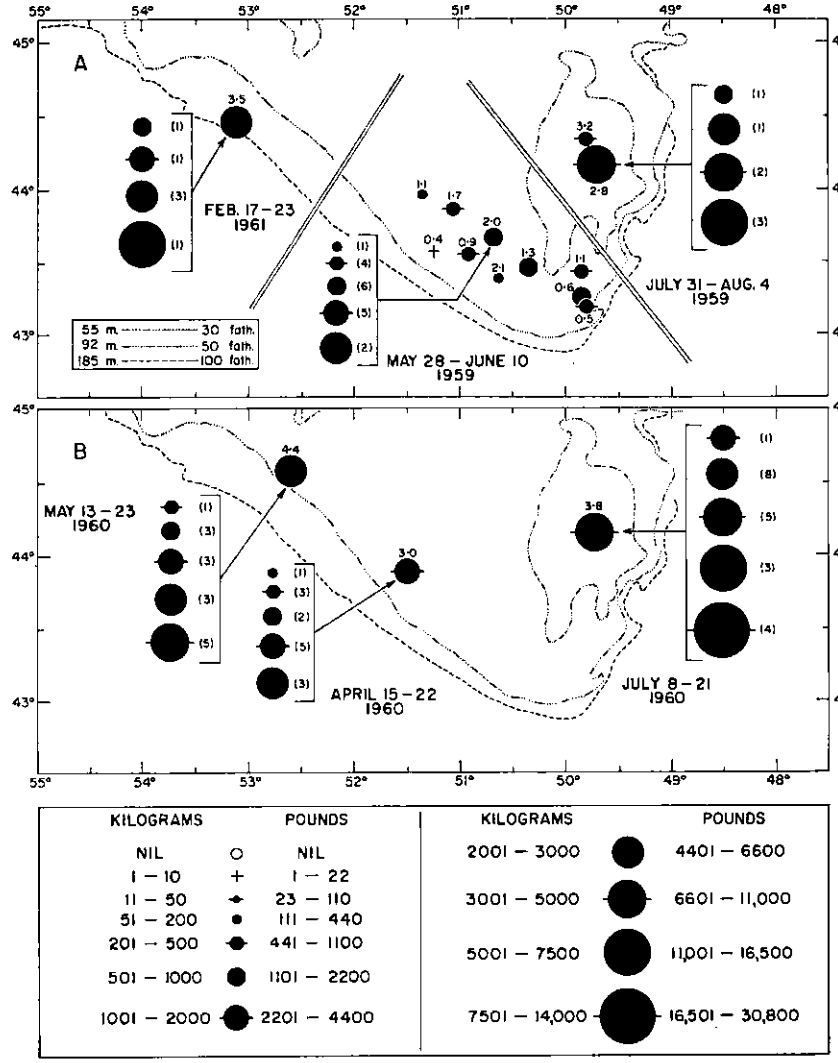

Fig. 10. Haddock catches per half-hour tow on bottom by *A.T.Cameron* from mesh selection cruises on the southern Grand Bank, February-August, 1959-61. (The figures in parentheses represent the number of tows and the arrow points to the average catch which is shown at the fishing location.)

usual, 4.1 to 4.7°C, only small quantities of haddock were present on the Southeast Shoal.

In late June and early July 1949 (Fig. 9) small quantities of haddock were found at most stations on the southwestern part of the plateau of the bank in 66-113 m (36-62 fathoms) at 1.3 to 4.1°C. In August considerably larger catches were made on and near the Southeast Shoal in depths of 46.-60 m (25-33 fathoms) at temperatures from 3.9 to 5.4°C and in one case at 2.8°C.

4: Mesh Selection Cruises

In addition to the survey cruises, several mesh selection cruises for haddock were made, some of the results of which are given in Fig. 10. During these cruises, after preliminary searches to find suitable quantities of haddock, many tows were made in the same area. These were usually 1-hr tows and occasionally, when catches were very large, 40-min tows. The catches have been reduced to the half-hour level to agree with the results of the survey cruises.

In February 1961 large catches were taken in 155-170 m (85-93 fathoms) on the slope south of Whale Deep at 3.5°C, and in May 1960 similar catches were obtained just north of the same location in 85 m (47 fathoms) at 4.4°C. In April 1960 and May-June 1959 only modest catches were obtained on the bank plateau just north of the 90-m (50-fathom) contour at 0.6 to 3.0°C.

In July-August 1959 and in July 1960 very large catches were obtained at 2.8 and 3.8°C on the Southeast Shoal in 46 m (25 fathoms). These large catches were taken in a capelin spawning area where the haddock were feeding heavily on capelin eggs and capelin (Templeman and Pitt MS, 1951; FRBC, 1952, Pitt, 1958, Noskov, MS, 1962).

5: Pelagic Movements

Although most feeding of haddock is on bottom organisms, it appears possible that on some occasions, at least, haddock may move long distances pelagically. Often in late June and early July there is some movement of Grand Bank haddock coastward to the Avalon Peninsula and northward reaching Bonavista usually in late July and early August. The quantity of haddock decreases as the movement northward progressea and small numbers have been taken at least as far north as Notre Dame Bay. In some years this coastward movement of haddock schools is very great. For example, at Fermeuse on 29 June-3 July 1959, most codtraps obtained 900-1,400 kg of haddock per haul and 1 trap had a catch of 9,000 kg. This migration occurs across the Avalon Channel which usually has a good deal of bottom or intermediate water below -1.0°C. Judging from the usual scarcity of cod (a fish which generally lives at lower temperatures than haddock) in these temperatures of -1.0°C and lower, it appears certain that these haddock travel pelagically across the Avalon Channel in the warmer surface layer. In their normal abode on the bank haddock are much more bottom related and less pelagic than cod. When they are caught together with cod in codtraps on the east coast of Newfoundland, however, their pelagic habit at this time is evident from their tendency to take up their position nearer the surface and in warmer water than the cod. Bottom temperatures on the bank were unusually low in early May 1959 (Fig. 2C) and haddock concentrations were retained longer than usual and mainly lay deeper than the barrier of the cold tongue. It appears likely that large quantities, in order to move shallower, rose into the warmer surface layer and dispersed pelagically in such numbers that large schools reached the southeastern coast of Newfoundland.

It is very likely, also, that some of the haddock migrations between the slope and the shallower parts of the bank are pelagic as such movements in more superficial warmer water would at times appear to be necessary if the haddock are not to pass through below 0°C water of the cold tongue.

DISCUSSION AND CONCLUSIONS

On the Grand Bank in winter haddock become concentrated at greater depths, often at 185-230 m (100-125 fathoms) and in lesser but sometimes significant quantities as deep as 275 m (150 fathoms), than on the Scotian Shelf where the winter concentrations occur at 80-130 m (45-70 fathoms) (Martin, 1960, 1961).

From otter-trawl surveys of Georges Bank by the *Albatross III* in the spring of 1950, during the spawning season most haddock of all ages occurred in water shallower than 55 m (30 fathoms) with only very small quantities in deeper water. At greater depths haddock gradually decreased in numbers but there was a secondary increase in numbers of larger haddock in the 112-165 m (61-90 fathom) range. Similar surveys in the summers of 1948-50 showed that the smaller haddock (ages 2-4) were principally in depths of 55-110 m (30-60 fathoms) whereas the older haddock were most numerous in water of 166-275 m (91-150 fathoms). Very few haddock of any age were found in the 112-165 m (61-90 fathom) depths in summer (Colton, 1955).

Presumably, as assumed by Colton, many of the large haddock of the Georges Bank area remain in deep water until late winter and rise into shallower water during the spawning season which occurs mainly in February-April (Bigelow and Welsh, 1925; Walford, 1938). The Grand Bank haddock begin to move towards the shallower water in April and spawn mainly in May and June.

Noskov (MS, 1962) shows the Soviet fishery for haddock on the Grand Bank in 1961 to have taken place on the shallower part of the southwest slope and on the southwest fringe of the plateau of the bank in April-June and mainly on the western part of the Southeast Shoal but also a little to the west of this shoal in July-November.

In the Bay of Fundy McKenzie (1932) found that the best catches of haddock on bottom longlines occurred in July-August at bottom temperatures of about 8°C but catches fell rapidly to near zero with temperatures of 9 to 11°C. In early winter catches increased again when the bottom temperature fell to about 4°C but were again reduced to near zero as the temperature fell to 2°C and lower. In experimental fishing near St. Andrews no haddock were caught with longline in water colder than 2.4°C. The greatest catches were made when the bottom water was between 7.3 and 10°C and catches almost as great were sometimes made when the bottom temperature was 11.9°C. On other occasions no haddock were taken with longline at 11.7°C although otter trawling in the same area showed that haddock were numerous.

Martin (1960, 1961) found largest catches of haddock of commercial size on the Nova Scotian Shelf in winter to occur in the vicinity of Sable Island and Emerald Banks in 80-130 m (45-70 fathoms) at bottom temperatures from 3 to 5°C. At bottom temperatures of 1 to 3°C small haddock predominated but there were no haddock in the shallow water on the tops of the banks where temperatures were less than 1°C. In cold years the haddock lay deeper and were more concentrated. In summer small haddock were most abundant in warm shallower water less than 55 m (30 fathoms) on top of the banks with bottom temperatures above 7°C.

Thompson (1939), from otter trawling on the southwest slope and edge of the Grand Bank by the research vessel *Cape Agulhas* in March-May 1934 and 1935, found the greatest average catches of haddock at 4 to 7°C.

A consideration of Fig. 5 and 6 shows that in different years, months and depths there is considerable variation in the temperatures at which the best catches of haddock are made but on the southern Grand Bank between February-June the best catches are usually obtained at bottom temperatures between 2 and 8°C. In any one month and place, however, only a limited part of this range of bottom temperatures is generally available. Consequently, haddock, if present, must usually occupy a more limited temperature range.

Haddock in late winter and early spring inhabit the southwest slope of the Grand Bank at greater depths than are required merely to evade low temperatures. Preceding spawning haddock desert the high temperatures of the deeper water, which are very favourable during winter, and move shallower usually into lower temperatures. Presumably the retention of haddock eggs and larvae on the bank is favoured by this northeastward pre-spawning migration away from the very deep water south and west of the slope. It is apparent that Grand Bank temperatures either in the deep or the shallow water are not usually high enough to be limiting for haddock, although they may doubtless form a temporary barrier to haddock already in low temperatures until they become accustomed to the impinging higher temperature water.

By April-June, when the haddock are moving northeastward from the southwest slope of the bank, the eastern Grand Bank branch of the Labrador Current usually has a well-developed tongue of water below 1°C extending westward along the shallower fringe of the southwest slope to about 51°W (Fig. 2D, 3A, 3B, 4D) or even farther westward to about 51°30'W - 52°30'W (Fig. 2C, 3C, 3D, 4A, 4B). The cold tongue of water, judging from Fig. 2-8, attains a greater development in May and June than in earlier months. Depending on the time of development of the cold tongue in relation to the existence of haddock on the slope or the passage of haddock to the shallower plateau of the bank, the following hypotheses are possible: the cold tongue may pass above or below the main haddock concentrations or may push through the concentrations with the haddock moving both deeper and shallower away from the cold tongue, thus separating them into concentrations above and below the cold tongue. Haddock concentrations are rarely found in the central coldest part of this cold tongue, but sometimes they are found at temperatures below 1.5 and even below 1°C on the fringes of the cold tongue. It is possible that in such cases the haddock concentrations have not migrated into the cold tongue but have moved both deeper and shallower away from it and thus become separated, but that sometimes the cold tongue has moved rapidly enough to engulf the haddock concentrations on its fringes and they have become acclimatized to the cold water before they could escape it. In such cases haddock concentrations occur deeper and shallower than the cold tongue at unusually low temperatures as in Fig. 2C, and Fig. 8, 1959 (Line D, Stations 6 and 3). On other occasions (Fig. 3A, 4A) the cold tongue seems to engulf the southern part of a haddock concentration on one or more of the eastern lines. The apparent separation of haddock by a cold layer of water at intermediate depths into concentrations in warmer water both shallower and deeper than the cold layer is similar to that found by Templeman and Fleming (1956) for cod on the east coast of Newfoundland.

Temperatures on the Grand Bank are often low enough, from less than 0 to 2°C, to interfere with northward movement of haddock over the bank plateau. Consequently, even in summer, apart from the pelagic coastward and coastal movements, large concentrations of haddock are found on the southern rather than on the northern parts of the bank.

In some months and years (Fig. 4A, 4B, 4D, 3D) there is an apparent intrusion of warmer slope water onto the bank from the southwest slope region, usually between 53° and 51°W. Often the haddock are included with or follow the pattern of the warm water intrusion. At other times (Fig. 2C, 2D, 3A, 4C) there may be an influx of warm slope water at various levels or there may equally well be warming from the surface. The intrusion or warm water mass has either a broad base on the southwest slope (Fig. 4C, 4D) or the base may be narrow forming a warm water tongue (Fig. 4A, 4B). The width of the base is largely determined by the extent of development of the cold tongue passing westward along the southwest slope and edge of the bank. With the intrusion (if it occurs) and the cold tongue both being deflected in their natural direction to the right, the haddock are directed by the isotherms of favourable temperature toward the shallowest part of the southern Grand Bank, the Southeast Shoal. The extent, shape, temperature, and other characteristics of this warm water mass during the spawning season in May and June and the resulting distribution of haddock at spawning time should have a considerable influence on the survival and retention on the bank of haddock eggs and larvae. In 1955 when haddock were well established on the plateau of the bank in May and June, with very few on the slope (Fig. 4D) there was the most successful year-class survival of haddock between 1950-1962. (For success of other haddock year-classes see Templeman, this symposium).

From lack of information on food and feeding of haddock in the Grand Bank area it has not been possible here to assess the relative effects of food and temperature in producing haddock concentrations. However, as in the instance given of the great haddock concentrations on the capelin spawning grounds of the Southeast Shoal, there can be no question that, especially after spawning, food as well as temperature will be important factors in concentrating haddock. Judging, however, by the work of Homans and Vladykov (1954) for haddock of the Nova Scotian area and allowing for later spawning (mainly in May-June) on the Grand Bank it is unlikely that the pre-spawning haddock on the southwest slope are concentrated mainly by food.

REFERENCES

BIGELOW, HENRY B. and WILLIAM W. WELSH. 1925. Fishes of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, 40(1): 1-567.

COLTON, JOHN B. 1955. Spring and summer distribution of haddock on Georges Bank. *U.S. Fish Wildl. Serv., Spec. Sci. Rep.-Fish.*, 156: 1-65.

F.R.B.C. 1952. Report of the Newfoundland Fisheries Research Station. *Ann. Rep. Fish. Res. Bd. Can.* for 1951: 43-65.

HOMANS, R.E.S. and V.D. VLADYKOV. 1954. Relation between feeding and the sexual cycle of the haddock. *J. Fish. Res. Bd. Canada*, 11 (5): 535-542.

MARTIN, W.R. 1960. Canadian research report, 1959: B, Subareas 4 and 5. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 10: 25-31.

1961. Canadian research report, 1960: B, Subareas 4 and 5. *Ibid.* 11: 31-37.

MCKENZIE, R.A. 1932. Water temperature and the haddock fishery of the Fundy area. *Fish. Res. Bd. Canada, Atl. Prog. Rep.* 4: 10-13.

NOSKOV, A.S. MS, 1962. Haddock observations in the south of the Great Newfoundland Bank. *Annu. Meet. int. Comm. Northw. Atlant. Fish. 1962.* Doc. No. 68, Ser. No. 1011: 1-6.

PITT, T.K. 1958. Distribution, spawning and racial studies of the capelin, *Mallotus villosus* (Müller), in the offshore Newfoundland area. *J. Fish. Res. Bd. Canada.*, 15(3): 275-293.

TEMPLEMAN, WILFRED. 1964. Relation of periods of successful year-classes of haddock on the Grand Bank to periods of success of year-classes for cod, haddock and herring in areas to the north and east. *This symposium, Contribution No. D-2.*

TEMPLEMAN, WILFRED and A.M. FLEMING, 1956. The Bonavista long-lining experiment, 1950-1953. *Bull. Fish. Res. Bd. Canada*, 109: 1-55.

TEMPLEMAN, W. and T.K. PITT, NS, 1951. Haddock and cod concentrations due to capelin spawning on the Grand Bank. *Ann. Rep. (mimeo.) Fish. Res. Bd. Canada Biol. Sta., St. John's, Nfld.* for 1951, App. No. 6, p. 12.

THOMPSON, HAROLD. 1939. The occurrence and biological features of haddock in the Newfoundland area. *Res. Bull. Nfld. Dept. Nat. Resources*, 6: 1-31.

WALFORD, LIONEL A. 1938. Effect of currents on distribution and survival of the eggs and larvae of the haddock (*Melanogrammus aeglefinus*) on Georges Bank. *Bull. U.S. Bur. Fish.*, 29: 1-73.

A-9

DISTRIBUTION OF HADDOCK ON ST. PIERRE BANK (ICNAF DIVISION 3Ps) BY SEASON, DEPTH AND TEMPERATURE[1]

By

Wilfred Templeman and V. M. Hodder[2]

ABSTRACT

The largest catches of haddock from research vessel operations on St. Pierre Bank from late ay to early July 1951-54 were in the shallow water. On the average the largest shallow-water atches were taken at temperatures between 2.5 and 7.0°C but a few large catches occurred at tempratures from 1.4 to as low as 0.7°C. Catches in the deep water were very low and the small numers of generally larger fish at depths below 119 m were usually at the higher temperatures between .5 and 6.4°C.

Information from Newfoundland trawlers during the years of great abundance of young fish of ne 1949 year-class showed that haddock were available in quantity on top of the bank in 37-72 m nd usually less than 60 m from June to January. In February-April the commercial fishing was conentrated on the western slope of the bank generally between 146-220 m.

Temperature surveys indicate that the bottom water on top of the bank usually ranges from less han 0°to 1°C in March-April, whereas at the same time on the western slope of the bank at 175 m nd deeper bottom temperatures were usually from 3 to over 6°C.

The retreat of haddock from the shallow water in January-February and the return to shallow ater again in May-June are apparently in response to low temperatures on top of the bank in winter nd early spring and to the subsequent warming in late spring and early summer.

INTRODUCTION

Surveys of St. Pierre Bank by bottom otter trawl have been carried out for many years, mainly n late spring, by the research vessels *Investigator II* and *A.T. Cameron*. Details of the ships, rawls, and hydrographic methods are set out in Templeman and Hodder (this symposium). Unless therwise noted all temperatures mentioned in this paper are bottom temperatures.

Statistics of landings, location of fishing and effort have also been obtained for Newfoundand trawlers fishing on St. Pierre Bank since 1953 and for several Newfoundland trawlers before hat time.

Only occasionally is St. Pierre Bank a major source of haddock. Before the autumn of 1953, hen the unusually successful 1949 year-class had reached small commercial size, haddock fishing y Newfoundland trawlers in this area was sporadic although some successful fishing for haddock as carried out in deep water in spring and early summer of the years after 1946. From the autumn f 1953 to the spring of 1956 there was excellent fishing on St. Pierre Bank for the very numerous 949 year-class. Since 1956 there has been little commercial haddock fishing on this bank.

DISTRIBUTION OF RESEARCH VESSEL CATCHES

. 1951-54

In the years 1951-54 the *Investigator II* obtained some large catches of haddock on St. Pierre ank (Fig. 1), almost all from the unusually large 1949 year-class. Although fishing was usually arried out in depths to 185 m and occasionally deeper, the large catches (greater than 1000 kg per

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[2] Fisheries Research Board of Canada, Biological Station, St. John's, Newfoundland.

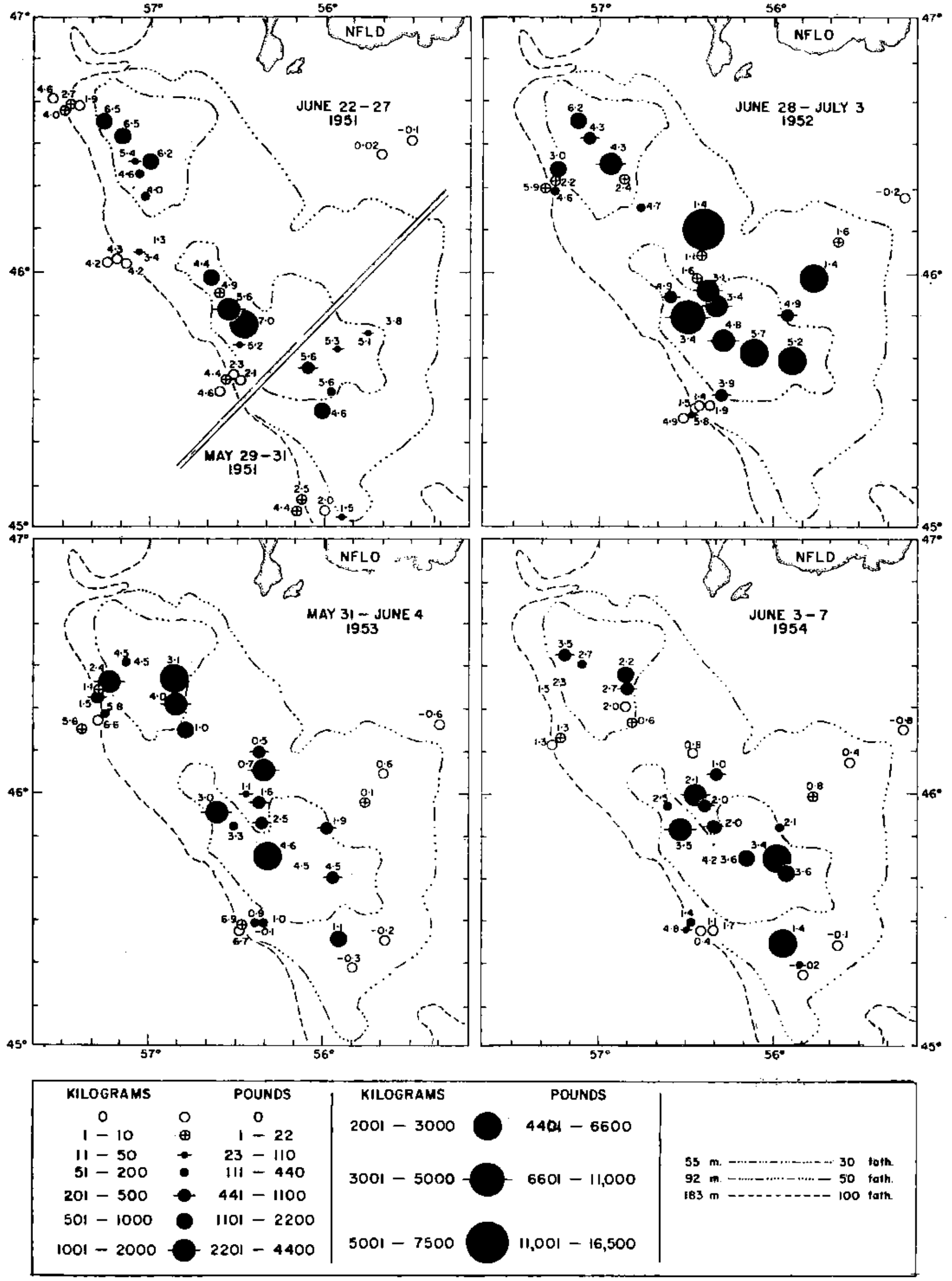

Fig. 1. Distribution of haddock from otter-trawl catches by the *Investigator II* on St. Pierre Bank, 1951-54, in relation to bottom temperature. (Catches are in kg of whole haddock per half-hour tow on bottom and temperatures are in °C.)

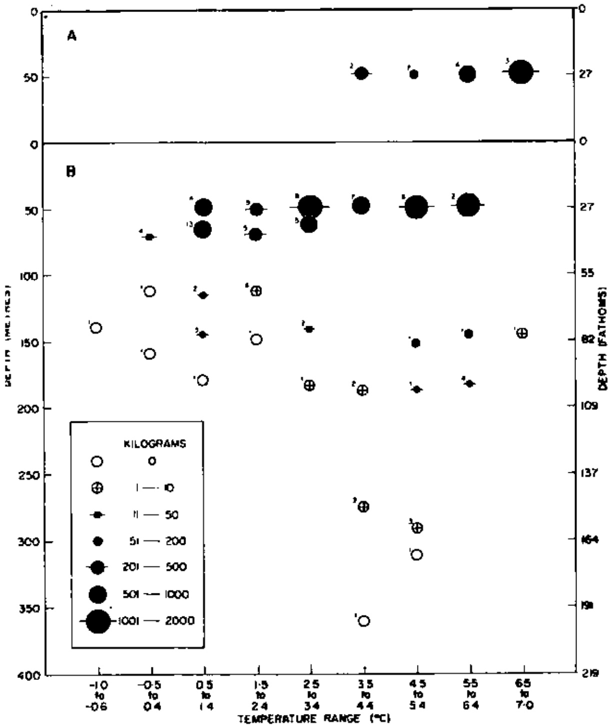

Fig. 2. Average catches of whole haddock per half-hour tow by the *Investigator II* on St. Pierre Bank in May-early July 1951-54 in relation to depth and bottom temperature. (At the upper left of each symbol is the number of sets involved in the average. A = 1951. B = 1952-54 for the shallowest depth range and 1951-54 for the remainder.)

hour tow) were all taken in shallow water on the plateaus of the bank mainly between 44-66 m. In May and June 1951 (a warm year) large numbers of haddock (mainly 2-yr-old fish) were obtained at high temperatures of 4.4 to 7.0°C. Between 28 June and 3 July 1952, although most of the good catches (chiefly of 3-yr-old fish) were taken at temperatures of 3.1 to 5.7°C, two large catches (one the largest for the survey) were taken at 1.4°C. From 31 May to 4 June 1953, good catches of mainly 4-yr-old haddock were taken chiefly between 2.4 and 4.6° C. Again on 3-7 June, 1954, some good catches of chiefly 5-yr-old fish were taken at temperatures from 1.4 to 3.5°C. Many sets in deeper water, both in cold water at intermediate depths (70-180 m) and in deeper warm water between 180-300 m produced zero or negligible catches.

In Fig. 2. where the catches are averaged in relation to depth and temperature range, it can be seen that the best fishing, mainly on haddock 2-5 yr old of the 1949 year-class, occurred in average depths of 45-50 m. In 1952-54 the largest catches, on the average, were obtained at temperatures between 2.5 and 6.4°C, whereas in 1951 (Fig. 2A), a warmer year, the haddock (mainly 2-yr-old fish) were most plentiful at the highest temperatures (5.5 to 7.0°C). At average depths of 60-70 m catches were reduced; the available temperature range was narrower and the largest catches were between 0.5 and 3.4°C. Catches at deeper levels were very low and the small numbers of generally larger fish at levels below 119 m tended to be at the higher temperatures between 2.5 and 6.4°C.

2. 1957-60

In recent years, 1957-60, survey sets on St. Pierre Bank mainly in May and June by both the *Investigator II* and the *A.T. Cameron* have produced negligible catches (Fig. 3). In this period, although temperatures on the shallower parts of the bank were generally suitable for haddock, the best of the very small catches were usually on the western slope of the bank, either in the deep warmer water of about 180 m or deeper or in the intermediate colder water usually at about 145 m. This scarcity is due to the great reduction in the haddock population on St. Pierre Bank following the heavy exploitation during 1954-56 and the poor year-class survival since 1949.

HADDOCK DISTRIBUTION AS INDICATED BY THE COMMERCIAL FISHERY

1. The Commercial Fishery

The commercial fishery by Newfoundland trawlers on St. Pierre Bank in 1954-56 was mainly for haddock of the 1949 year-class. From June to January (Fig. 4, 5) fishing was concentrated in shallow water between 37-72 m. At first most of the fishing occurred in the shallowest part of this range where bottom temperatures in late spring and summer are highest. As the year advanced fishing gradually progressed downward to 55-60 m in December and January. The downward movement to deeper water appeared to occur very rapidly in January, so that from February to April haddock were caught on the western slope of the bank usually between 146-220 m.

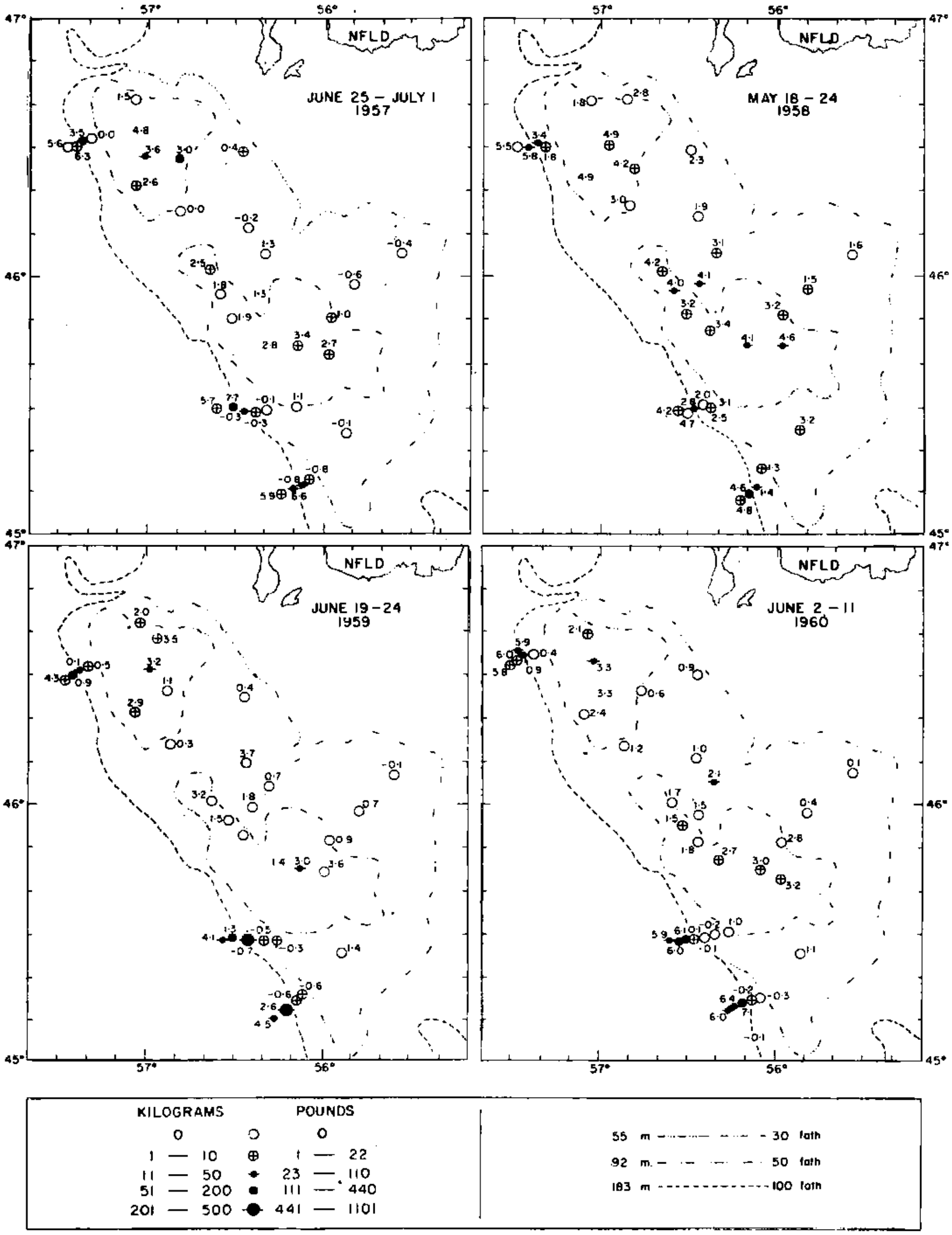

Fig. 3. Distribution of haddock from otter-trawl catches by the *Investigator II* 1957-59 and by the *A.T. Cameron* 1960, in relation to bottom temperature. (Catches are in kg of whole haddock per half-hour tow on bottom and temperatures are in °C.)

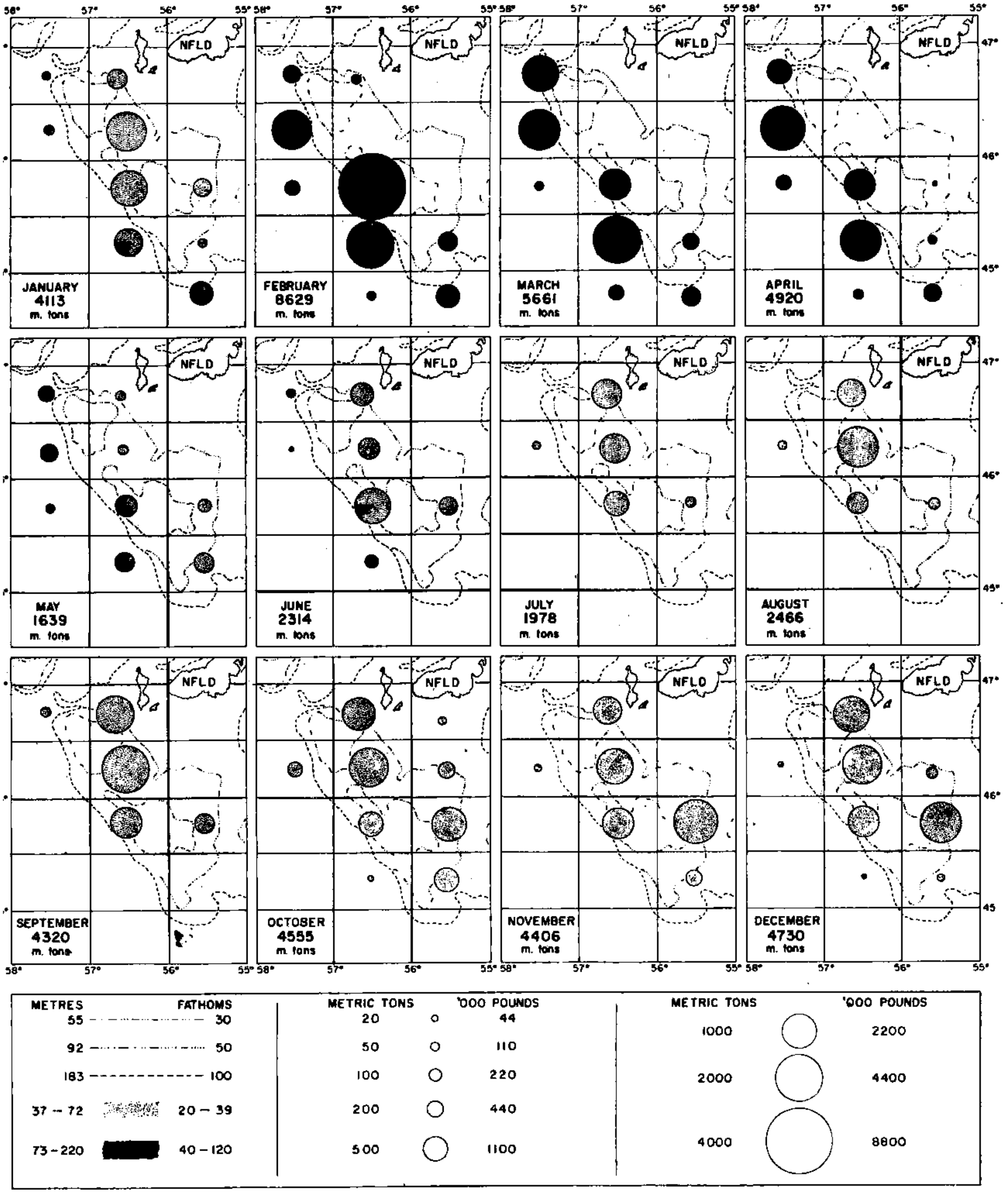

Fig. 4. Monthly distribution of haddock landings by Newfoundland trawlers (151-400 tons) in 1954-56 by 1° longitude, 1/2° latitude rectangles and depth range. (The symbols are in relation to the size of the landings and are placed in the middle of the appropriate rectangle.)

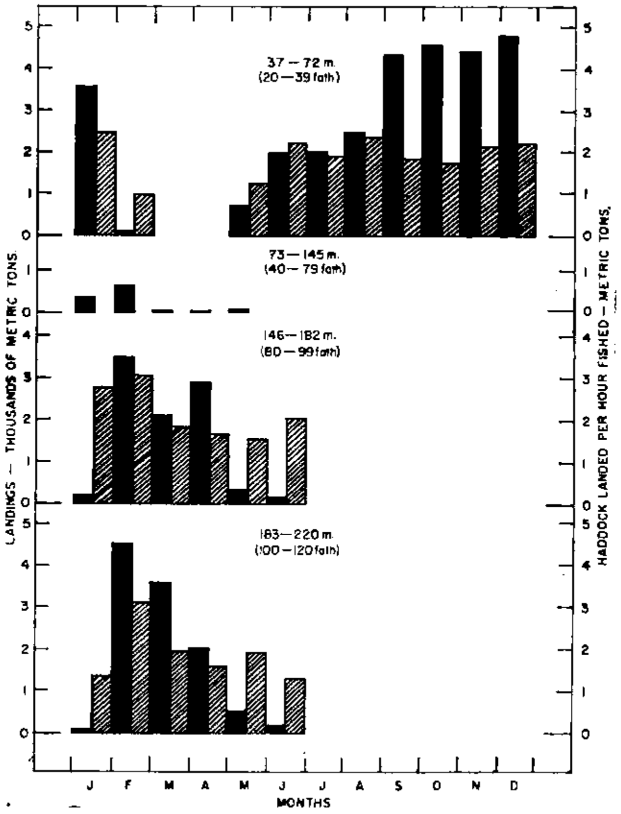

Fig. 5. Average monthly landings and landings per unit effort of whole haddock by Newfoundland trawlers (151-400 tons) at various depth ranges on St. Pierre Bank, 1954-56. (Black bars represent landings and cross-hatched bars the landings per unit effort.)

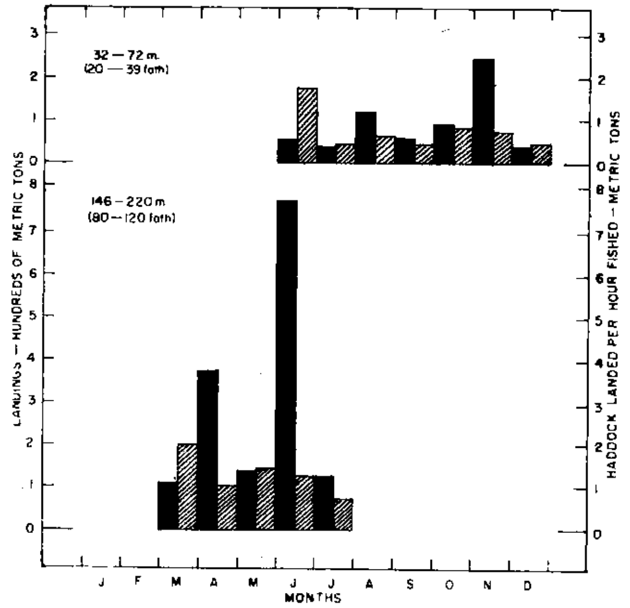

Fig. 6. Average monthly landings and landings per unit effort of whole haddock by several Newfoundland trawlers (151-400 tons) at various depth ranges on St. Pierre Bank, 1946-50. (Black bars represent landings and cross-hatched bars the landings per unit effort).

Landings per unit effort (Fig. 5) indicate that quantities of haddock were present in the intermediate deep water (146-182 m) in January, but as similar quantities were available in shallow water the fishermen continued to fish there because they preferred the shallower depths. In January the haddock had not penetrated in quantity to the deepest water of 183-220 m. By February both the landings from the shallow water and the landings per unit effort were considerably reduced whereas there was a considerable increase in both of these at the deepest fishing level. When fishing in the shallow water was resumed in May there was only a slight increase in the landings per unit effort beyond those of February. By June the fishery had mainly returned to the shallow water, and the landings per unit effort declined at the deepest level but increased in the intermediate deep water and in the shallow water.

These data indicate that in January and February haddock rapidly migrated downward from the shallow water of St. Pierre Bank to the deep water along the western slope with a gradual return to the shallow water in May-June. Due to lack of fishing in the shallow water in March-April and in the deep water from July to December the record is not complete, but research vessel catches, carried out mostly in June 1951-54 (Fig. 1, 2), showed only small quantities of haddock in the deep water compared with the large amounts in the shallow water on top of the bank.

In the period of sporadic effort in 1946-50, for which data are available for only a few trawlers, most of the fishing for haddock was carried out in deep water (146-220 m) along the western slope of the bank from March to July and a little from June to December on top of the bank in 37-72 m (Fig. 6). Landings at the rate of a ton or more per hour's fishing were made from the deep water in March-June and from the shallow water in June. Catches undoubtedly were considerably larger because at this time almost all haddock below 45 cm and some up to 50 cm in length were discarded.

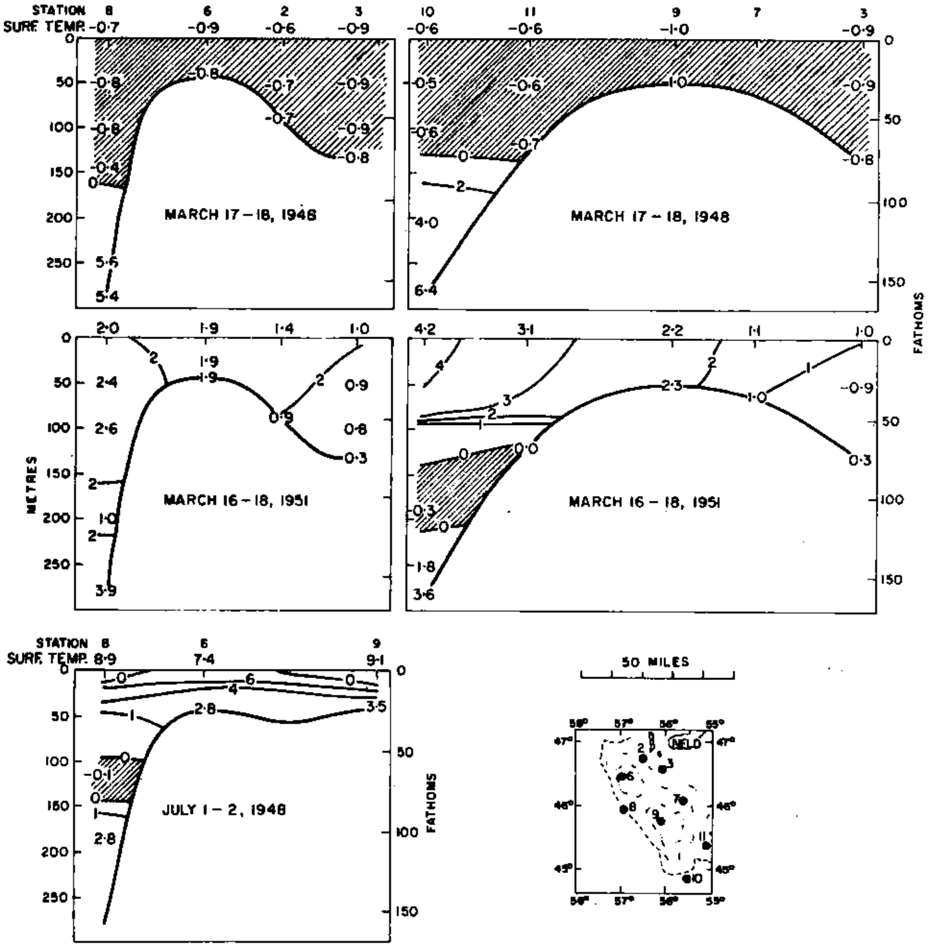

Fig. 7. Temperatures (°C) on St. Pierre Bank in March 1948, 1951 and in July 1948 (from hydrographic cruises of the *Investigator II*.)

Bottom Water Temperatures in General Relation to the Commercial Fishery

Temperatures were not taken during the commercial cruises but are available from hydrographic ruises of the *Investigator II* for 1948 and 1951 and for 1954-55 (Fig. 7,8). In March (1948) temperatures from the surface to about 150 m were below 0°C and in April (1954 and 1955) bottom temperatures ranged from about 1°C at 40-50 m on the plateaus of the bank to about 0°C at 100 m. In hese months temperatures on the western slope of the bank in 175 m were at 3.0°C or higher and sually 5 to 6°C or higher at 200 m in warmer years such as 1954-55 and at 250 m in 1948, a cold ear.

Even in cold years such as 1948 temperatures in the shallowest water at 40 m on top of the ank were close to 3°C or higher by July. By August these temperatures may be 4 to 5°C or higher. eanwhile in these summer months temperatures in the deep water were usually high as in winter and hroughout the year, but centred in the vicinity of about 100 m there was a cold intermediate layer ith temperatures usually below 1°C. Minimum temperatures in this intermediate layer varied from elow 0°C in cold years (Fig. 7,8) to about 2°C in warm years such as 1951 (Fig. 1).

In March 1951 temperatures were unusually high (1.9 to 2.3°C) in the shallow water on the top f the bank, but cold water extended deeper than usual on the western slope. In exceptional years uch as 1951 (Fig. 1) bottom temperatures on top of the bank may reach as high as 6 to 7°C by late une-early July.

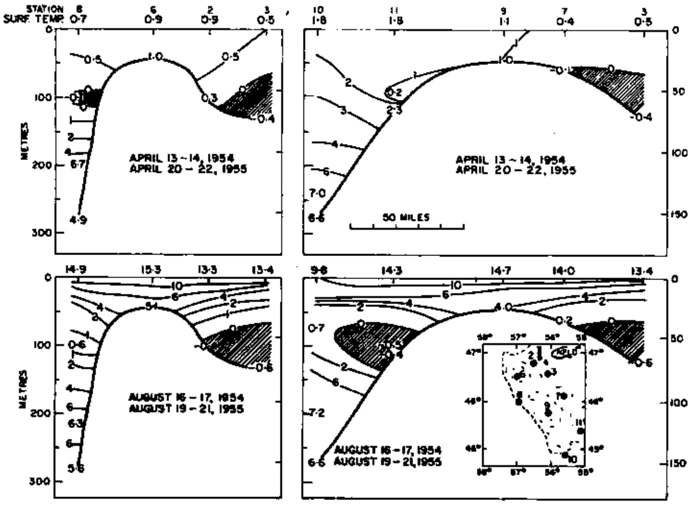

Fig. 8. Temperatures (°C) on St. Pierre Bank in April and August 1954 and 1955 (from hydrographic cruises of the *Investigator II.*)

Both in spring and in summer haddock were restricted in bottom distribution by the presence of water below 0°C in the St. Pierre Channel to the north of the bank. There is some summer migration of St. Pierre Bank haddock, however, to the Burin Peninsula and their shoreward passage to this peninsula is probably pelagic.

DISCUSSION AND CONCLUSIONS

For the Grand Bank, Templeman and Hodder (this symposium) found haddock to occupy the deep water of the southwest slope in late winter and early spring, with the larger concentrations mainly between 120-275 m and temperatures between 2.5 and 9°C. Haddock concentrations were at higher or lower temperatures in this range in different years depending on the prevalence of high or low temperature water on the southwest slope. In movements onto the top of the bank in April-June the 2°C contour was usually restrictive and in the latter part of this movement concentrations were usually at temperatures of 3°C and over. Occasionally a good catch was made at temperatures as low as 0.4°C, but this was unusual. The temperature distribution shown in Fig. 7 and 8 and the related depths and landings per unit effort throughout the year (Fig. 4-6) show that the St. Pierre Bank haddock follow a pattern generally similar to that of Grand Bank haddock in depth and temperature relationships.

The largest catches of haddock from research vessel operations on St. Pierre Bank from late May to early July 1951-54 were in the shallow water. On the average the largest shallow water catches were taken at temperatures between 2.5 and 7.0°C but a few large catches occurred at temperatures from 1.4 to as low as 0.7°C.

The retreat of haddock and the haddock fishery from the shallow water in January-February and the advance into shallow water in May-June are apparently a retreat from low temperatures on the surface of the bank and a return again to the shallower water of the bank as the water on top of the bank warms up.

The relatively greater commercial catches in deep water than in shallow water in June-July 1946-50 (Fig. 6) compared with the same months in 1954-56 (Fig. 5) may be due to several causes: The haddock population at the earlier period consisted, to a much greater degree than in the latter period, of large haddock over 10 yr of age whereas the haddock caught in 1954-56 were chiefly 5-7 yr old. These large fish may have had a greater tendency to remain in deep water during summer as do large cod off the northeast coast of Newfoundland (Templeman and Fleming, 1956). On the whole the earlier period had more cold years. The year 1948 was a cold year in the shallow water of St. Pierre Bank (Fig 7.) whereas 1954 and 1955 were moderately warm years (Fig. 8). The year 1950 was also cold in the early part of the year in the shallow water on St. Pierre Bank with below 0°C temperatures in March approximately the same as in 1948. These low temperatures in the upper water layers may have kept the fish in deep water somewhat longer in the earlier period.

ACKNOWLEDGEMENT

The authors are grateful to Mr A. M. Fleming for the provision of statistics of haddock catches by Newfoundland trawlers fishing on St. Pierre Bank.

REFERENCES

TEMPLEMAN, WILFRED, and A. M. FLEMING, 1956. The Bonavista long-lining experiment, 1950-1953. *Bull. Fish. Res. Bd. Canada*, 109: 1-55.

TEMPLEMAN, WILFRED and V. M. HODDER, 1964. Distribution of haddock on the Grand Bank in relation to season, depth and temperature. *This Symposium Contribution No. A-8.*

A-10

INFLUENCE OF COLD WATER ON FISH AND PRAWN STOCKS IN WEST GREENLAND[1]

By

Sv. Aa. Horsted[2] and Erik Smidt[2]

ABSTRACT

Redfish is especially sensitive to low temperatures and it is for this species that there are most records of mass mortality after severe winters. Mass mortality because of extraordonarily cold water has also been recorded among other species of fish (cod, lumpfish etc.), but the most catastrophic effect of winter-cooled water in West Greenland was the total destruction of the stocks of deep sea prawns, *Pandalus Borealis*, in the fjords at Holsteinsborg after the very severe winter 1948/49.

In many fjords cod follow the capelin when the latter arrive there in May and June to spawn. In some years, however, when the coastal water is colder than normal, capelin arrive in the fjords without being followed by the cod which cannot go through the cold water barrier.

In certain threshold fjords the bottom water is constantly cold. In these fjords cod and redfish are very rarely found in the trawl catches and *Pandalus borealis* has a very slow growth rate, late sex reversal and negligible reproduction. *Pandalus borealis* is partly replaced by *Spirontocaris machilenta* in these fjords.

MORTALITY DUE TO EXTRAORDINARILY LOW TEMPERATURES

1. Redfish *(Sebastes marinus)*, cod *(Gadus morhua)* and other species.

On several occasions mass death of redfish *(Sebastes marinus)* in West Greenland fjords has been stated as being an effect of heavy winter cooling of the sea. In a paper about *S. marinus* the late Professor Ad. S. Jensen (1922) refers to a letter written on 20 February 1889 by Colonial Manager R. Müller in Sukkertoppen to Professor in Zoology Chr. Lütken, in which it was mentioned that an enormous quantity of dead or dying redfish were covering the surface of the sea off Sukkertoppen. In a letter of 4 April of the same year Müller added that larger or smaller numbers of redfish had been found in different places every day from the middle of February till that date. The Greenlanders told Müller that it was not uncommon at that place for the redfish to rise to the surface in this manner, and that it does not happen to any other fish. Sometimes redfish rise every year in greater or smaller numbers, sometimes after an interval of several years, but always between January and April inclusive and mostly in February and March. About 12 yr before redfish was said to have risen so profusely and so widely that the fjord, seen from the mountain, was red with dead specimens.

Jensen (*loc. cit.*) discussed the phenomenon with the hydrographer, Dr J. N. Nielsen. He was of the opinion that it was caused by the cooling of the water, since the *Tjalfe*-expedition showed that -1°C could be recorded down to 100 m or more off Sukkertoppen towards the end of the winter. Further Nielsen believed that the fish while possibly hunting for food for instance had risen to higher levels than usual and became so weak in the cold water they could not descend again, and so slowly died.

In the warm period which has existed in Greenland waters since about 1920, mass death of redfish does not seem to have been so common. Still we have records after the two severe winters 1937/38 and 1948/49 when many redfish and fish of other species were killed.

After the severe winter of 1937/38 records from Sukkertoppen show that great quantities of dead *S. marinus, Gadus morhua, Reinhardtius hippoglossoides, Cyclopterus lumpus* and *Anarhichas sp.* were found in the spring (Hansen, 1939). In Amerdloq Fjord at Holsteinsborg a great many dead or dying cod were taken by the prawn trawlers at the beginning of the summer. All had a hole in the side through to the body cavity and the intestines had disappeared (Hansen, *loc. cit.*). The most

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[1] Originally Contribution No. A-3, ICNAF Environmental Symposium, Rome 27 January-1 February 1964.

[2] Greenland Fisheries Investigations, Charlottenlund, Denmark.

probable explanation is that the fishes had been paralysed by the cold water and attacked by a predator, which Dr Paul Hansen, in accordance with Greenlandic fishermen and hunters , thinks is the harp seal (verbal information).

The winter of 1948/49 was more severe than the winter of 1937/38 and winter cooling of the water went down to the bottom of the Amerdloq and Ikertoq Fjords (Holsteinsborg district) and killed the redfish and the prawns (Hansen, 1951, Horsted and Smidt, 1956). In the spring of 1949 great quantities of dead and dying redfish were seen on the surface of the fjords, and once in March the sea off the mouth of Amerdloq was quite red with redfish. As late as the first of July some dead redfish were observed on the surface from the research cutter *Adolf Jensen*.

In the innermost part of Godthåb Fjord, inside the outpost of Kapisigdlit, the fishermen in the middle of March 1959 observed many dead cod. They had never seen this in previous years. This observation corresponds with the fact that unusually cold water, from -1.5 to -1.3°C, was observed from the surface down to 90 m depth.

2. Deep sea prawn *(Pandalus borealis)*

Since 1935 prawns have been trawled in Amerdloq and Ikertoq Fjords at Holsteinsborg, but in 1949 the fishery had to be given up as the prawn stocks were totally destroyed by the cold bottom water. This occurrence, however, must be regarded as abnormal, as the prawns survived the severe winter of 1937/38. After the catastrophe in 1949 it was 4-5 yr before the prawn stocks recovered, which is about the same time it takes a prawn to grow from an egg to fishable size (Horsted and Smidt, *loc. cit.*).

3. Temperature observations showing the effect of the extremely cold winters 1937/38 and 1948/49.

As mentioned the biological effects of the severe winters of 1937/38 and of 1948/49 were very important. No temperature observations, however, were made in winter then, but as can be seen from two series of observations made in summer, one from Fylla Bank (Table 1) and one from Amerdloq Fjord (Table 2), the effect of the winter cooling was still very pronounced in the summers of 1938 and 1949.

TABLE 1. FYLLA BANK (63°58'N. 52°44'W.). BOTTOM TEMPERATURES (°C) AT ABOUT 40 M IN JUNE OF VARIOUS YEARS.

Year:	1925	1926	1928	1934	1936	1937	1938	1947	1948
Temp.:	0.8	2.2	1.8	2.7	2.0	1.3	0.0	3.4	1.3
Year:	1949	1950	1953	1954	1956	1957	1959	1960	
Temp.:	0.1	1.0	1.4	2.2	0.8	1.3	1.6	2.6	

TABLE 2. AMERDLOQ FJORD (66°54'N. 53°35'W.). TEMPERATURES (°C) AT 300 M IN VARIOUS YEARS FROM MAY TO AUGUST INCLUSIVE

Year:	1909	1934	1935	1936	1937	1938	1939	1947	1949	1950
Temp.:	1.0	1.4	1.4	0.9	1.0	-0.9	0.7	2.5	-1.6	0.0
Year:	1951	1952	1953	1954	1955	1956	1957	1959	1960	
Temp.:	0.9	1.0	1.8	-0.2	1.0	2.7	0.8	1.2	1.4	

EFFECT OF UNUSUALLY COLD WATER ON FEEDING MIGRATIONS OF COD

Under normal temperature conditions in Southwest Greenland waters the cod follows the capelin *Mallotus villosus)*, its favourite food, when the latter migrates in the early summer (May and une) to the shore of the fjords in order to spawn. At that time there is an important cod fishry with pound nets in several fjords. In some years, however, when the coastal water is colder han normal the capelin arrives in the fjords without being followed by the cod, which cannot go hrough the cold water barrier. From recent years we have good instances of this phenomenon in 949 and 1954 and possibly in 1963.

After the severe winter of 1948/49, shoals of capelin arrived in Amerdloq and Ikertoq Fjords ear Holsteinsborg in May and June, but they were not followed, as usual, by the cod because of he cold water, so that the cod fishery in the fjords failed at that time.

Ameralik Fjord in Godthåb district is a threshold fjord with constantly cold bottom water. he local cod stock is only small, but when the capelin enters the fjord for spawning it may be ollowed by great quantities of cod from the coastal region. This was the case in 1951, when a ound net fishery was started, but in 1954 the fishery failed completely as the cod kept out of he fjord in spite of a normal invasion of spawning capelin. The coastal water was very cold that ear and must have been the reason the cod could not enter the fjord. The following biological obervations give a clear picture of the conditions in 1954.

From 26 April to 2 June 1954 Ameralik Fjord was visited five times by fisheries biologists, and hroughout that period very few cod could be fished. However, some cod eggs were taken in the 1m tramin net in the surface water at the end of April. On 21 May much roe of capelin was observed on he bottom at the shore, and later, on 2 June good catches of capelin were made with a hand seine. emperature observations were made on 12-13 May showing cold water with negative temperatures from he bottom up to between 30 and 20 m depth inside and outside the threshold. Table 3 and 4 give ome temperature observations made in the coastal region in May since 1954, and clearly show that 954 was a very cold year.

TABLE 3. ENTRANCE TO THE GODTHAB FJORD. TEMPERATURES (°C) AT VARIOUS DEPTHS AND DAYS DURING MAY OF 1954-62.

Depth in m	1954 17th	1955 25th	1956 16th	1957 14th	1958 14th	1959 16th	1960 21st	1961 12th	1962 29th
0	0.8	1.4	1.4	0.9	1.5	3.3	2.3	2.2	2.5
20	0.7	1.2	1.0	0.8	0.9	1.6	1.7	1.7	1.5
50	0.5	1.2	1.0	0.8	0.6	1.3	1.5	1.5	1.3
100	0.4	1.2	1.0	0.8	0.6	1.2	1.6	1.3	1.4
200	0.2	1.2	1.0	0.8	0.3	1.1	1.6	1.3	1.3
300	0.1	1.3	1.0	0.8	0.3	1.0	1.6	1.2	1.3

TABLE 4. COASTAL WATER SOUTH OF GODTHAB (63°53'N.51°28'W). TEMPERATURES (°C) AT VARIOUS DEPTHS AND DAYS DURING MAY OF 1954-58, 1961 AND 1962.

Depth in m	1954 15th	1955 27th	1956 28th	1957 23rd	1958 13th	1961 4th	1962 30th
0	1.2	2.3	1.0	3.8	1.4	1.1	2.8
20	0.0	1.7	1.0	1.0	0.1	0.6	1.8
50	-0.3	1.4	1.0	0.7	0.1	0.6	1.8
100	-0.6	1.2	0.9	0.2	0.2	0.6	0.9
200	-1.0	0.8	0.5	-0.1	0.4	0.3	0.5

TABLE 5. ARFERSIORFIK FJORD: TEMPERATURES (°C) 4-6 SEPTEMBER 1949.

Depth in m	Station A	Station B	Station C
10	2.83	2.58	3.38
50		2.27	1.63
100	2.99	1.80	-1.09
150	2.48	1.66	-1.32
200	2.21	1.04	-1.15
225		0.93	
250	2.15		
300	2.17		

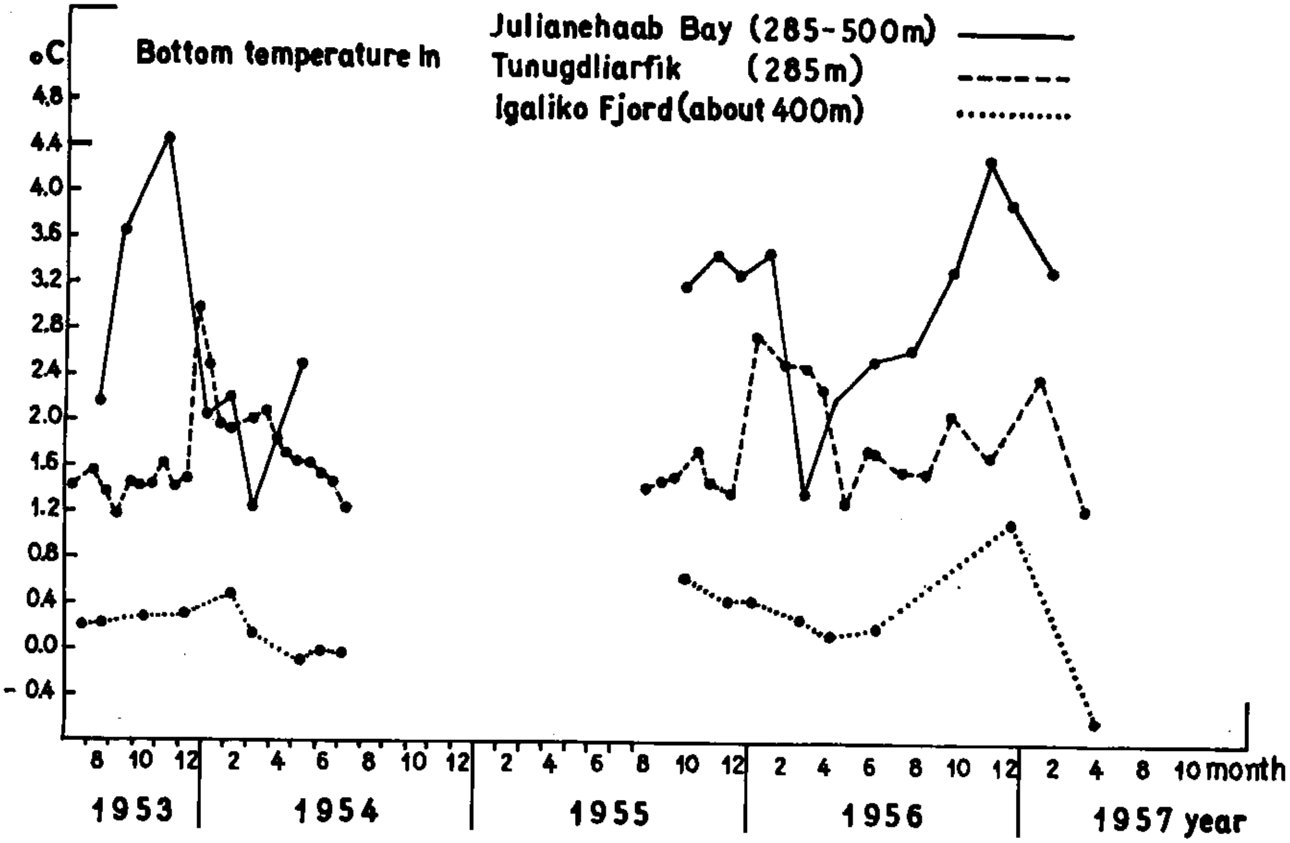

Fig. 1. Bottom temperatures (°C) in Igaliko Fjord (60°46'N.45°40'W.), Tunugdliarfik Fjord (60°56'N.45°47'W.) and Julianehåb Bay. (In Julianehåb Bay the station position has normally been 60°35'N.46°19'W. but in periods with ice other positions near the main station have been used).

EFFECT OF CONSTANTLY COLD WATER ON THE COMPOSITION OF ANIMAL COMMUNITIES AND ON THE BIOLOGY OF PRAWNS ON THE PRAWN GROUND

The depth of the prawn grounds in the West Greenland fjords is normally 250-400 m. The most important of these grounds are found in fjords without a threshold (open fjords) where relatively warm bottom water can enter. The bottom temperature in open fjords is normally above zero throughout the year. Some of the West Greenland fjords, however, are threshold fjords with one or more thresholds in the outer part of the fjord and one or more deeper basins in the inner part of the fjord. The warm deep currents do not enter these threshold fjords. The bottom temperature in the threshold fjords is often below zero and always lower than the bottom temperature in the open fjords. In this section examples of the hydrography of the threshold fjords and of the influence of the constantly cold bottom water on the animal communities are given.

1. Examples of the hydrography of threshold fjords.

1.1. *Arfersiorfik Fjord* (lat 68°10'N.) has several basins divided by thresholds. Threshold depths are 50-100 m while the depth of the trawling grounds in the basins is 220-285 m. Observations were taken in September 1949 (Table 5). Station A is outside the threshold in the mouth

TABLE 6. TEMPERATURES (°C) AT VARIOUS DEPTHS AND DAYS IN IGALIKO FJORD IN 1951, 1953-57.

	1951	1953				1954			
Depth in m	Sept. 14	July 29	Aug. 27	Oct. 19	Dec. 6	Feb. 10	March 9	May 3	June 3
0	5.1	10.1	5.8	2.2	-0.5	-1.0	-1.1	0.6	1.9
10	4.75	4.37	3.90	2.41	0.06	-0.86	-1.09	-0.11	1.17
20		2.52	2.51	2.30	0.80	-0.86	-1.06	-0.47	1.06
25	3.82								
30		1.81	1.92	2.32	0.80	-0.85	-1.10	-0.54	0.74
50	2.24	1.22	1.89	2.51	1.67	-0.56	-1.03	-0.53	-0.23
75		0.87	0.35	1.90	1.91	-0.60	-1.17	-0.57	-0.55
100	0.86	0.45	0.23	1.38	1.83	-0.37	-1.18	-0.72	-0.53
150	0.13	0.32	0.28	0.54		-0.12	-1.01	-0.69	-0.49
200	0.16	0.22	0.21	0.26	0.43	0.40	-0.37	-0.37	-0.23
250	0.17	0.23	0.23	0.35	0.26	0.41	0.18	-0.13	-0.17
300	0.20	0.20	0.18	0.22	0.19	0.36	0.40	-0.07	-0.09
350		0.38	0.24	0.27*	0.21	0.43	0.14	-0.18	-0.06
385-400	0.22+	0.22	0.22		0.33	0.48	0.13	-0.09	-0.01

*) at 325 m +) at 375 m

	1955			1956					1957
Depth in m	July 2	Oct. 6	Dec. 5	Jan. 9	March 9	Apr. 24	June 29	Dec. 21	Apr. 3
0	10.0			-1.1		2.2	6.1	-1.5	0.3
10	3.94	1.84	0.47	-0.60	-0.28	1.19	2.25		
20	2.03	1.69	0.64	-0.55	-0.23	0.70	1.92		-0.35
25									
30	1.19	1.65	0.70	-0.53	-0.27	-0.45	1.46		-0.42
50	0.03	1.21	0.85	-0.39	-0.30	-0.39	1.01		
75	-0.42	0.55	0.84	0.50	-0.29	-0.28	0.32		-0.42
100	-0.22	0.55	0.69	0.66	-0.31	-0.05	0.12	1.04	-0.71
150	-0.53	0.08	0.49	0.91	0.02	-0.01	0.05		
200	-0.27	0.32	0.47	1.17	0.15	0.11	0.11	0.58	-0.74
250	-0.17	0.50	0.49	0.42	0.15	0.10	0.16		-0.77
300	0.02	0.56	0.52	0.43	0.32	0.16	0.20		
350	-0.07	0.65†	0.47	0.43	0.32	0.18	0.22		-0.61
385-400	-0.03			0.43	0.25	0.15	0.22	1.14	-0.63

†) at 330 m

TABLE 7. BOTTOM TEMPERATURES (°C) AND CATCHES OF COD, REDFISH AND *Pandalus borealis* AT 400 M IN IGALIKO FJORD IN 1951, 1953-55.

	Bottom temp.	Cod	Redfish	*Pandalus*	Trawling time
	°C	*no. per hr*	*no. per hr*	*kg per hr*	*hr*
1951					
Sept. 14	0.22	0	0	20	2.25
1953					
July 29	0.20				0
Aug. 27	0.22				0
Oct. 19	0.27				0
Oct. 30		0	0	29	1
Dec. 6	0.33				0
Dec. 15		0	0	57	1
1954					
Feb. 10	0.48	24	4	50	0.50
March 9	0.13	1	0	44	1.25
May 3	-0.09	0	0	15	1
June 3	-0.01	0	0	31	1
July 2	-0.03	0	0	67	0.58
1955					
Oct. 6	0.65	0	0	20	0.75
Dec. 5	0.47	0	0	24	0.58
1956					
Jan. 9	0.43				0
March 9	0.25	0	1	15	0.75
Apr. 24	0.15	0	0	25	0.92
June 29	0.22	0	0	53	1
Dec. 21	1.14	0	1	20	1
1957					
April 3	-0.63	0	1	2	1

of the fjord; Station B inside the first threshold (depth of threshold about 100 m); and Station C in the innermost part of the fjord (threshold depth about 50 m).

1.2. In *Julianehåb district* (southern Greenland) trawling grounds are found in most of the fjords. Of these Tunugdliarfik (60°56'N. 45°47'W.) among others, is an open fjord with depths about 300 m while Igaliko Fjord (60°46'N. 45°40'W.) is a threshold fjord with a trawling ground depth of about 400 m.

The hydrographic conditions in the district are characterized by a mixing of the warm Irminger Current and the cold East Greenland Polar Current. The latter is found mainly nearest the coast and lies above the former.

In the offshore area the warm Irminger Current dominates the deeper water layers in autumn and the beginning of winter, while the cold water dominates in spring and in summer, when Irminger water is found only at great depths (Fig. 1). In the open Tunugdliarfik Fjord these fluctuations appear 1-2 months later. In Igaliko Fjord, however, there is only a very slight inflow of the warm, deep current due to a threshold (Fig. 1, Table 6). The temperature conditions in the threshold fjord depend more upon local warming and cooling of the water as well as upon the extent of he cold surface Polar Current.

. Effect on cod and redfish abundance.

Horsted and Smidt (this symposium p. 435-437) showed that redfish normally occur in the prawn atches in the open fjords throughout the year, and cod occur in the same catches in winter time. n catches from the cold threshold fjords this is not the case.

In Arfersiorfik Fjord trawling was carried out at Stations B and C (Table 5). At Station B, 7 small redfish were caught in one hour. At Station C the fish fauna was poor apart from 233 *ycodes seminudus*. Only one redfish (8 cm) was caught. At both stations cod were absent, but at his time of the year cod is not at all likely to be found at great depths in the fjords (Hansen *oc. cit.*).

In Igaliko Fjord several trawling experiments were undertaken. Catches of cod, redfish and *andalus borealis* per one hour's trawling were recorded together with the bottom temperatures Table 7). Normally cod and redfish are absent in the catches or appear only as single specimens. he exception is February 1954 when 12 small cod and 2 redfish were caught in half an hour's trawing. At this time the bottom temperature was relatively high and the upper water layers down to 50 m had negative temperatures.

Normally, however, no cod and redfish are taken in trawl catches in Igaliko Fjord. The ermilik Fjord (about 60°30'N. 45°00'W.) has a threshold depth of about 50 m. A trawling experient was carried out on 14 August 1953. The depth of the trawling ground was about 350 m and the ottom temperature -0.4°C. Cod and redfish were absent from the catch.

. Influence on prawn stocks (growth rate, sex reversal, reproduction, composition)

The prawn fishery in Greenland is based on *Pandalus borealis*. This prawn has sex reversal protandric hermaphrodity) as shown by various authors. Sex reversal occurs when the prawn has rown to a carapace length of about 25-30 mm. Growth rate, however, is affected by temperature nd consequently the age at which sex reversal occurs is also affected by the temperature (Horsted nd Smidt, 1956, p.43). Thus, in Tunugdliarfik sex reversal takes place at 4 yr of age, but in galiko Fjord one fraction of the prawns have sex reversal at 4 yr of age and another fraction at yr of age. In Sermilik Fjord sex reversal is found only in the 5 yr olds. By comparison, the ame prawn species in the Skagerak has sex reversal at 2 yr of age.

Temperature, however, is not the only factor affecting the growth rate and age at sex reveral. In Disko Bay (about lat 69°N.) sex reversal occurs at 5 yr of age but temperature conditions ere are just as favourable as in Tunugdliarfik where reversal occurs at 4 yr of age. Perhaps in isko Bay the long, unproductive winter season is decisive. There are several deciding factors of hich temperature is the best known, but quantity of food and the length of the period of producivity are certainly just as important (Horsted and Smidt, *loc. cit.*). Reproduction takes place n the prawn stocks in Disko Bay and in the open West Greenland fjords. In some of the threshold jords, however, sex reversal takes place and later on spawning, but many and in some years proably all, females lose their eggs before hatching.

TABLE 8. IGALIKO FJORD. *Pandalus borealis*. DEVELOPMENT OF FEMALES (AND TRANSITIONALS) IN % OF TOTAL FEMALES AND TRANSITIONALS.

Year	1951	1953		1954					
Month	Sept.	July	Oct.	Jan.	Feb.	March	May	June	July
Day	15	3	30	14	10	9	3	3	3
% no roe	54.6	36.5	84.4	100.0	61.4	9.8	10.0	27.9	50.0
% head roe	0.0	4.8	0.0	0.0	29.5	85.3	90.0	19.4	0.0
% ovigerous, embryos eyes not visible	45.5	52.2	15.5	0.0	6.8	0.0	0.0	36.2	44.4
% ovigerous, embryos eyes visible	0.0	0.0	0.0	0.0	0.0	4.9	0.0	0.0	0.0
% no eggs, setae on pleopods	0.0	6.4	0.0	0.0	2.3	0.0	0.0	16.7	5.6
Numbers of transitionals and females	33	63	58	25	44	41	20	36	18

This phenomenon was quite apparent in Igaliko Fjord in 1953-54 (Table 8). Head roe developed during the spring months and spawning is completed by the end of June. Few of the females, however, succeeded in becoming ovigerous. While 90% of the females had head roe in the spring of 1954 only 44% of the females were ovigerous on 3 July 1954. At the same time many females with setae on the pleopods were found but none of them had roe of any kind. Apparently the spawned eggs did not adhere at all or adhered only for a short time to the pleopods. Possibly fertilization was unsuccessful. Even if eggs adhere in some individuals they are gradually cast off so that ovigerous females become fewer and almost none of them carry the eggs at the time when hatching should take place. Only on 9 March 1954 were ovigerous females found, and these comprised only 5% of the females.

Thus reproduction in Igaliko Fjord is negligible. Larvae hatched on other grounds however, are transported here by surface currents and maintain the stock.

A wide distribution of larvae also explains why *Pandalus borealis* occurs so far to the north in West Greenland as southern Upernavik district. Here, at the island of Skaløen, trawling experiments were carried out in July 1949 and in July 1957. The composition of the prawn stock in 1957 is shown in Fig. 2. The most striking feature of this composition is not the small amount of large prawns (females) but the total absence of prawns with carapace length 24-27 mm. Since prawns of this length are 4 yr old, the 1953 year class is totally absent from the stock. The stock is presumably recruited by drift of larvae from more southerly areas (Disko Bay) and it must be supposed that the conditions for this drift were very bad in 1953. Unfortunately we have not enough observations to say more about this phenomenon.

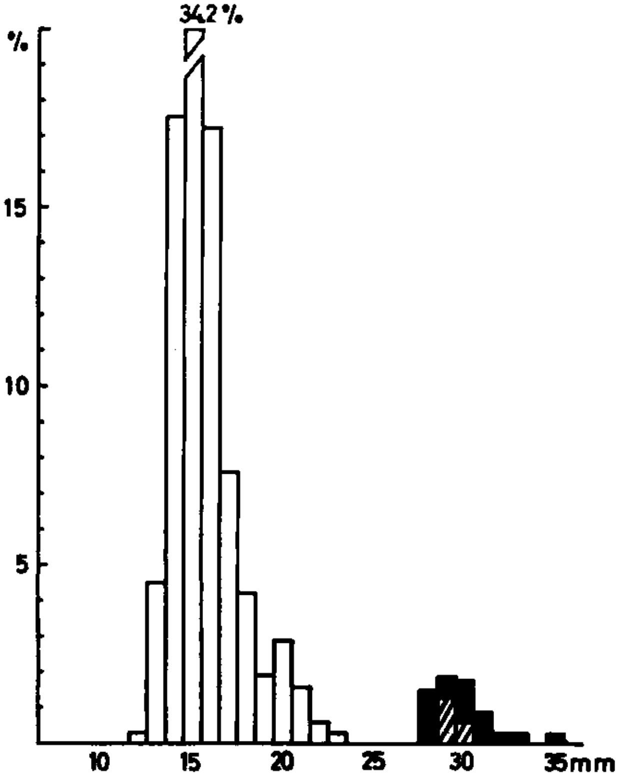

Fig. 2. *Pandalus borealis*. Carapace length of 315 specimens taken 10 July 1957 SE of Skaløen, (71°53'N. 55°26'W.) Symbols: White; juveniles and males. Crosshatching, transitionals. Black; females. Carapace is measured from eye lobe to posterior lateral edge.

On most of the West Greenland prawn grounds *P. borealis* is by far the predominant species. *Spirontocaris machilenta* is another common species but, because of its small size, is of no commercial value. Experimental trawling was carried out with 18mm mesh size of cod end which retains a great deal of the *Spirontocaris*. In Tunugdliarfik the catch per hour of *Spirontocaris* varied in 1953-54 in the following way. In August-September 1953, 1,000-3,000 individuals per hour were caught, the rest of the year less than 500 per hour and in March 1954, 80 per hour. Looking at the bottom temperatures (Fig. 1) it is evident that *S. machilenta* occurs in the greatest quantities when the bottom temperature is lowest. In this connection *S. machilenta* shows just the opposite to *P. borealis*. Consequently one can expect *S. machilenta* to be particularly dominant in fjords with cold bottom water. In Sermilik Fjord *Spirontocaris* was the predominant species and in Igaliko Fjord it was nearly of the same abundance as *P. borealis*. In Arfersiorfik Fjord (Table 5) *Pandalus* dominated at Station B with *S. machilenta* as a common species. At Station C in the same fjord only a few *Pandalus* were caught but *S. machilenta* was numerous. In Fig. 3 the number of *S. machilenta* in percent of the number of *P. borealis* is given from the various grounds in Julianehåb district and is correlated with the actual bottom temperature. With temperatures less than -0.2°C *S. machilenta* is the dominant prawn species. Between -0.2°C and 2.0°C it must still be, considered as a characteristic animal but *P. borealis* dominates and more so as the temperature rises. Only one out of 46 samples fits poorly into this picture (1.8°C - 70% *S. machilenta* 60°21'N. 45°25'W., 15 September 1953). With temperatures from 2°C to 3°C *S. machilenta* still occurs rather commonly but at temperatures higher than 3°C it is rarely found.

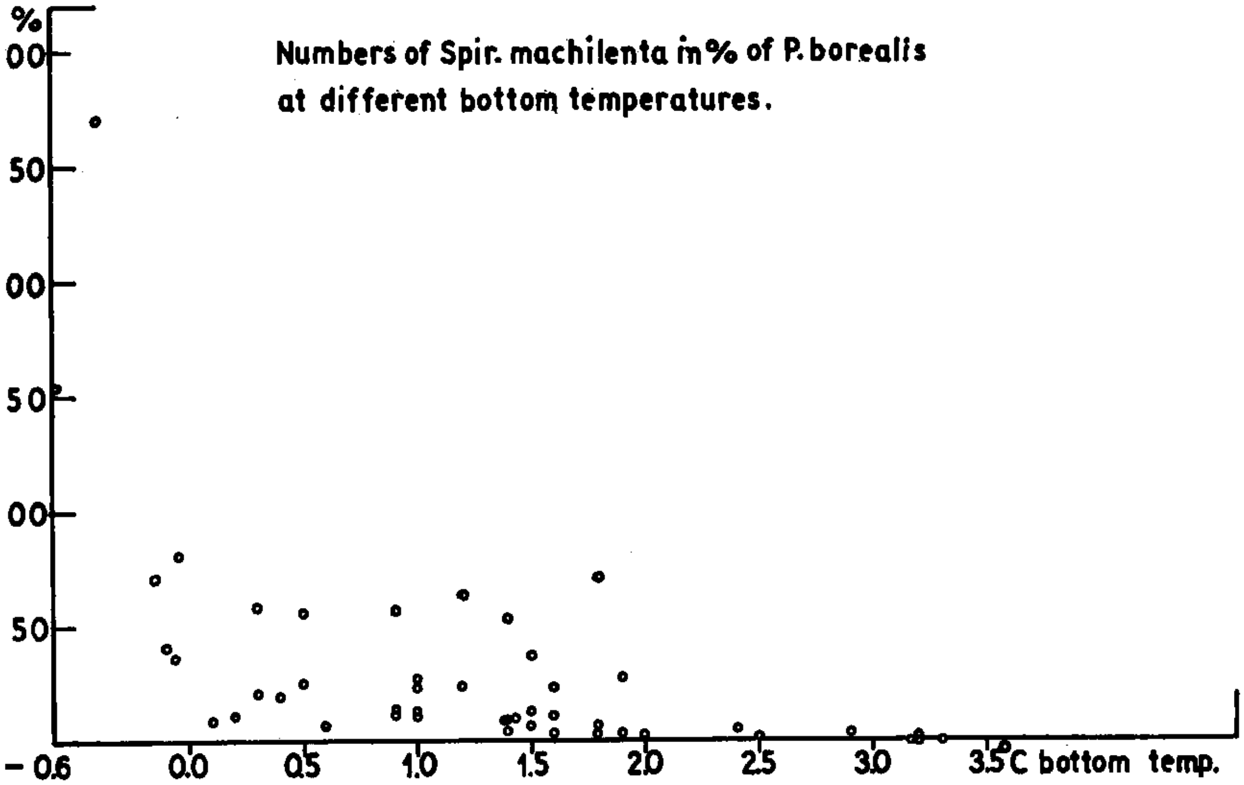

Fig. 3. Numbers of *Spirontocaris machilenta* as a percent of numbers of *Pandalus borealis* at different temperatures from various grounds in Julianehåb district.

REFERENCES

HANSEN, P.M. 1939. Fiskeriundersøgelser i 1938. *Beretninger vedr. Grønlands Styrelse.* 1: 199-200.

1951. Fiskeribiologiske undersøgelser 1949. *Beretninger vedr. Grønland.* 1: 70-71.

HORSTED, SV. AA. and E. SMIDT. 1965. Remarks on Effect of Food Animals on Cod Behaviour. *This Symposium, Contribution No. C-1.*

1956. The Deep Sea Prawn (*Pandalus borealis* Kr.) in Greenland Waters. *Medd. Danm. Fisk. Havundersøg. N.S.*, 1 (11).

JENSEN, AD. S. 1922. Research on the Distribution, Biology and Systematics of the Greenland Fishes. I. *Sebastes marinus*. *Vidensk. Medd. dansk. naturh. Foren. Kbh*, 74: 89-109.

A-11

INFLUENCE OF THE TEMPERATURE REGIME ON THE BEHAVIOR OF REDFISH OFF WEST GREENLAND IN SPRINGS 1959-1961[1]

By

L.N. Pechenic[2] and I.I. Svetlov[2]

ABSTRACT

The authors of this report attempt to show the influence of the temperature conditions on the distribution of redfish (*Sebastes marinus* L.) on the Banana and Lille Hellefiske Banks in spring during the period 1959-61. They state that the location of redfish concentrations during this season is mainly influenced by the intensity of the Canadian Polar Current.

CONDITIONS IN 1959

The results of our investigations (Pechenic, 1960) showed that in April 1959 the redfish concentrations were as usual on the slopes of the Banana Bank and also on the eastern and western slopes of the Lille Hellefiske Bank (Fig. 1B). It is evident that redfish concentrated in the channel between the Banana and Fyllas Banks with the near-bottom temperature between 4.0° and 4.6°C. Scouting vessels caught more than two tons per trawling hour. In 1961 there were no redfish concentrations north west of the Lille Hellefiske Bank (Fig. 3B).

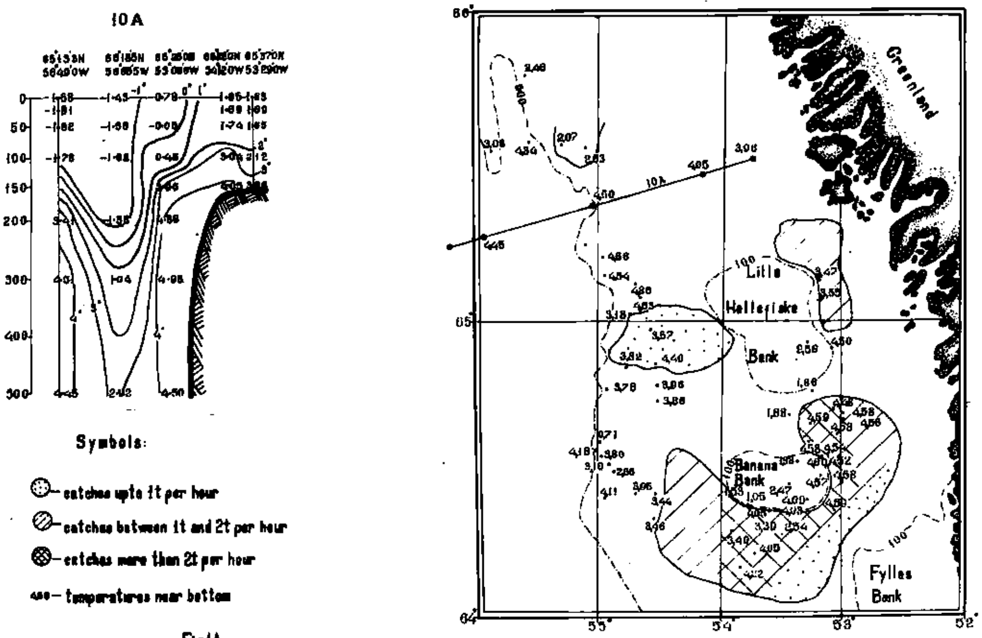

Fig1A

Fig1B

Fig. 1. (A) Isotherms on Section 10a on 26 April 1959 north of the Lille Hellefiske Bank.
(B) Distribution of the redfish concentrations and near-bottom temperatures in April 1959.

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We suppose this peculiarity was mainly due to the temperature conditions. Temperatures recorded on Section 10A (Fig.1A) on 26 April 1959 across the Lille Hellefiske Bank north of the areas of redfish concentrations, enable us to conclude that the redfish behaviour was influenced by the extent of the cold Canadian Polar Current. According to Killerich (1943), in early summer this current is often influenced by the north western winds and protrudes far to the east over the western slopes of the Store and Lille Hellefiske Banks to a depth of 150-200 m. On reaching these banks the Canadian Polar Current usually has the temperature of 0° to 1.0°C and salinity of 33.50 to 34.00°/00. However, in April 1959, the waters of the current were much colder than indicated by Killerich and had temperatures of -1.8° to 1.5°C. The cold water penetrated to a depth of 250 m (Fig. 1A) and, on reaching the area northwest of the Lille Hellefiske Bank, evidently hampered the formation of redfish concentrations in that area.

CONDITIONS IN 1960

In the spring (April-the beginning of May) of 1960 the main redfish concentrations were, as previously, found on the Banana Bank, but if we compare 1960 with 1959, the catches were smaller. We ascribe this to some changes in the hydrological conditions north west of the Lille Hellefiske Bank.

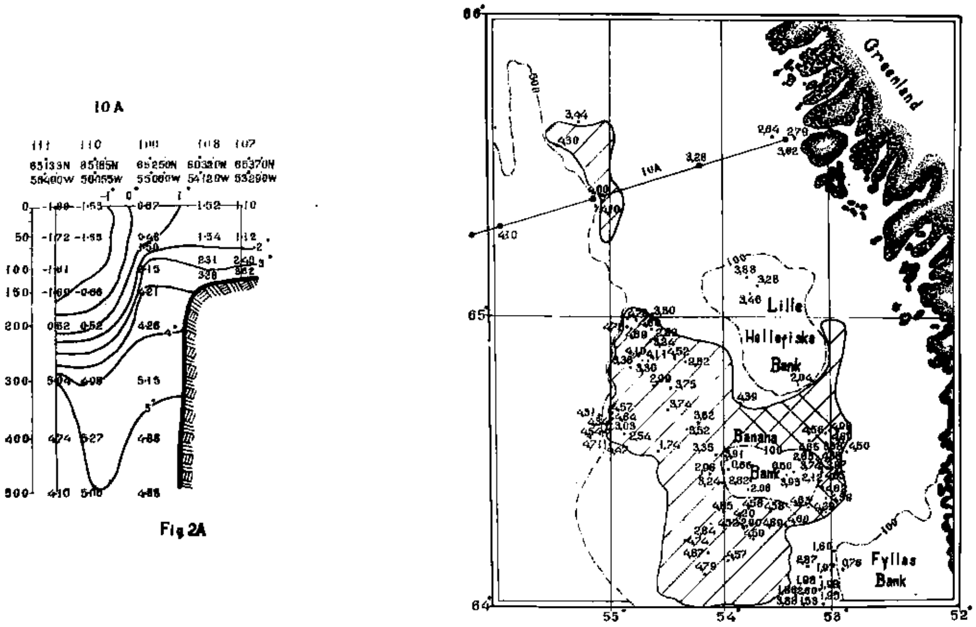

Fig 2A

Fig 2B

Fig. 2 (A) Isotherms of 5 May 1960 on Section 10a.
(B) Distribution of the redfish concentrations and near-bottom temperatures in April 1960.

The temperature distribution on Section 10A (Fig. 2A), carried out in May 1960, shows a de- :rease from the same period in 1959 in the amount of cold water from the Canadian Polar Current, ınd it only penetrated down to 150-175 m. In the warm waters of the Irminger Current in 1959 :he temperature was 3° to 4°C. at depths of 200-400 m, while in the spring of 1960 the temperature ncreased by 1°C. All these conditions favoured, to a certain extent, the more extensive distri-)ution of the commercial redfish concentrations, their advance in a north westerly direction and :heir appearance on the slope. These concentrations were not observed at all in April 1959.)uring both the above mentioned years the feeding of redfish at the places of concentrations was)oor.

CONDITIONS IN 1961

In contrast to 1959 and 1960, the most dense redfish concentrations were met in 1961 on the 'estern slope of the Lille Hellefiske Bank and to the north west. On the Banana Bank concentra- :ions were less dense and catches were poorer.

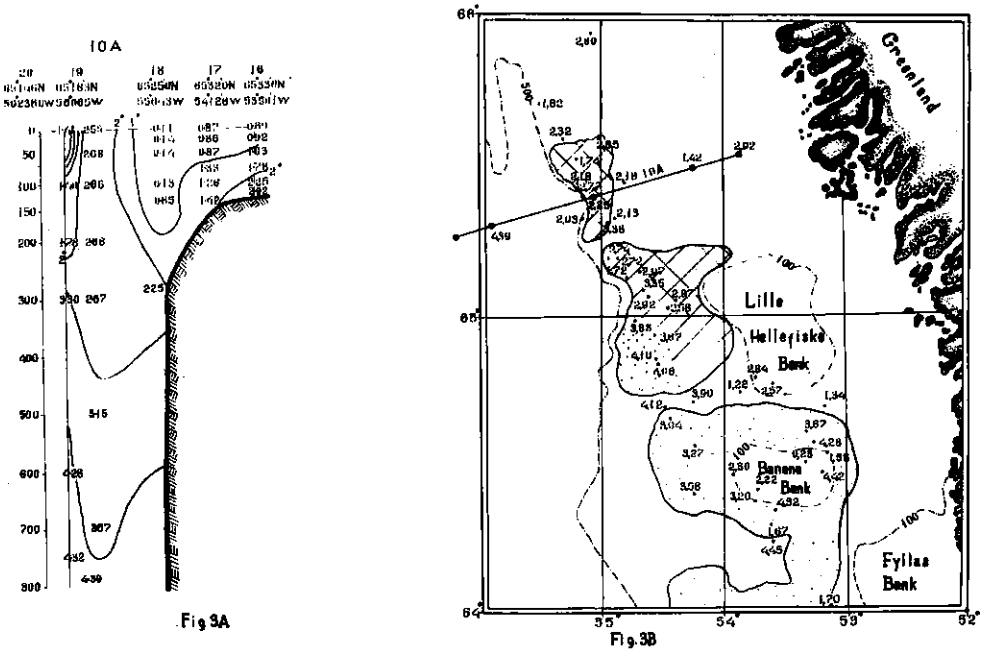

Fig 3A

Fig 3B

ig. 3 (A) Isotherms on 21 April on Section 10a.
(B) Distribution of the redfish concentrations and near-bottom temperatures in April 1961.

Analysing the distribution of waters on 22 April 1961 on the Section 10A (Fig. 3A), we see hat the cold Canadian Polar Current is less developed than in the two previous years. Cold aters with a temperature of -1.5°C. penetrated only to depths of 50-75 m and did not reach the ille Hellefiske Bank. This allowed a more north westerly redfish movement than in the two revious years. There were good food resources for redfish in this area; they fed on krill *Euphausiacea*) and, despite the temperature of 2.5° to 3.5°C. in the near-bottom layer, formed omparatively stable concentrations (Fig. 3B).

DISCUSSION

Figures 1B, 2B and 3B distinctly show that redfish keep to a certain level of temperature (4° to 4.6°C) at which their concentrations are more dense and stable. This is also confirmed by Meyer (1960) who states that the best redfish concentrations were observed in the spring of 1960 on the Lille Hellefiske Bank with water temperatures of 4.7° to 5.0°C and that in the areas, where the waters of the near-bottom layers were warmer, the catches were larger.

SUMMARY

1. The analysis of data obtained in the springs of 1959-61 revealed a certain relationship between the temperature conditions and the distribution of redfish (*Sebastes marinus* L.) in the area of the Banana and Lille Hellefiske Banks off the western coast of Greenland.

2. During some years in spring the cold Canadian Polar Current, depending on its strength, affects the temperature conditions on the Store and Lille Hellefiske Banks and the redfish distribution in these areas. When the inflow of cold waters brought by this current is intensive, redfish have the southern distribution and concentrate on the southern and south-eastern slopes of the Banana Bank and the eastern slope of the Lille Hellefiske Bank (1959). When the inflow of the cold waters is not intensive, redfish have a more northerly distribution and their main and dense concentrations occur on the north-western slope of the Lille Hellefiske Bank and to the north west of it (1960/61).

3. The most favourable temperature conditions for the formation of redfish concentrations are between 4° and 4.6°C in the near-bottom layer.

REFERENCES

PECHENIC, L.N. 1960. Natural Resources of the Davis-Strait. *Fishery Economy.*

KILLERICH, A. 1943. The hydrography of the West Greenland Fishing Banks. *Medd. Komm. Danm. Fish. Havundersøg.*, Ser. Hydrogr. 3 (3).

MEYER, A. 1960. Die Suchereise mach Gronland. *Allg. FischwZtg*, No. 42.

A-12

THE RELATION BETWEEN TEMPERATURE CONDITIONS AND FISH DISTRIBUTION IN THE SOUTHEASTERN BARENTS SEA[1]

By

Lars S. Midttun[2]

ABSTRACT

The distribution of cod and haddock in the south eastern Barents Sea, as observed during echo surveys, has been compared with the temperature conditions at 150 m. In the autumn the fish are mainly located in water of temperature above 2°C along the central cold water front and in the warm water tongues bending eastwards. In spring the fish are migrating towards the Finnmark-Murman Coast.

There is an east-west long-term fluctuation in the fish distribution. In 1954 the fish had an easterly distribution. During the following year the fish gradually moved westwards until 1958, when it reached an extreme westerly location. Later, as observed up to 1960, the fish again moved easterly. Similar long-term variations have been observed in the temperature conditions.

OBSERVATIONS AND METHODS

Echo surveys covering the central and south eastern Barents Sea have been undertaken twice a year regularly in order to study the distribution of cod and haddock in this area. Normally, the surveys are made in spring (March-April) and in autumn (September-October). The results of four cruises in the period autumn 1958-spring 1960 are shown in Figs. 1-4. The fish concentrations are illustrated as light, medium and heavy.

Echo-sounding is a suitable method for fish recording, when the fish are pelagic. On the other hand, echo-sounding has proved to be an unreliable method of recording for bottom concentrations. Especially in autumn the cod and haddock show a tendency to be located near the bottom. Even though the echo surveys have been supplemented by a network of trawl stations, one must make some reservations concerning undetected bottom concentrations of fish from the cruises made in the autumn. In spring the fish are more frequently found in pelagic formations, probably because they are heading towards the coast.

THE DISTRIBUTION OF TEMPERATURE

The distribution of cod and haddock in the Barents Sea is to be compared with the temperature conditions. In Figs. 1-4 the temperature conditions are illustrated by means of isotherms at 150 m depth. This depth represents the layer where the major part of the fish normally is located. The temperature conditions in the Barents Sea are characterized by comparatively warm water flowing in from the west and meeting with cold water formed in the eastern areas. The transition area between the warmer western water and the cold eastern water seems at most places to be stationary and is apparently related to the bottom configurations. Thus it is located above the north-south Central Ridge at about 35°E. The warm western water flows into the eastern Barents Sea mainly along two branches, one following the Murman coast, the other passing Skolpen Bank and proceeding eastwards towards Novaya Zemlya. The influence on the temperature conditions caused by these currents is clearly shown by the tonguelike forms of the isotherms.

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Whereas the temperature of the cold water in the north-east shows little change from time to time, there is a considerable variation in that of the warmer inflowing western water. The thin, solid line with the scale to the left in Fig. 5 shows the temperature observed at 150 m on Skolpen Bank (71°00'N, 37°20'E); the broken line with its scale to the right represents the

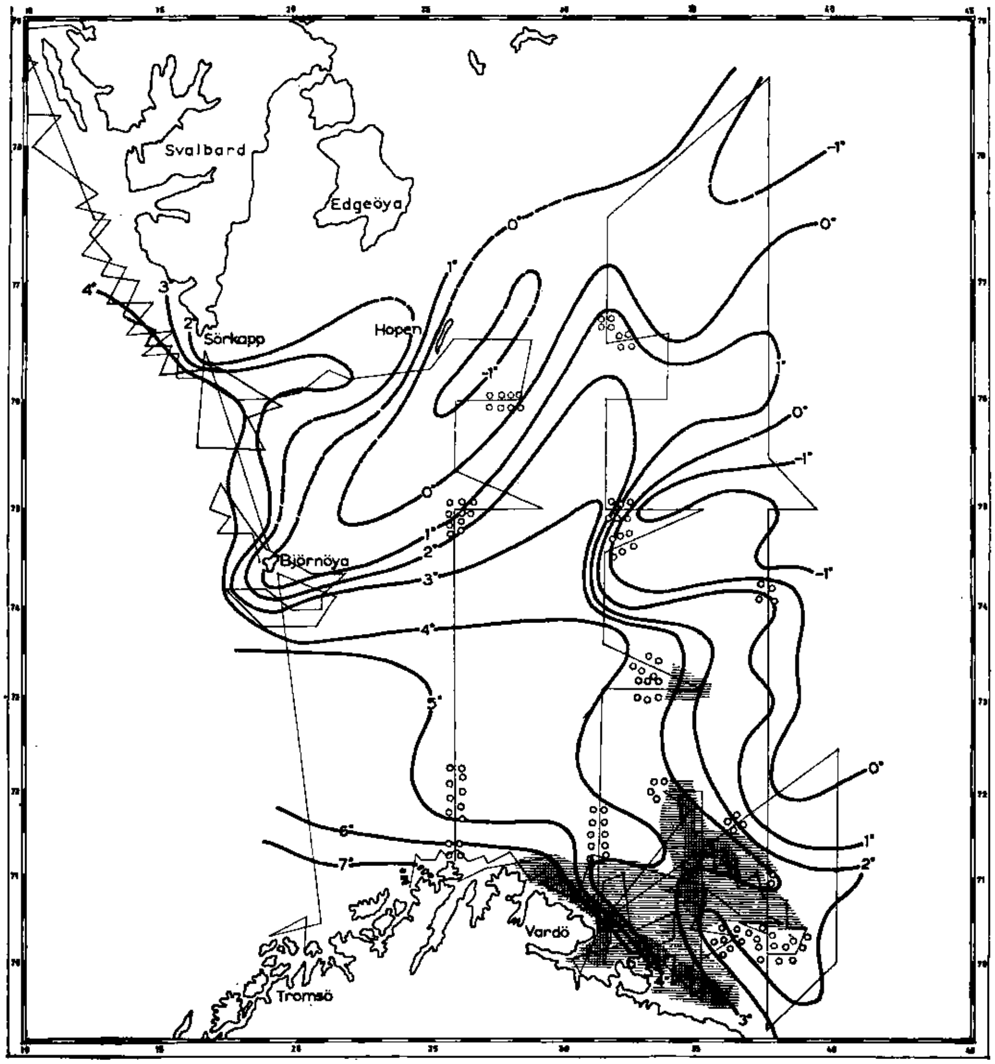

Fig. 1. Fish distribution and temperature (150 m), autumn 1958: *G. O. Sars* 20 September-24 October, 1958. Fish recorded in the Bear Island - Spitsbergen area are not included.
heavy lines = isotherms
thin lines = route of *G. O. Sars*
circles = light concentrations of fish
horizontal lines = medium concentrations of fish
combined horizontal and vertical lines = heavy concentrations of fish.

average temperature at 150 m in a section running northwards from Vardø in 31°13' E between 70° 30' and 73°00' N. Disregarding some irregularities (*i.e.* the spring temperature of 1957), there is a clear trend in the curves, from high values in 1954, decreasing to a minimum in 1958 and then again increasing up to 1960.

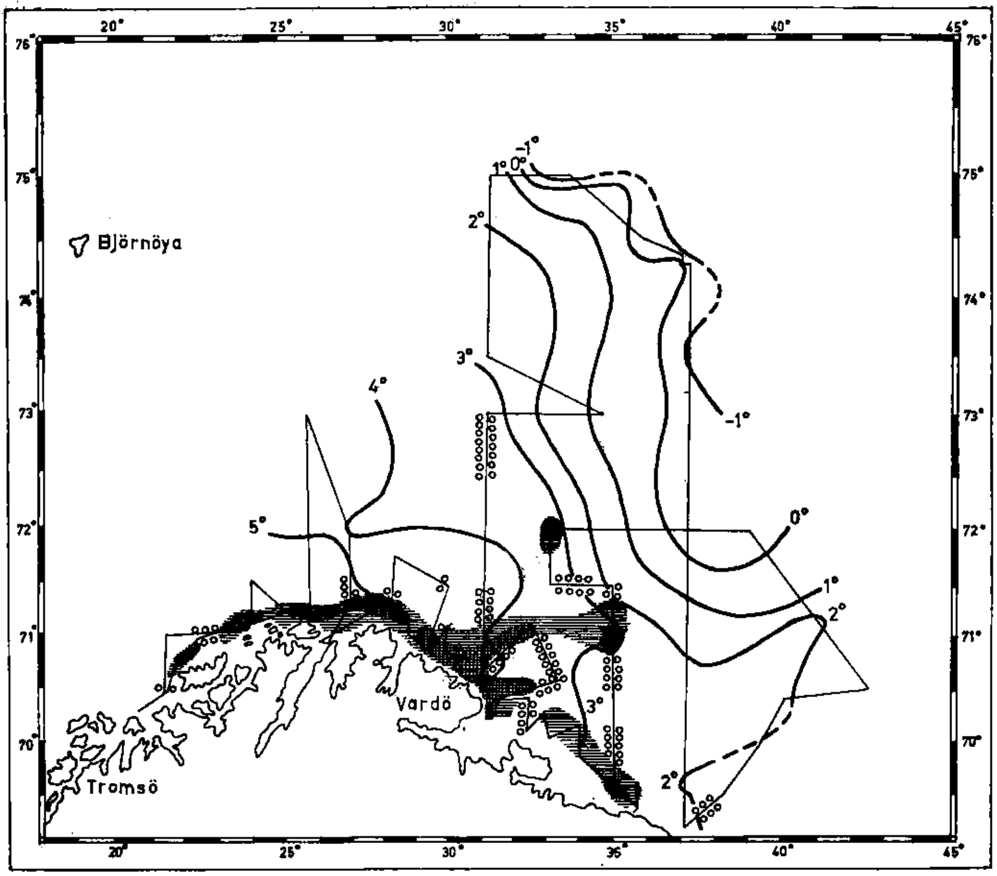

Fig. 2. Fish distribution and temperature (150 m), spring 1959: *G. O. Sars* 23 March - 20 April, 1959. Fish recorded in the Bear Island - Spitsbergen area are not included.
heavy lines = isotherms
thin lines = route of *G. O. Sars*
circles = light concentrations of fish
horizontal lines = medium concentrations of fish
combined horizontal and vertical lines = heavy concentrations of fish

THE DISTRIBUTION OF COD AND HADDOCK IN RELATION TO TEMPERATURE

Let us now consider the distribution of cod and haddock compared with the temperature conditions (Figs. 1-4). The figures show that the fish are located in the warmer western water. In spring the main concentrations are found near the coast of Finnmark and Murman. When surveyed again in the autumn, the fish have moved away from the coast and are now found against the cold water front above the Central Ridge, and in the warm water tongue, extending eastward. This is clearly seen by comparing Fig. 2 and Fig. 3. The fish are reluctant to move into water of temperature below about 2°C.

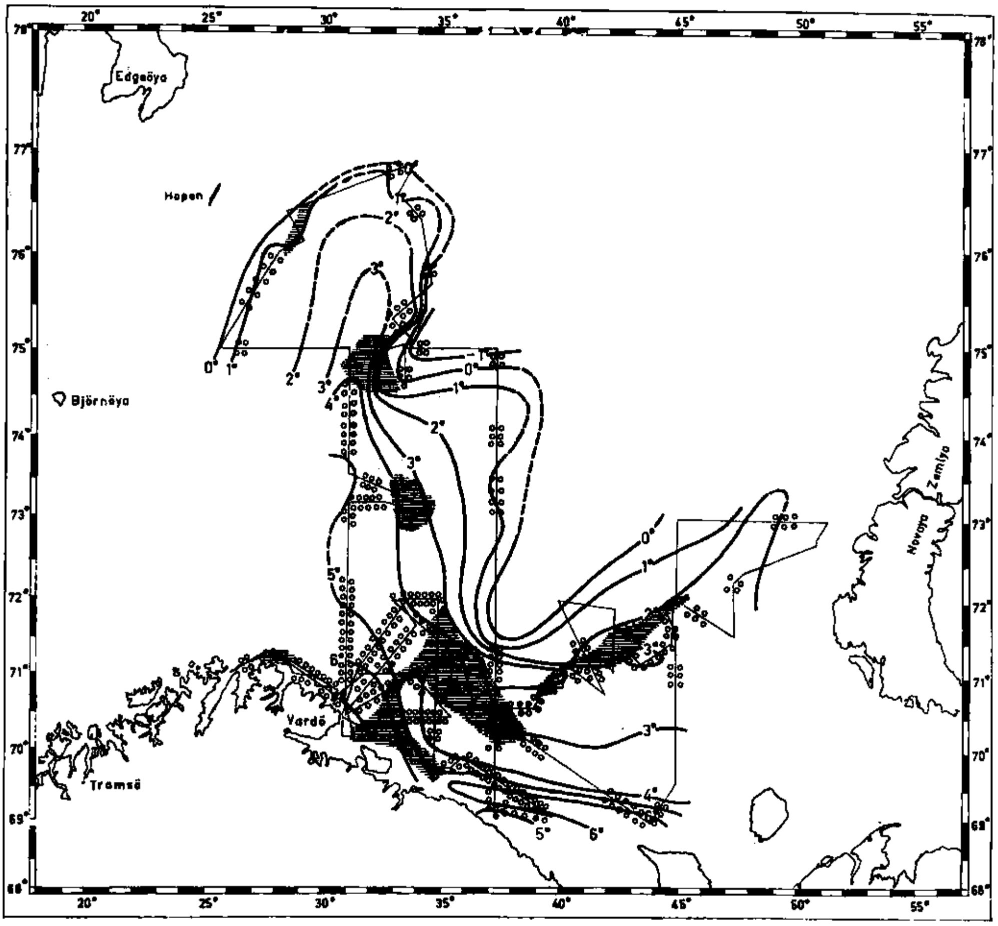

Fig. 3. Fish distribution and temperature (150 m), autumn 1959: *Johan Hjort* 23 September - 20 October, 1959. Fish recorded in the Bear Island - Spitsbergen area are not included.
heavy lines = isotherms
thin lines = route of *Johan Hjort*
circles = light concentrations of fish
horizontal lines = medium concentrations of fish

In addition to this seasonal variation in distribution there is, as well, a year-to-year variation. This variation is obviously connected with long-term temperature variations. The above mentioned trend in the temperature variations (Fig. 5) is reflected also in the fish distribution. Results from fishing and echo-sounding observations have shown that the fish in the warm year, 1954, were found far to the eastward in the sea. Gradually they moved westwards until in the cold year, 1958, they had their extreme westerly distribution. Later, as observed to 1960, the fish again moved towards the east. This can also be seen from Figs. 1-4: for example the fish were located farther to the east in 1960 (Fig. 4) than in 1959 (Fig. 2). A similar displacement can be seen by comparing Fig. 1 with Fig. 3. There is one irregularity in this general picture; the relatively high temperature measured in the spring of 1957 did not bring about a corresponding easterly distribution of the fish concentrations. However, the warmer period of 1957 was very short and there might be a lag or slowness in the displacement of the fish distribution.

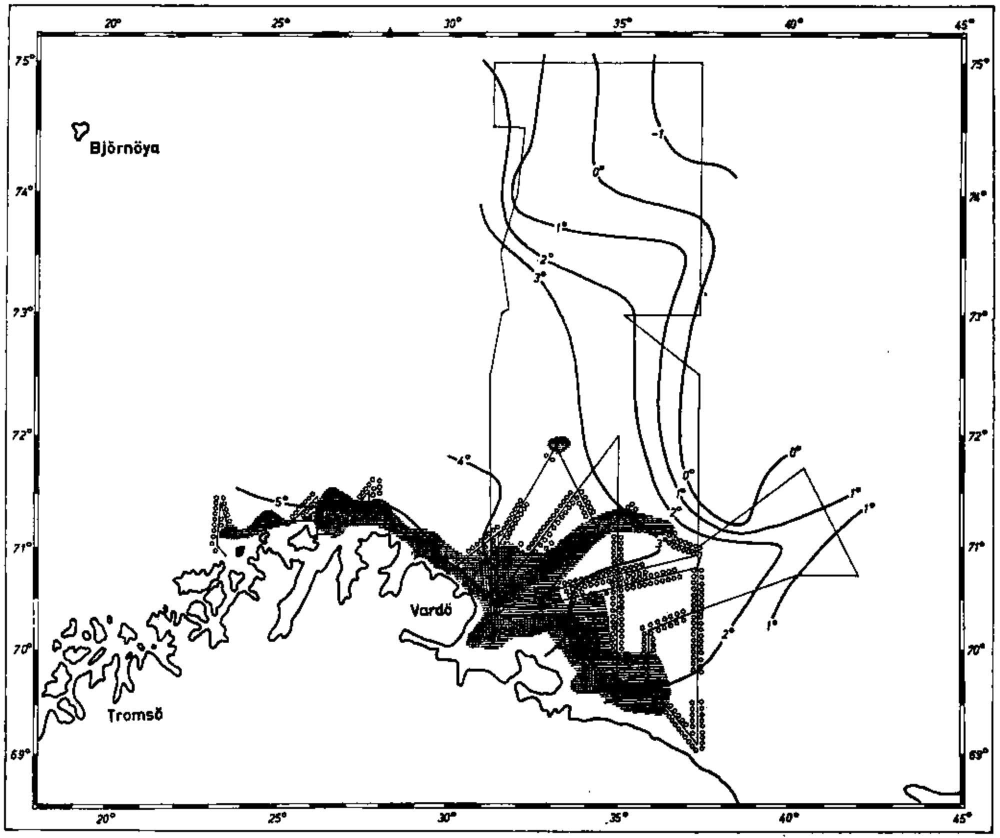

Fig. 4. Fish distribution and temperature (150 m), spring 1960: *Johan Hjort* 22 April-12 May, 1960. Fish recorded in the Bear Island - Spitsbergen area are not included.
heavy lines = isotherms
thin lines = route of *Johan Hjort*
circles = light concentrations of fish
horizontal lines = medium concentrations of fish
combined horizontal and vertical lines = heavy concentrations of fish

Figure 5 shows the total yield of the Norwegian spring cod-fisheries for the years 1954 - 60 (scale to the left). This yield over the seven year period corresponds to the main trend of the long-term temperature variations in such a way that low temperatures give high yields and high

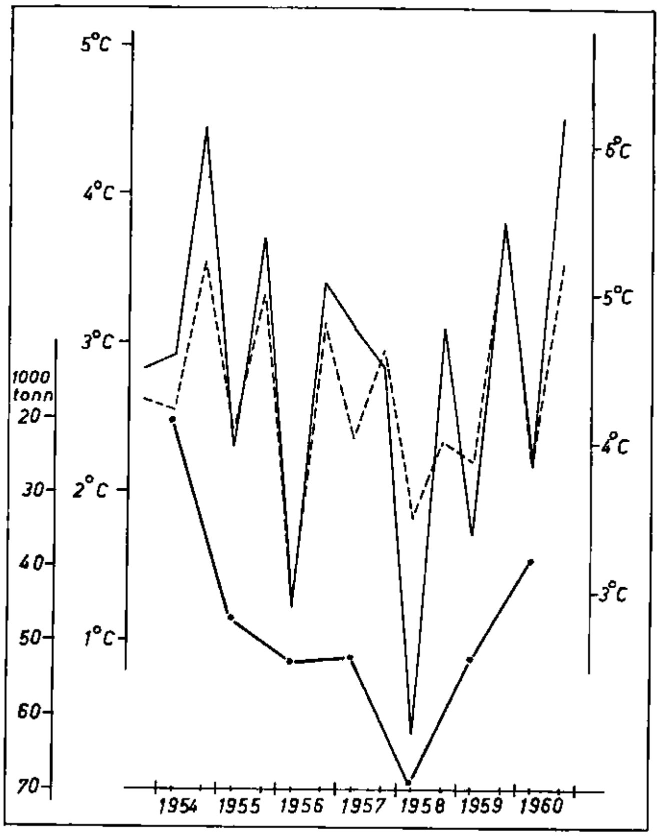

Fig. 5. Yield of the Norwegian spring cod fishery in thousands of tons (heavy solid line) in relation to temperature variations from 1954-60 of

(a) western water at 150 m in a section running northwards from Vardø in 31°13"E and between 70°30" and 73°00" N. Temperature curve in broken line with its scale to right of the figure. And

(b) water on Skolpen Bank (71°00"N, 37°20"E). Temperature curve is thin, solid line with its scale at the left of the figure.

temperatures low yields. When the fish in periods of high temperatures are distributed eastward, they are not so available for the Norwegian fishing fleet as in the colder periods when they are distributed westward.

To obtain a more detailed picture of the distribution of fish near a sharp temperature front, a local concentration of cod, found in October 1956 on the north-eastern Skolpen Bank, was investigated more closely. Figures 6 and 7 show the results of this detailed survey. The cod were located in a layer between 150 and 220 m, with the largest concentrations between 170 and 200 m. The horizontal distribution of fish is illustrated in Fig. 6. Fish concentration is given by numbers referring to an arbitrary scale where high numbers mean high concentration. Isotherms represent the temperature at 200 m depth. Figure 7 shows the temperature and fish distribution in the cross-section indicated by a dotted line in Fig. 6. The figure shows that the main concentration of fish is found between 2 and 3°C, but fish are also found at lower temperatures, even lower than 0°C.

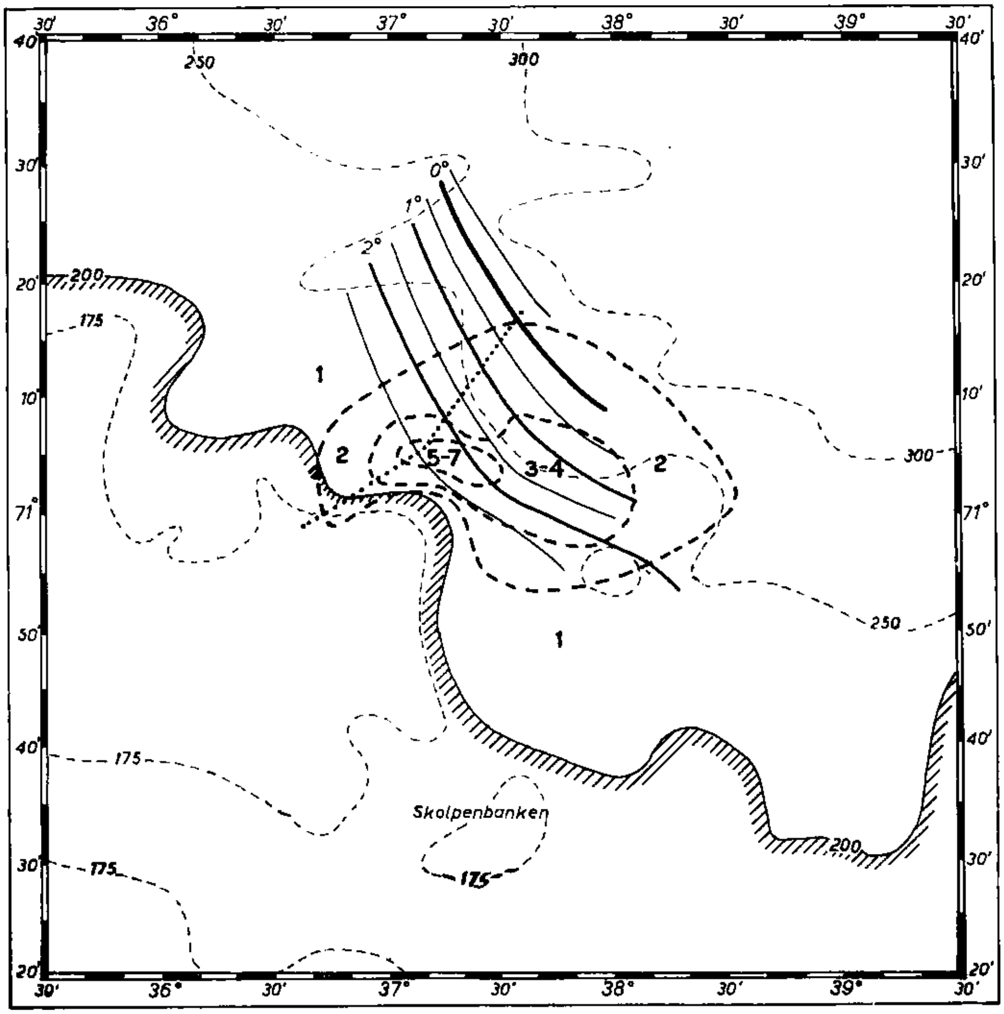

Fig. 6. Local concentration of cod in a temperature transition area on the north-eastern Skolpen Bank, October 1956. Solid lines are isotherms at 200 m. Broken lines circumscribe areas of increasing fish density as indicated by the numbers 1-7. Dotted line shows the location of the cross-section illustrated in the Fig. 7.

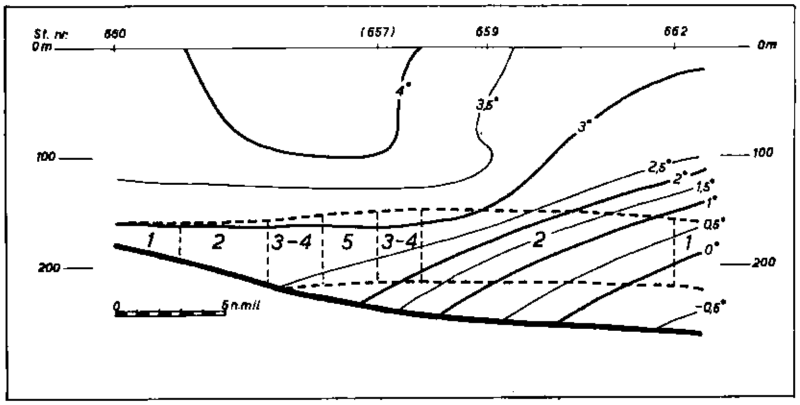

Fig. 7. Temperature and fish density in a cross-section through the same concentration of cod as is shown in Fig. 6. Solid lines are isotherms at 200 m. Broken lines circumscribe areas of increasing fish density as indicated by the numbers 1-7.

A-13

WATER TEMPERATURE AS A FACTOR GUIDING FISHES DURING THEIR MIGRATIONS[1]

By

K. G. Konstantinov[2]

ABSTRACT

When undertaking seasonal migrations, fish are usually guided by the water temperature. There- re, temperature observations enable us to foresee the paths and time of migrations of commer- al fishes. Thus, the water temperature in November in the 150-200 m layer on the Kola hydro- gical section accounts for the area where capelin and capelin cod approach the coasts of the rents Sea in March-April of the next year. The water temperature in the 50-200 m on the same ction in February-March make it possible to judge upon the mass movements of capelin cod via e Murman Shelf in May of the same year.

ABIOTIC CONDITIONS AS ORIENTING FACTORS FOR THE MIGRATORY ANIMALS

Performing complex and lengthy migrations, fish are in need of some guide posts. In the pro- ss of evolution precise responses to the environment were formed. With the help of these res- nses fish can reach points within the area of their distribution where there is more food or ss enemies, or where the conditions are safer for the development of deposited eggs. Neither minosity nor almost inappreciable admixtures of mineral or organic matter themselves (*ipso facto*) e of vital importance for migrants, they only help in searching for migratory ways, thus, serving orienting factors (Konstantinov, 1958). The point of view developed here is particularly well lustrated in the case of white bass (*Roccus chrysops*) which finds its way to the spawning grounds the sun (Hasler, 1960*a*, 1960*b*; Hasler & Henderson, 1963).

In a great number of cases water temperature is a guiding factor for fish. It is generally own that some fish occur only within a definite, often very limited temperature range (this cilitates detection of fish concentrations). Meanwhile, aquarium observations indicate that sh can safely stand temperatures that are never encountered in nature. Vladykov (1933) showed is for haddock, Gerasimov (1961) for herring, Kelly and Barker (1961) for redfish and McCracken 963) for flatfish. So there are no reasons to suppose that there is a purely physiological rmfulness in the temperature being avoided by the free-living fishes. The choice of a particular mperature helps a fish to reach the area with the optimum biotic conditions in due time. From is point of view it is quite obvious that in nature the range of preferred temperatures changes gularly throughout the year. Thus, the Atlantic cod (*Gadus morhua*) are not found at a temp- rature below +2°C in winter, while in the summer-autumn months they do not avoid the areas even th 0°C temperature (Woodhead and Woodhead, 1959). Certainly, a more extensive distribution of sh is expedient in the main feeding period than in the period of wintering. An attempt is made low to consider the afore-mentioned ideas in more detail with special reference to capelin cod.

DEPENDENCE OF THE MIGRATORY PATH OF CAPELIN COD UPON THE WATER TEMPERATURE IN THE BARENTS SEA.

At the beginning of spring, mainly in March-April, the concentrations of capelin (*Mallotus llosus*) and "capelin cod" living on capelin come to the southern coast of the Barents Sea. As rule, specimens of 40-70 cm, immature, with the liver weight not over 5-6% of fish weight, pre- il in the stock of capelin cod. Stomachs of the cod are packed full with capelin. Concentrating ar shores, capelin cod are subjected to an extensive fishery. In the years of severe hydrologi- l regime both cod and capelin migrate to the coast by more westerly routes than in the warm ars. Favourable fishing conditions may prevail either off the Finmark or Murman coasts.

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Polar Institute of Marine Fisheries and Oceanography (PINRO), Murmansk, USSR.

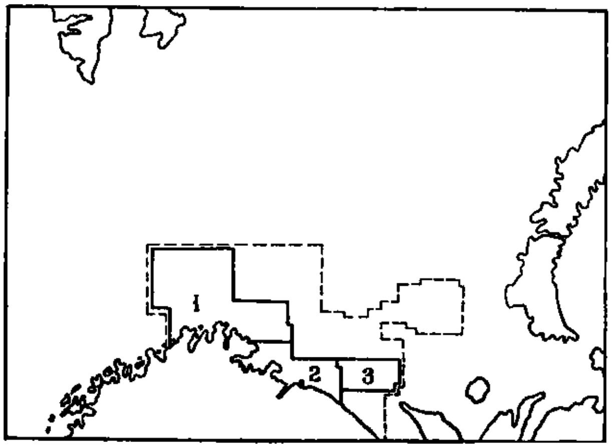

Fig. 1. Areas of the trawl fishery in the Barents Sea: 1 - the Finnmark Coast, 2 - the Murman Coast, 3 - the Murman Shallow. Dotted line - the boundary of the southern part of the Sea within the limits of which the main cod fishery is carried out in March-April.

Therefore, the increase in the Soviet catches of capelin cod and capelin is usually accompanied by the drop in the Norwegian catches and vice versa (Konstantinov, 1961; Prokhorov, 1963*a* and 1963*b*).

Using the hydrological data, one can foresee the route of the spring migration of capelin cod several months before its beginning. The methods proposed are as follows.

The southern coast of the Barents Sea is divided into two zones: western (Finnmark) and eastern (Murman). The importance of each zone for the Soviet trawl fishery in March-April is defined by the percentage of the catch taken in the given zone to the total catch in the whole southern part of the Barents Sea. If compared with ICES, Area I, our boundaries in the southern part of the sea are somewhat smaller (Fig. 1), and some areas where cod are not usually fished in spring are not included.

The whole area treated in the present paper as "the southern part of the Barents Sea" is usually free from ice in spring and is available to fishing trawlers of any type. As a rule each great concentration of cod appearing within the limits of the area described is immediately found and fished by the trawl fleet. Therefore, the commercial importance of some areas in the southern part of the sea the actual distribution of cod shows well. The commercial importance of the coastal zones compared varies considerably: from 0.2 to 87.7% in the western zone and from 4.3 to 37.8% in the eastern zone. From Figs. 2 and 3, it is not difficult to see a rather close relation between the commercial importance of each of the coastal zones in March-April and the water temperature in the 150-200 m layer on the Kola hydrological section in November of the previous year. As a rule, the higher this temperature, the greater the commercial importance of Murman and the lower the commercial importance of Finnmark.

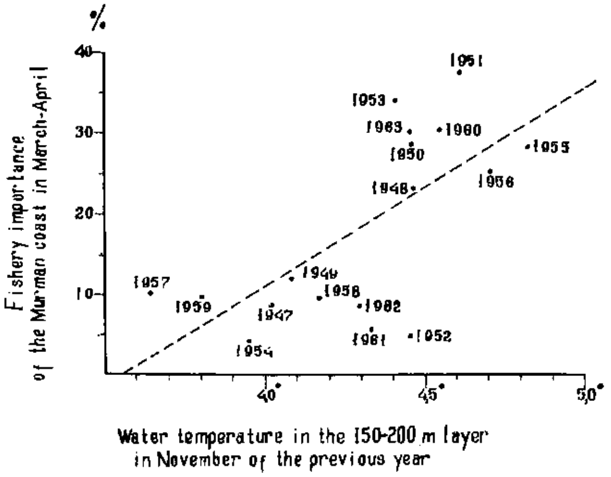

Fig. 2. Commercial importance of the Murman Coast in March-April in relation with the water temperature in November of the previous year.

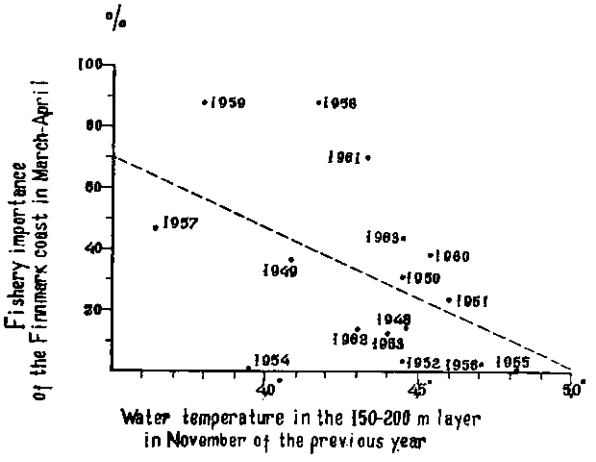

Fig. 3. Commercial importance of the Finnmark Coast in March-April in relation with the water temperature in November of the previous year.

The equations of quantitative relation between the compared indices are given below:

$$y = 24.5x - 86.9 \qquad (1)$$
$$y = 3.8x^2 - 7.6x - 19.5 \qquad (2)$$

In these equations "x" designates the November temperature on the Kola section and "y" the mmercial importance of the Murman Coast in March-April of the following calendar year. The oken line in Fig. 2 corresponds to equation (1): the correlation coefficient (r) = 0.67 ± 13. The parabolic curve corresponding to equation (2) is not represented in the Fig. as it lmost coincides with the straight line, having only slight curvature. However, forecasting by e equation (2) provides somewhat more exact results than by equation (1).

In equation

$$y = -45.3x + 227.7 \qquad (3)$$

" also presents the November temperature on the Kola section, while "y" shows the commercial imrtance of the Finnmark Coast in March-April of the following year. The correlation coefficient) = -0.50 ± 0.19. The straight line in Fig. 3 corresponds to equation (3). Despite the comratively low correlation coefficient, equation (3) is of a certain practical interest as together with the more reliable equations (1) and (2) it helps to forecast the spring migration routes of capelin cod. For instance, the November temperature in the 150-200 m layer was highest in 1954 and 1955. Using equations (1) and (2), it was easy to forecast the outstanding commercial importance of the Murman Coast in March-April 1955 and 1956. At the same time equation (3) enabled us to forecast the very insignificant commercial importance of the Finnmark Coast. As is obvious from Figs. 2 and 3, the actual run of the fishery corresponded to the expected one.

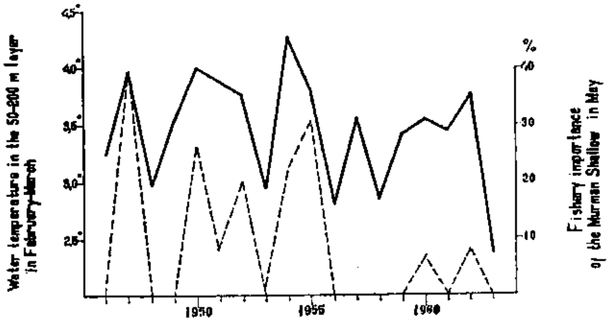

Fig. 4. Commercial importance of the Murman Shallow in May (dotted line) in relation to the water temperature in February-March (solid line).

An even closer relation exists between the thermal regime of the sea and the cod distribution on the Murman Shallow. This area, which is very suitable for the trawl fishery, is shown in Fig. 1. Figure 4 indicates that the higher the temperature is in the 50-200 m layer on the Kola hydrological section in February-March, the greater will be the commercial importance of the Murman Shallow in May. In the cold years cod are distributed west of the Murman Shallow in May, whereas in the warm years they are found within the limits of this area.

In equation

$$y = 18.2x - 53.8$$

x" designates the water temperature in February-March while "y" shows the commercial importance f the Murman Shallow in May: the correlation coefficient (r) = 0.71 ± 0.11.

The measure of reality of the relation between the varying values is usually expressed by he formula $\frac{r}{E}$, where $E = \pm 0.67 \frac{1 - r^2}{\sqrt{N}}$. If $\frac{r}{E} = 6$, the relation is considered to be resent. In our case $\frac{r}{E} = 9.1$; *i.e.* the relation is undoubtedly there.

As the migratory paths of both capelin cod and capelin itself as a rule coincide, the methods proposed can be applied to forecasting the spring arrivals of capelin to the coast of the Barents Sea. The above equations evidently cannot provide an absolutely precise forecast. It is not difficult to see that the dots in the Figs. are considerably scattered. The methods proposed require further development. However, they are successfully used even now to judge whether the commercial importance of Murman (and Finnmark) will increase or drop compared with the previous year. The forecast obtained some months in advance by the methods proposed must be controlled and corrected later, if possible, by means of field observations on the migratory concentrations of cod and capelin.

REFERENCES

GERASIMOV, V.V. 1961. In Studies of Murman herring in aquarium. Collection of articles, Hydrobiological and biological peculiarities of the coastal Murman waters. *Murmansk Book Publishers*, pp. 212-219.

KONSTANTINOV, K.G. 1958. Diurnal vertical migration of cod and haddock. *Trudy VNIRO*, 36: pp. 62-82.

1961. On the relation between water temperature and distribution of bottom fish. *Sci. and Tech. Bull. of PINRO*, 4 (18): pp. 25-28.

PROKHOROV, V.S. 1963*a*. Capelin of the Barents Sea. *Murmansk Book Publishers*. 1963*b*. Some ecological peculiarities of the Barents Sea Capelin (*Mallotus villosus villosus Müller*). *Trudy PINRO*, p. 15.

MCCRACKEN, F.D. 1963. Seasonal movements of the winter flounder, *Pseudo-pleuronectes americanus* (Walbaum), on the Atlantic Coast. *J. Fish. Res. Bd. Canada*, 20(2): 551-586.

HASLER, A.D. 1960*a*. Homing orientation in migrating fishes. *Ergebn. Biol.*, 23: 94-115.

1960*b*. Guideposts of migrating fishes. *Science*, 132, No. 3430: 785-792.

HASLER, A.D. and H.T. HENDERSON. 1963. Instrumentation problems in the study of homing in fish. In Bio-Telemetry. *Oxford-London-New York-Paris, Pergamon Press*, pp. 195-200.

KELLY, G.F. and A.M. BARKER. 1961. Observations on the behaviour, growth and migration of redfish at Eastport, Maine. *Rapp. Cons. Explor. Mer.* 150: 263-275.

VLADYKOV, V.D. 1963. Young haddock in the vicinity of Halifax, N.S. Contribution, *Canadian Biol. Fish., N.S.*, 8 (29).

WOODHEAD, P.M.J. and A.D. WOODHEAD, 1959. The effects of low temperatures on the physiology and distribution of the cod, (*Gadus morhua* L.) in the Barents Sea. *Proc. Zool. Soc. Lond.*, 133 (2): pp. 181-199.

A-14

THE INFLUENCE OF HYDROGRAPHIC AND OTHER FACTORS ON THE DISTRIBUTION OF COD ON THE SPITSBERGEN SHELF[1]

By

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SUMMARY

1. New information is presented on the distribution and movement of cod on the Spitsbergen Shelf in relation to hydrographic and biological factors.

2. Results of a series of cruises covering the edge of the shelf north-east of Bear Island during 1953-55 show the contrasting effects of a cold year (1953) changing to an exceptionally warm one (1954) and back to cold (1955). The observations throughout this period, with only minor exceptions, showed that cod were confined in the relatively warm Atlantic water above 1.5° to 2.0°C. Their distribution varied in accordance with that of the position of the boundary between the warm and cold water, both on a broad scale and locally when a sharply defined temperature structure built up during the warm spring of 1954.

3. Echo-surveys in the late spring and summer of 1956 showed that the short-term movement of cod onto the western edge of the shelf was related to the surge of Atlantic water. At a later stage *in situ* warming on the banks proper appeared to allow a widespread migration of cod from Atlantic to Arctic water.

4. There is evidence that the occurrence of local concentrations of a preferred food (herring and, to a lesser extent, euphausids) within an otherwise tolerable and featureless hydrographic area caused aggregation of cod on them. There was no obvious relation between cod density and intensity of feeding in the absence of a particular preferred food or when the latter was of widespread occurrence (*e.g.* capelin in 1953).

5. The earlier findings of a lack of cod in water below 1.5° to 2.0°C are confirmed by these results. There were no signs of the migration of large concentrations of cod into cold shallow water in the summer that were found in 1949-51 and which constituted the exception to this general rule. The later evidence emphasizes the influence of water movements and lessens the importance of an intrinsic seasonal depth cycle in determining cod distribution in the Spitsbergen Shelf region.

6. Attempts to establish the precise mechanism (*e.g.* response to a temperature gradient or to current shear at the interface) by which cod appear to be restricted mainly to one water mass are largely inconclusive from evidence of this kind. It is suggested that the detailed analysis of fish distribution in relation to a sharply-defined temperature regime (such as is described for the area east of Bear Island in 1954), by modern techniques of fish detection, temperature and current measurement, might provide an answer.

INTRODUCTION

Some of the results of an investigation of the influence of certain environmental factors on the distribution of cod on the Spitsbergen Shelf (Bear Island - Hope Island - Spitsbergen region) carried out from the Research Vessel *Ernest Holt* during the period 1949-59 have been given by Lee (1952), Graham *et al.* (1954), and Trout (1957). The first two of these papers considered the influence of temperature on the cod distribution and the third dealt with the roles of daylight radiance in the sea and of water movement.

The purpose of this contribution is to examine data concerning the distribution of cod in relation to water temperature and other factors for later periods than those covered by the papers referred to above. Two situations are considered. The first relates to the area to the east and north-east of Bear Island, along the eastern edge of the Spitsbergen Shelf, which was covered on a number of cruises during 1953, 1954 and the first half of 1955. A particular study was made of the local distribution of cod in the region of the South-east Gullies (Fig. 1), where a temperature picture of sharp contrasts formed during 1954. The second deals with three cruises made in the summer of 1956 when the distribution and movement of cod along a broad front on the western edge of the Spitsbergen Shelf between Bear Island and Spitsbergen, and later onto the shelf itself, was followed by echo-sounder surveys.

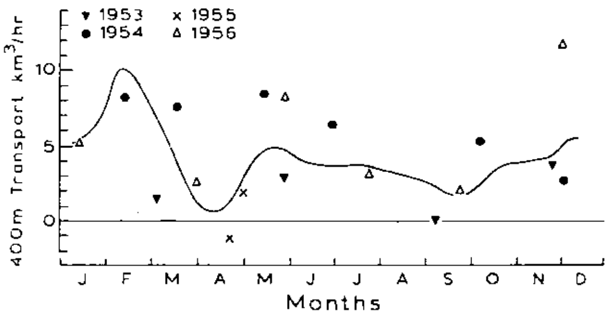
THE GENERAL HYDROGRAPHIC SITUATION IN THE BEAR ISLAND REGION DURING 1953-56.

Figure 1 shows the geography of the Western Barents Sea and the main features of the current system in that area. Warm water is transported northwards along the western edge of the shelf by the West Spitsbergen Current and along the eastern edge by the northernmost arm of the North Cape

ig.1. The western Barents Sea and its current system.

1.Bear Island	2.South-east Gullies
3.Hope Island	4.Spitsbergen
5.Spitsbergen Shelf	6.North-west Gully
7.Storfjordrenna	

. West Spitsbergen Current	B. North Cape Current
. Bear Island Current	D. Atlantic Current



ig.2. The annual cycle of volume transport of the West Spitsbergen Current and the values observed in 1953-56.

Current. The bottom temperature in the Bear Island region is determined by two opposing effects - on the one hand by the strengths of these two currents which, since both derive from the Atlantic current, vary together, and on the other by the strength of the Bear Island Current which is cold and of Arctic origin.

The volume transport of the West Spitsbergen Current above 400 m depth along a section running for 93 km due west of Bear Island has been measured on 46 occasions during the period 1949-59 (Lee, 1962), and its magnitude gives a good indication of the general temperature conditions on the edge of the shelf. Figure 2 shows the mean annual cycle of volume transport for these years (Lee, 1961), and the particular values for the years in question (1953-56). This shows that the volume transport was below average during most of 1953 but increased to about average in December. This increase continued to give above average transports until the end of 1954 when it subsided until, by the spring of 1955, the transport was again below average.

Although these 12 observations of volume transport are a guide to the strength of the West Spitsbergen Current during 1953-55, they are not a complete one. They give an index of the geostrophic transport only and are probably correct to no more than ± 2 km hr^{-1}, for the reasons discussed by Lee (1962). Further, they only refer to 12 points in time over a period of 26 months. Hill and Lee (1958) established a positive correlation between the volume transport (v) and the southerly wind component (s) during the 10 days preceding the working of the section. The regression line of v on s was found to be

$$v = 3.85 + 0.29 s.$$

Since then Lee (1962) has found that the correlation does not hold in the months of July and August, during which there is thermal stratification of the surface layers. In Fig. 3 we have plotted for each month of the period March 1953 - May 1955 the anomaly of the southerly wind component at Bear Island from the 35-year mean based on the years 1920-40, 1946-59. Ignoring the months of July and August in each year, it can be seen that during the spring and summer of 1953 the southerly wind component was below normal in all but one month, but that during the period September 1953 - June 1954 it was above normal for most of the time, particularly in the last months of 1953. From September 1954 through the first half of 1955, but with the exception of the month of November, it was much below normal, particularly in January and April-June. The 12 observations

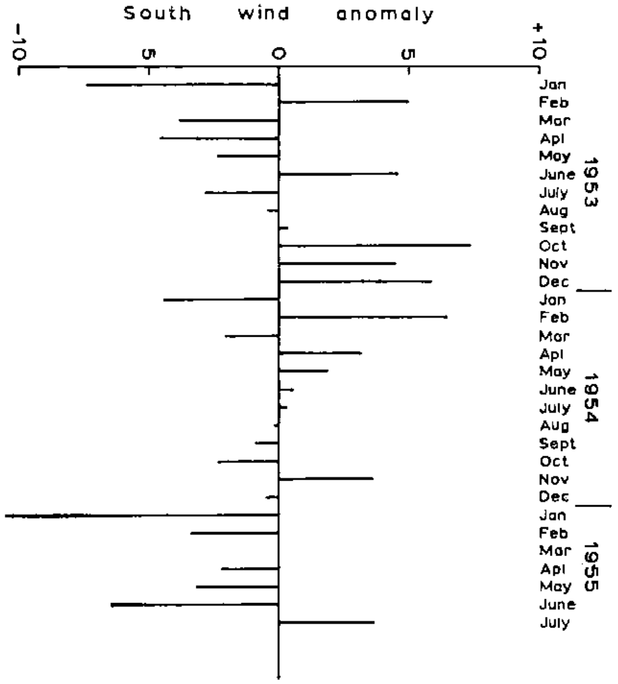


Fig.3. The anomaly of the south component of the wind at Bear Island: 1953-55.

of the volume transport of the West Spitsbergen Current, which we have, agree well with this wind picture and we can reasonably infer from them and the wind picture as a whole, that the influx of warm water into our area was low in spring and summer 1953, high from autumn 1953 to autumn 1954, and low in the first half of 1955. Furthermore, Lee (1961) has shown that the thermal effect of the wind on the ocean in the Bear Island-Spitsbergen region supplements and acts in the same direction as the dynamic effect. Southerly winds not only increase volume transport of the warm current but they also cause increased air temperature and humdity and so reduce the cooling of the sea in winter. Northerly winds reduce volume transport, lower air temperature and humidity, and increase cooling. Bearing this in mind we can use the wind picture as a guide to the sort of hydrographic regime which we can expect in the Bear Island area.

We have some evidence that the actual regime conformed with the expected one. The higher temperatures at the end of 1953 compared with those at the beginning can to some extent be seen in Figs. 4-10 and 12-14, which show the bottom temperature and fish distributions for the period under investigation, but the increase in bottom temperature during 1954 and its decline in 1955, which we would also expect from our consideration of the wind regime and the strength of the West Spitsbergen Current, are much more notable features.

THE SOUTH-EASTERN EDGE OF THE SPITSBERGEN SHELF, 1953-55.

1. Cod and Temperature Distribution to the East of Bear Island, 1954-55.

Figures 4-10 show the research vessel catches of cod and the bottom temperature isotherms from cruises made to the east of Bear Island during 1954 through to the spring of 1955. Catches are given in baskets per hour (40 baskets = 1.5 metric ton); no attempt has been made to contour them and no adjustment has been made for diurnal effects (Woodhead, 1964).

23-29 March 1954; Fig. 4.

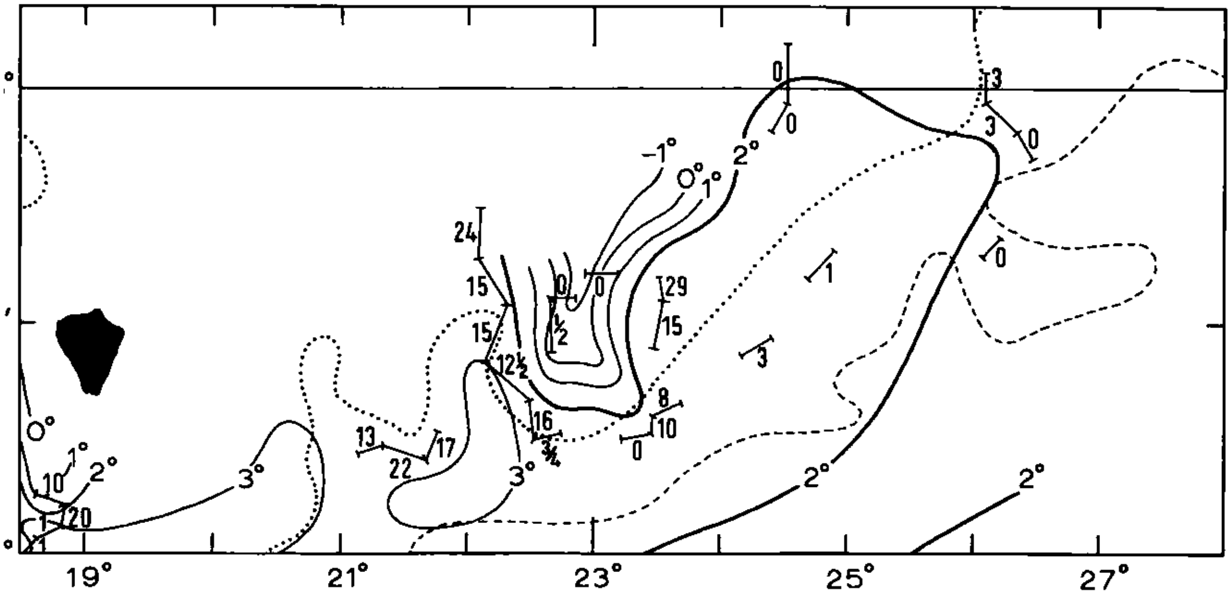
The sharply defined temperature structure in the region of the South-east Gullies is already established in this first cruise with a cold tongue bounded on both sides by water several degrees higher in temperature. Fish were virtually absent in the cold tongue but catches up to 29 baskets per hour were obtained within a few miles on either side in water between 2° and 3°C.

5-13 May 1954; Fig. 5.

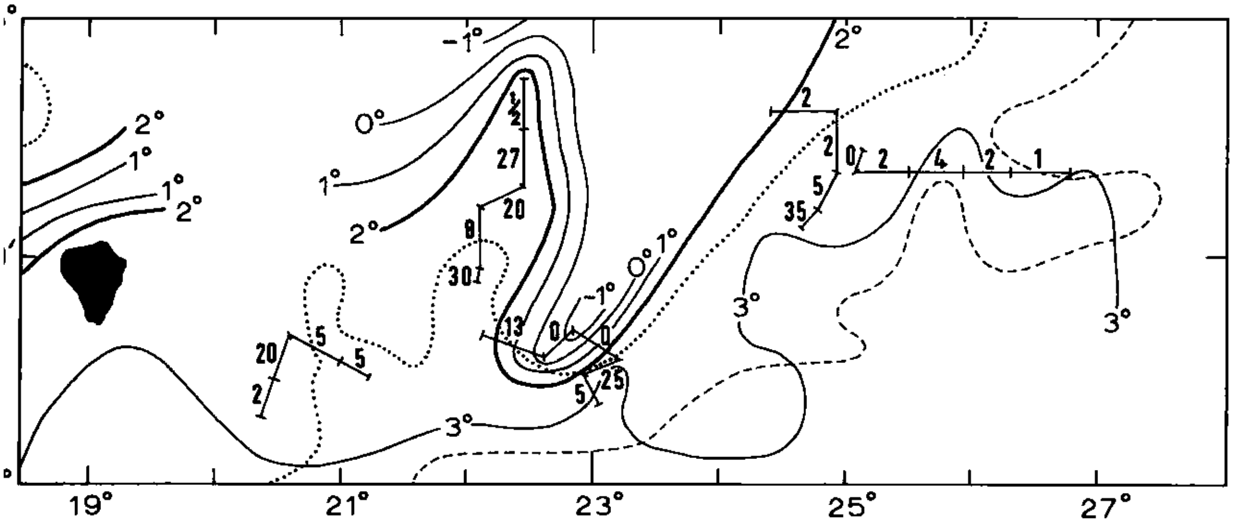
The coincidence of the fish and temperature boundaries is maintained. On this occasion the boundary of the fish distribution at the head of the gullies can be seen, and while not coinciding exactly with the temperature gradient is nevertheless close to it. The absence of fish across the tip of the cold tongue with concentrations on either side is again evident.

18-26 June 1954; Fig. 6.

By now the temperature boundaries have become less sharp, the temperature falling both in the gullies themselves and to the east. There is also a general decline in catches except in one locality where exceptionally heavy catches up to 320 baskets/hr were taken in a depth of 100 fm



ig.4. Catches of cod and the distribution of bottom temperature east of Bear Island 23-29 March 1954. (Catches are in baskets/hr in Figs. 4-10 and 12-14: 1 basket = 0.038 metric tons).



ig.5. Catches of cod and the distribution of bottom temperature east of Bear Island 5-13 May 1954. (Catches are in baskets/hr in Figs. 4-10 and 12-14: 1 basket = 0.038 metric tons).

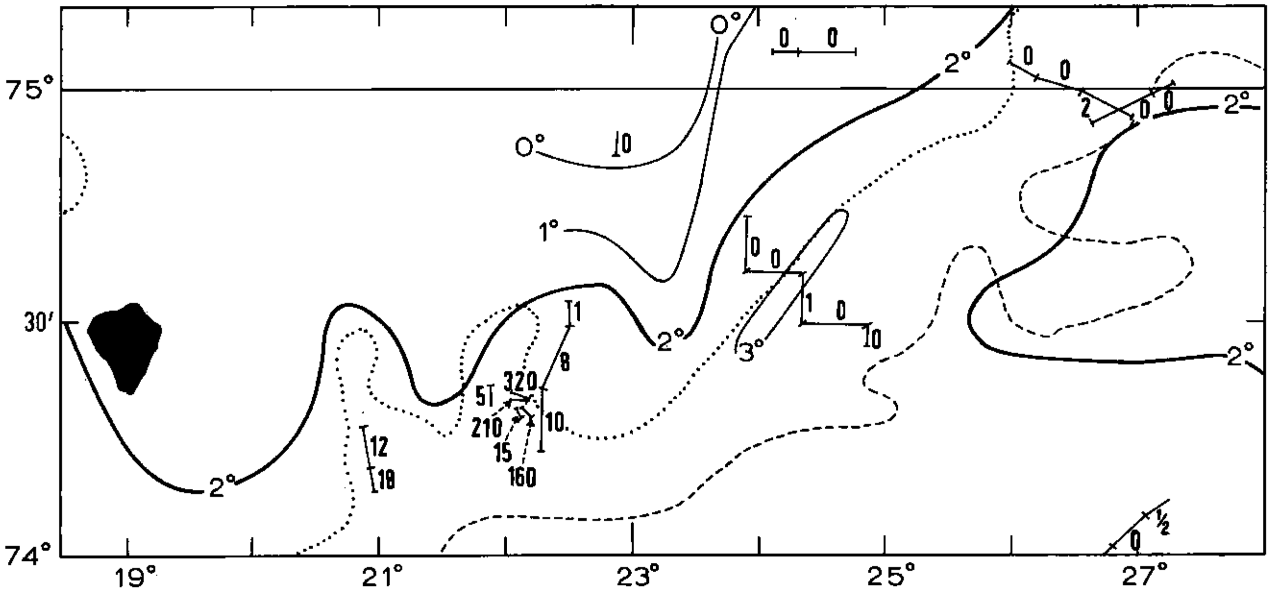


Fig. 6. Catches of cod and the distribution of bottom temperature east of Bear Island 18-26 June 1954. (Catches are in baskets/hr in Figs. 4-10 and 12-14: 1 basket = 0.038 metric tons).

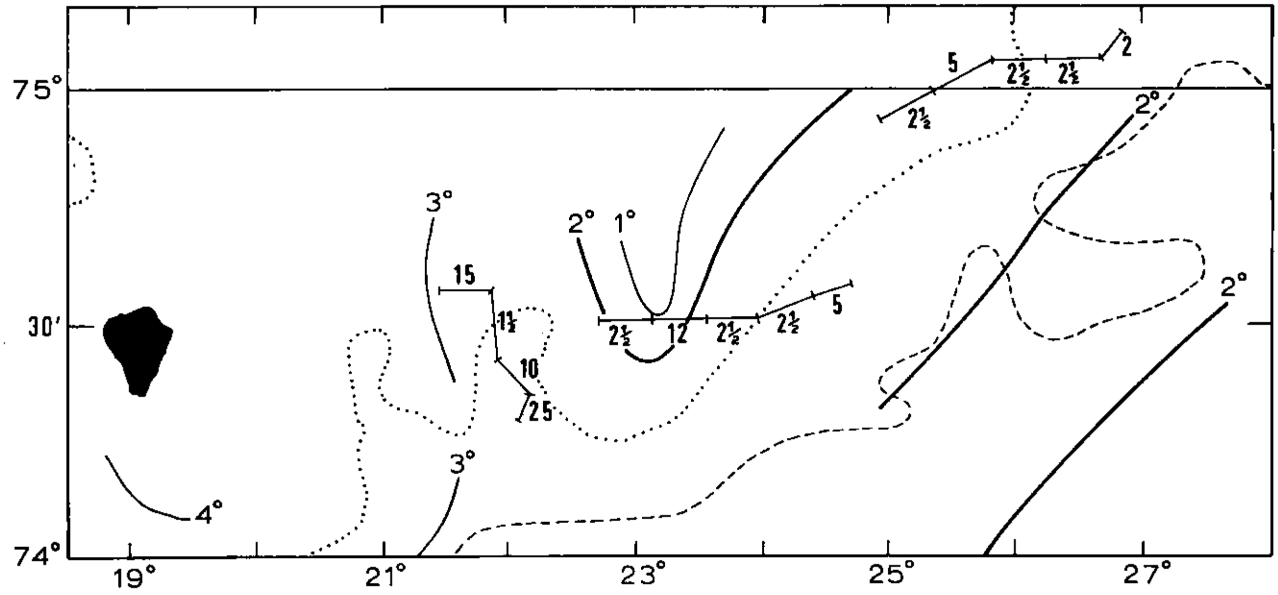


Fig. 7. Catches of cod and the distribution of bottom temperature east of Bear Island 19-21 October 1954. (Catches are in baskets/hr in Figs. 4-10 and 12-14: 1 basket = 0.038 metric tons).

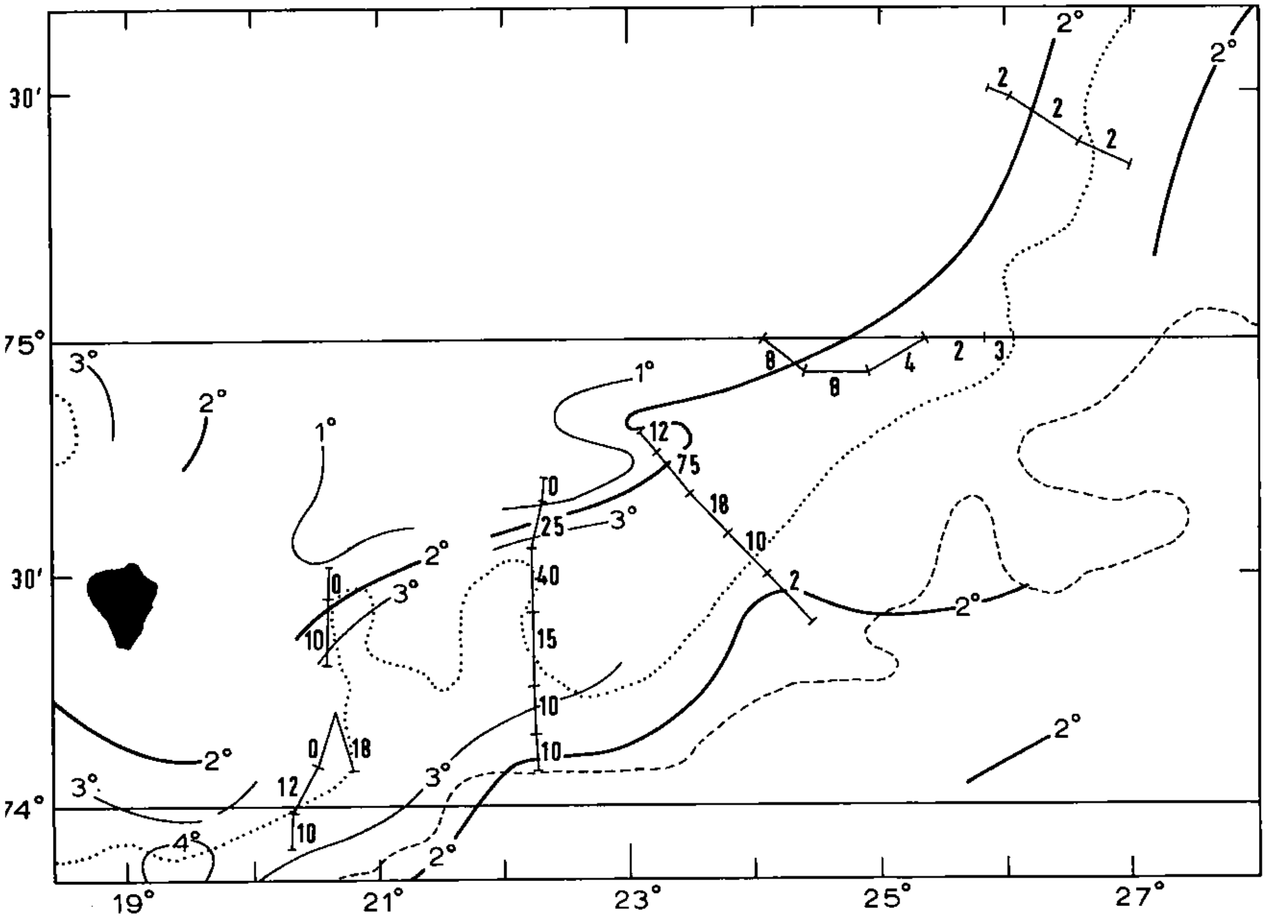


Fig. 8. Catches of cod and the distribution of bottom temperature east of Bear Island 26 November-2 December 1954. (Catches are in baskets/hr in Figs. 4-10 and 12-14: 1 basket = 0.038 metric tons).

(183 m). This was near the end of the cruise, about a week later than the rest of the catches shown in Fig. 6. Whether these fish were there throughout or whether the concentration formed during this short time cannot be established; but in either case there is no correspondingly sharp hydrographic feature to explain it. There seems to have been a movement of fish away from the head of the gully since the previous cruise. This may have been due to the onset of cooler conditions there, but we have no evidence to show conclusively that this has led to the build-up of the concentration in deeper water.

19-21 October 1954; Fig. 7.

There were, unfortunately, no cruises to the area during July-September. By October the temperature structure in the South-east Gullies had begun to return to something similar to that earlier in the year, but the number of stations are too few to establish either the fish or temperature gradients with any precision.

26 November - 2 December 1954; Fig. 8.

The temperature gradients have steepened since the previous cruise, partly through a decrease in temperature on the shallower parts of the bank and partly through an increase in the deeper water. Catches are substantially higher than before and indicate the existence of a band of maximum fish concentration in the region of the 2° and 3°C isotherms and decreasing towards the north-east. Where hauls extended to the 1°C isotherm catches declined sharply.

6 - 14 March 1955; Fig. 9.

The cooling of the shoal water has intensified and most of the deeper parts of the shelf to the south as well as the east of Bear Island are now also covered with water below 2°C. The band of maximum fish concentration also appears to have moved south and is still in the region of the 2° C isotherm. Compared with the corresponding period of 1954 (Fig. 4) the cold water is more extensive and the temperature gradients in the region of the South-east Gullies are consequently less steep. The fish gradients also appear less pronounced and appreciable quantities were caught in cold water, especially to the south of Bear Island. The impression is that the fish distribution has not changed as rapidly since the previous cruise as has the hydrographic regime, and it is interesting to note that over a considerable part of the area the surface water is colder than the bottom. This indicates that some, at least, of the decrease in temperature of the bottom water since December is due to *in situ* cooling as opposed to a southerly transport of Arctic water *en masse*, and this may explain why the fish distribution does not follow the temperature boundaries as sharply as during the period of high transport (in the opposite direction) earlier in the year.

28-30 April 1955; Fig. 10

The progressive cooling of the water on the shelf noticed on both the previous cruises is continued even further, until by now the greater part of the shelf to the south and south-east of Bear Island is covered with water less than 2°C and much of the shoaler parts (*i.e.* the South-east Gullies proper) by water below zero. The two lines of trawl hauls to the east of Bear Island coincide almost exactly with those of the previous cruise (Fig. 9) and show that there has been a dramatic decrease in fish density since then. The only catches of any size (15 and 40 baskets) were again taken near the 2°C isotherm; but now, in contrast to the previous cruise, the fish gradients are sharper and hardly any fish were caught in water colder than this. In contrast to the previous cruise cold bottom water now covers a large area in the bottom of the gullies (Fig. 10), due to the cascading of cold Arctic water downwards from the bank. It is reasonable to suppose that the rapid retreat of fish to the south since the previous cruise is related to this advance of cold water.

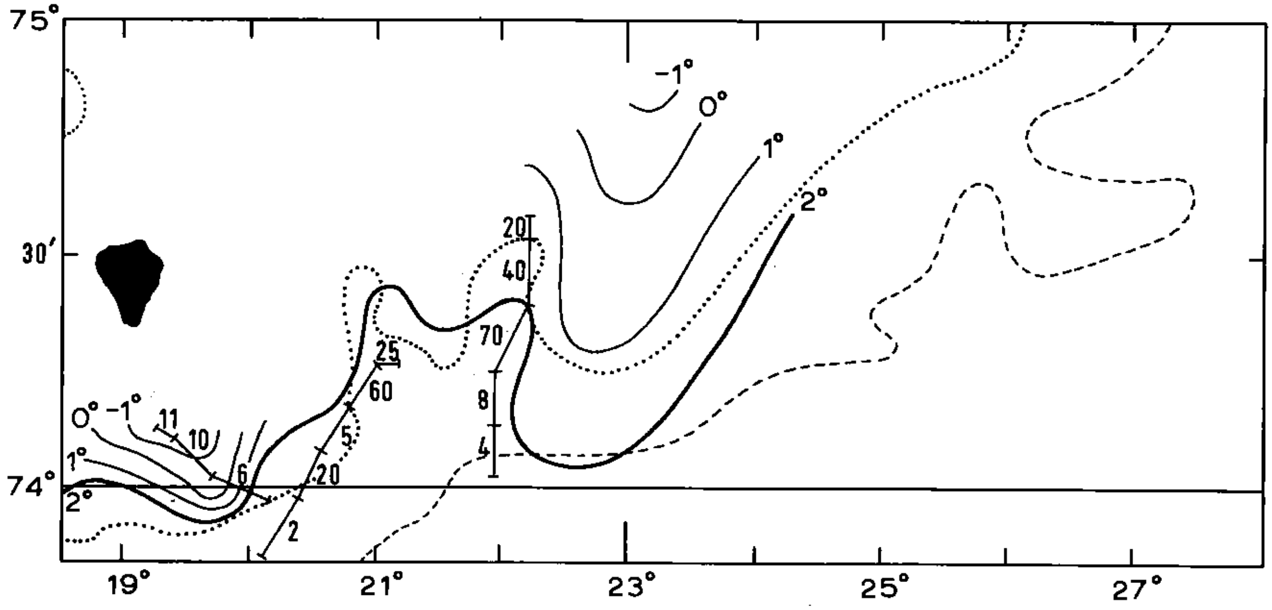
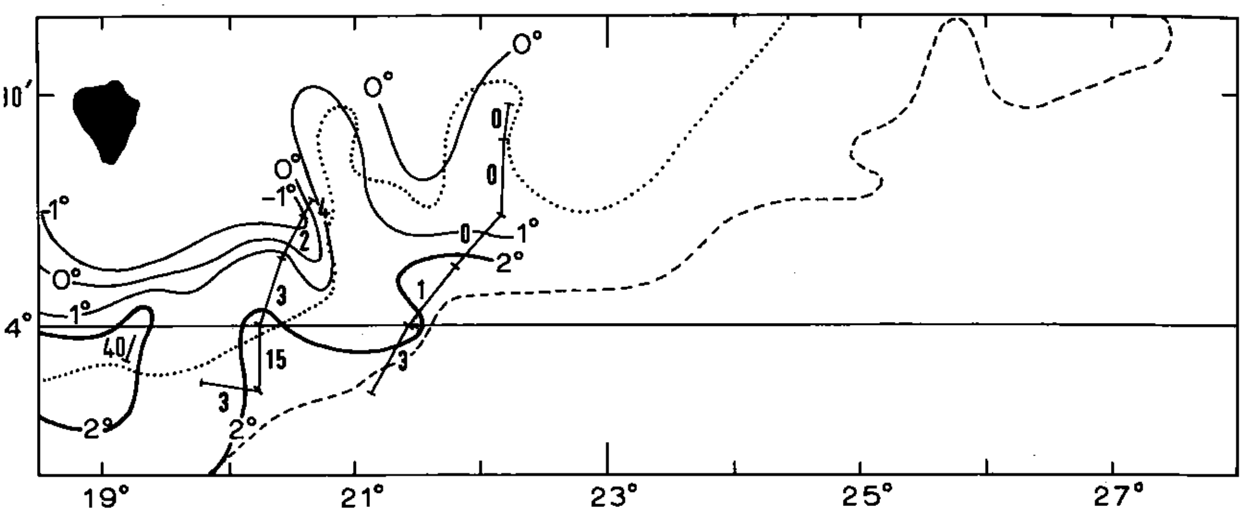


Fig. 9. Catches of cod and the distribution of bottom temperature east of Bear Island 6-14 March 1955. (Catches are in baskets/hr in Figs. 4-10 and 12-14: 1 basket = 0.038 metric tons).



ig. 10. Catches of cod and the distribution of bottom temperature east of Bear Island 28-30 April 1955. (Catches are in baskets/hr in Figs. 4-10 and 12-14: 1 basket = 0.038 metric tons.)

. Temperature or Depth?

The Spitsbergen Bank receives cold Arctic water from its shallow region to the north and east, nd warm Atlantic water from the deeper areas to the south and west. Consequently, there is usually strong association between temperature and depth on the edge of the bank (the shallowest areas eing the coldest), which complicates what might otherwise appear to be a straightforward relation etween fish distribution and temperature. It is therefore necessary to re-examine the evidence resented in Figs. 4-10, to see how far it is possible to distinguish between temperature and depth s the more significant indicator of the limits of cod distribution.

A formal bivariate analysis giving all the data equal weight is of doubtful value if not posiively misleading for this purpose, because sampling was not distributed, temporally or spatially, n either a systematic or a random way with respect to temperature or depth. The evident lack of ish to the north-east, irrespective of temperature and depth, means that many of the data are inonclusive, and it is necessary to examine the rest selectively, although this precludes rigorous tatistical evaluation. To support the hypothesis that cold water rather than shallow depth is he limiting influence (direct or indirect), the crucial evidence is the existence of appreciable oncentrations of fish in shallow but warm water; to refute it, concentrations of fish in cold ater, irrespective of depth, must be demonstrated. Both of these are rare occurrences, but forunately the striking contrast between the "warm" conditions of 1954 and the "cold" of 1955 proides a clue. Since detailed depth contours could not be shown on Figs. 4-10, catches are given n Table 1 by half degree temperature and ten fathom depth intervals. Months are also given in able 1 since the effect of temperature or depth on fish distribution may vary seasonally.

It has been noted above that a feature of interest in the spring of 1954 was the sharply-efined cold tongue of water in the South-east Gullies region, and the absence of fish in it but heir presence in the warm water to each side only a few miles away. The depths in the cold ongue were, however, a little less than where the fish occurred, ranging from 55 to 70 fm. (100-28 m) compared with 65-80 fm. (119-146 m). Whether this depth difference could have been suficient to generate the very sharp boundary of the fish distribution is problematic. Warm water n precisely the same depths as the cold tongue was not found in the South-east Gullies locality, ut immediately to the south of Bear Island a line of trawl hauls extended into even shallower ater (45 - 60 fm: 82-110 m) where the temperature ranged from 1° to 2.5°C (Fig. 4 and Table 1); hese gave catches of 10 and 20 baskets, which are not much different from those in rather deeper ater of similar temperature on each side of the cold tongue. Moreover, this line of hauls did ot close the fish boundary towards the shallow water.

TABLE 1. CATCHES OF COD (BASKETS/HR ; INDIVIDUAL HAULS), SOUTH AND EAST OF BEAR ISLAND DURING THE PERIOD 1954-1955, GROUPED BY HALF DEGREE TEMPERATURE INTERVALS AND 10 FM. (=18.3 M) DEPTH INTERVALS.

Temp. °C	Depth (Fathoms)											
	40-49	50-59	60-69	70-79	80-89	90-99	100-109	110-119	120-129	130-139	140-149	150+
-1.0 to -0.51		11 M/5	0 My/4 10 M/5									
-0.50 to -0.01		0 M/4 0 J/4										
0.00 to 0.49		½ M/4	0 M/4 2 A/5	0 A/5	4 A/5							
0.50 to 0.99		0 D/4		0 My/4	0 A/5							
1.0 to 1.49	10 M/4		0 D/4	20 M/5	0 J/4 5 A/5	13 My/4 0 J/4 12 A/5						
1.50 to 1.99		12½ D/4	2½ 0/4	3 A/5	0 M/4 12 /4 7½ D/4	1 D/4 40 M/5		3 M/4		0 A/5		0 M/4 2 A/5
2.00 to 2.49		20 M/4	25 D/4	½ My/4 75 D/4 5 M/5	0 M/4 2½ My/4 100 A/5 50 A/5	0 J/4 2 D/4 7½ D/4 60 M/5	4 D/4 25 M/5	0 J/4 1½ D/4 70 M/5 7½ A/5	1 M/4 0 J/4 15 A/5	10 M/4 0 M/4	8 M/4 2 J/4 1 A/5 3 A/5	0 M/4 2½ D/4 10 D/4 4 M/5 7½ M/5 3 A/5
2.50 to 2.99		½ J/4	1½ My/4	29 M/4 15 M/4 24 M/4 20 My/4 8 J/4 15 0/4	15 M/4 7½ My/4 27 My/4 20 My/4 10 D/4	12 M/4 15 M/4 16 M/4 30 My/4 10 0/4 17½ D/4 20 M/5	1 M/4 25 My/4 2½ My/4 5 My/4 210 J/4 15 J/4 5 0/4 2½ 0/4 2½ 0/4 25 0/4 1½ 0/4	22 M/4 5 My/4 5 My/4 0 J/4 160 J/4 2½ 0/4 2½ 0/4 2½ 0/4 2½ D/4 12½ M/5	50 M/4 ½ M/4 13 M/4 17 M/4 35 My/4 0 My/4 5 J/4 2 0/4 5 0/4 3 D/4	1 M/4 15 M/4 3 M/4 5 My/4 1½ My/4 ½ J/4 20 M/5 2½ M/5	3½ My/4 0 J/4 15 M/5 11 M/5	2½ My/4 1 My/4 0 J/4 0 J/4 0 J/4 2½ D/4
3.0 to 3.49 +				1 M/4	½ M/4 5 My/4	1 M/4 8 My/4 15 J/4 15 D/4	10 My/4 12½ J/4 10 J/4 320 J/4	6 M/4	1 M/4		10 D/4	
3.50 to 3.99					40 D/4 12½ D/4 0 D/4	17½ D/4 25 D/4				2½ My/4 10 D/4 30 D/4		

<u>Key:</u> M- March, A- April, My- May, J- June, O- October, D- December. /4 = 1954 , /5 = 1955.

The fact that the maximum catches south-east of Bear Island in the spring surveys of 1954 were aken in depths between 70-90 fm. (128-165 m) but in water between 2° and 3°C is itself significant. his is the time when the average depth of the commercial fishing is greatest (usually in the region f 220 fm.: 402 m) (Trout 1957); it is also the middle of the "hydrographic winter" in average con- itions. At this time in 1954, however, the main commercial fishing (to the south and south-west of ear Island) was at depths between 100-150 fm. (183-274 m). The inference that the unusual occur- ence of both fish and warm water in exceptionally shallow depths during the spring of 1954 was not ortuitous is strengthened by comparison with the situation in the spring of 1955 (Fig. 10), by which ime the influx of warm water had weakened and cold water extended over much of the bank which at he same period in 1954 had been covered with warm water. Correspondingly, hardly any fish were aught in 1955 in places where good catches had been taken in 1954.

Inspection of Table 1 shows that, throughout the period, only two of the thirteen hauls made in ater below 1°C gave any quantity of fish (10 and 11 baskets). Both of these were in March 1955 in hallow water (50-70 fm.: 91-128 m) close to a very steep temperature gradient with warm water only few miles away. Indeed, the gradient here was so steep and irregular that there is some doubt hether the temperatures at the beginning and end of the two hauls (ranging from -0.5° to -1.0°C) ecessarily reflect the actual temperatures where the fish were, which could have been higher than his. Nevertheless, it has been noted above that the general distribution of fish in March 1955 ppeared to be lagging behind the rapid spread of cold water down the bank which was occurring then, nd it is possible that these fish had been overtaken by a relatively thin sheet of cascading cold ater. No hauls were made in exactly this locality on the following cruise (April 1955) because it as close to the ice edge, but heavy catches (50-100 baskets) were obtained at the edge of the warm ater (2° to 2.5°C) which by then had retreated further down the bank to depths of 80-90 fm.(146- 65 m). Thus it could be that by April fish had become concentrated at the new boundary between the old and warm water, but detailed information on the gradients of this concentration is lacking.

. Feeding.

Notes on the main food of cod, and a rough indication of the intensity of feeding, were recor- ed on most of the 1954-55 cruises. Detailed descriptions of the food of cod in the Bear Island area ave been given by Brown and Cheng (1946) and Graham *et al.* (1954); we now examine the information or the period 1954-55 in the area shown in Figs. 4-10, to see whether the kind and intensity of eeding can throw any light on the distribution of cod.

Inspection of these records showed that the broad distinction could be made between

(a) *mixed feeding*	(ctenophores, sagittae, euphausids, *Pandalus borealis*; small gadoid fish; polychaetes, amphipods and other benthic organisms)
(b) *specialised feeding*	(herring and euphausids).

ixed feeding, usually classified as "light" or occasionally "moderate" in intensity without any bvious seasonal change, was predominant on all cruises except the last (April 1955) when euphausids ere the main or exclusive food throughout the area in question. The possibly significant obser- ations concern the first three cruises of 1954 (March-June; Figs. 4-6), when although in the major- ty of hauls cod were feeding lightly on mixed food organisms, in certain hauls they were feeding eavily on herring or a combination of herring and euphausids. In such instances the catch was arkedly greater than the average of the remaining hauls. This was especially pronounced in May Fig. 5) when the cod taken in the four very heavy catches made at the end of the cruise were eeding heavily on young herring (12-14 cm), although this food species was not recorded on any of he earlier hauls.

The information on this point for the first three cruises is summarised in Table 2 below, which ompares the average catch of "specialised feeding" cod with that of "mixed feeding" cod in the ame general locality and temperatures.

There was no clear association with catch size when feeding was "mixed" in character, either on he cruises shown in Table 2 or on subsequent ones. In November-December 1954 (Fig. 8) for example, hen feeding was exclusively "mixed" in character, the intensity of feeding decreased from "moderate" o "very light" from north-east to south-west of the area shown, which is opposite to the gradient f fish density. Neither was a relation between catch size and feeding intensity observed in April

TABLE 2. COMPARISON OF "SPECIALISED FEEDING" AND "MIXED FEEDING" CATCHES OF COD. NUMBER OF HAULS IN BRACKETS.

Period	Specialised feeding			Mixed feeding	
	Average catch (baskets/hr)	Kind of food	Intensity of feeding	Average catch (baskets/hr)	Intensity of feeding
March 1954 (Fig.4)	18 (5)	Herring	Heavy	11 (19)	Light-moderate
May 1954 (Fig. 5)	21 (5)	Herring and Euphausids	Moderate-heavy	7 (19)	Light
June 1954 (Fig. 6)	175 (4)	Herring	Heavy	9 (6)	Light-moderate

1955, although feeding was again specialised (on euphausids) in character. In contrast to the spring of 1954, however, the specialised feeding in 1955 was general throughout the area.

Taken together, these observations suggest that the presence of young herring and to a lesser extent euphausids, in local concentrations in the spring of 1954 may have played a significant role in causing cod to aggregate for feeding in areas where there were no sharp hydrographic features. This is, in fact, the only apparent explanation of the very high but localised concentration of cod in June of that year. By the same token, if evidently preferred foods such as these are widespread, as were euphausids in April 1955, it is unlikely that they would act as concentrating agents. It may be noted that the occurrence of young herring east of Bear Island is not usual and their presence in 1954 is a further indication of the exceptionally strong influx of Atlantic water in that year. This is in contrast to the situation in the spring of 1955, when no herring were recorded in cod stomachs, and to that throughout 1953 until December of that year, as is mentioned in section 5 below.

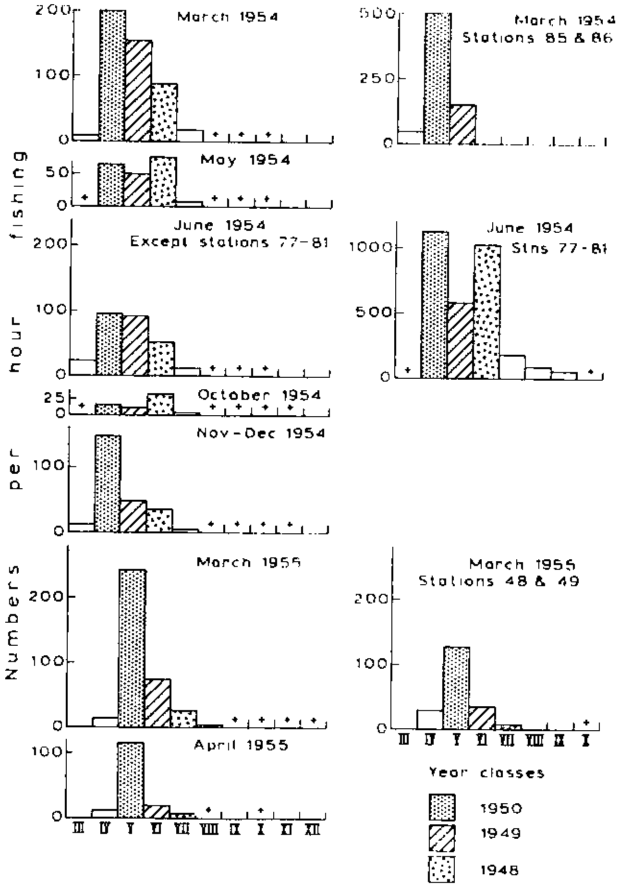


Fig. 11. Age composition of the cod in 1954-55 to the east of Bear Island.

4. Age-Composition.

Since in cod, as in other species, there is a marked tendency for older fish to be found in deeper water and since the physiological effect of temperature may possibly also be age-specific, a brief mention of the age-composition of the cod stock to which this account refers is given here.

The average age-composition of the catches taken on each cruise, expressed as numbers per hour fishing, are shown in the histograms on the left-hand side of Fig. 11. Throughout the period catches consisted almost entirely of three year-classes, those of 1948, 1949 and 1950, which comprised age-groups IV, V and VI in 1954 and V, VI and VII in 1955. Nearly all these fish were immature. The three year-classes ere represented in roughly equal proportions until November-December 1954; thereafter, the 1950 ear-class became dominant as the catches of the two older year-classes declined.

The right-hand histograms show the age-composition of hauls which, for one reason or another, ave been specially mentioned in the preceding account. Thus, stations 84 and 85 in March 1954 ere those in shallow but relatively warm water; the 1950 year-class was about twice as abundant ere as in the area generally, and the 1948 year-class was absent. Stations 77 to 81 in June 1954 ere those where the very high concentration of cod was located; the same three year-classes are ominant but there are more older fish in addition, though these stations were not deeper than the verage for the cruise as a whole. Lastly, stations 48 and 49 in March 1955 were those where fish ere caught in water both shallow and cold; their age-composition was very similar to that for the ruise as a whole, and also to those for the cruises immediately preceding and following.

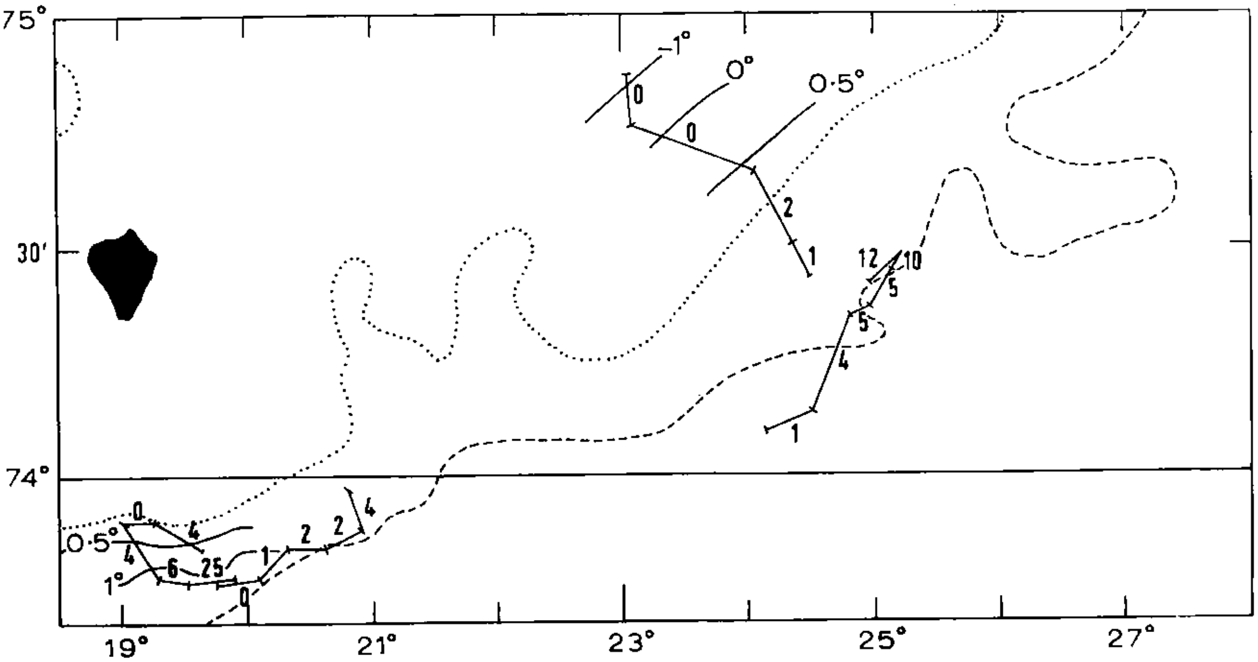
Generally speaking, the age-composition of the stock throughout the period was therefore fairly omogeneous, and the changes observed in its distribution cannot be attributed to any major dif- erences in the constituent year-classes, in time or space.

. The Distribution of Cod and Temperature to the East of Bear Island in 1953.

The area in investigation in 1953 extended much further north-east than in 1944, and no detailed nformation for the South-east Gullies region is available. Nevertheless, there is enough to show hat in several respects the two years were sharply contrasted.

Figures 12-14 show the distribution of cod and temperature for three 1953 cruises during which bservations were made in at least part of the area in question; these were in April, July and ctober. Comparing the times of these cruises with those in 1954, the first (Fig. 12) falls be- ween Figs. 4 and 5 and the last (Fig. 14) corresponds with Fig. 7: the second, the July cruise, s of particular interest since no cruises were made to the area in the high summer of 1954.

The most striking feature of all the 1953 cruises is that cold Arctic water covered practically



ig. 12. Catches of cod and the distribution of bottom temperature east of Bear Island, 13-23 April 1953.

all the shelf, all temperatures being below 2°C, even in water as deep as 200 fm. (366 m). In April, pack ice prevented access to the shoaler parts of the bank in the South-east Gullies region which were covered with warm Atlantic water in 1954. The only catches of any size taken in this month were in water of about 150 fm. (274 m) south of Bear Island where the temperature was about 1°C, and in water between 160-180 fm. (293-329 m) further east, where the water was between 0.5° and 1°C (Fig. 12). The situation in May 1953, not shown here, was the same. These depths of maximum catch contrast markedly with the spring of 1954 when the highest catches were taken in warmer water at depths between 75-95 fm. (137-174 m).

By July (Fig. 13) the temperatures on the shelf had dropped even lower. Several lines of trawl hauls covering depths from 80-180 fm. (146-329 m) failed to find fish except in moderate quantity on two hauls on the most northerly line in about 120 fm. (220 m).

On the last cruise, in October (Fig. 14), only a few observations were made, but they are sufficient to show the beginnings of the influx of warm water which led to the unique features of the following year. A cluster of trawl hauls just east of the South-east Gullies at the end of the cruise gave up to 30 baskets/hr, the largest catch recorded throughout the year on the surveys east of Bear Island, including the banks east of Hope Island not shown in the diagrams.

Apart from the unusually cold conditions, 1953 also differed from 1954 in the almost universal occurrence of capelin (*Mallotus villosus*) over all the area from the South-east Gullies eastward. This was by far the dominant food of cod, which were noted as feeding heavily on them in nearly all hauls, irrespective of the quantity caught. Abundant echo traces were also recorded throughout the area and positively identified as capelin on a number of occasions. Here again, therefore, a presumably preferred food of widespread occurrence failed to act as a concentrator of cod. On the last cruise, however, the cod caught just east of the South-east Gullies (Fig. 14) were feeding heavily on herring, so that in this respect also the pattern of 1954 was beginning by the autumn of 1953.

The general temperature conditions in 1953 are similar to those of 1949, in July of which year exceptionally heavy catches of cod were taken at several points on the bank in cold (0.5° to -0.5°C) but shallow water (80-100 fm: 146-183 m) north-eastwards from the South-east Gullies as reported by Graham *et al.* (1954): it was these catches which proved the first clear exception to the general temperature rule for cod distribution. The presence of these fish in cold water at this season became explicable in physiological terms by the later work of Woodhead & Woodhead (1959); yet there were no signs of fish migrating onto the shelf in 1953. In fact, catches comparable in size to those of 1949 were never obtained again east of the South-east Gullies in any subsequent year, cold or warm, except in May 1950 when, as reported by Lee (1952), up to 150 baskets/hr of cod feeding heavily on capelin were taken in the area between 90-110 miles east of Bear Island in bottom temperatures between 2° and 3°C in 160-170 fm. (293-311 m), and again in the summer of 1951 when catches up to 40 baskets/hr were obtained south of Hope Island (just north of the area shown in Figs. 12-14) in cold shallow water. Commercial fishing concentrations also occurred still further to the north-east on the banks east of Hope Island in the late 1940's, but these too appeared largely to have ceased during the early 1950's and did not start again in these areas until 1957.

There is no immediate explanation for this change beyond the fact that in these earlier years (*e.g.* 1949) the fish were mainly of age-groups VI-IX and many had spawned at least once, and that the general abundance of these age-groups in the Arcto-Norwegian stock as a whole had certainly declined by the 1950's. Even so, there should still have been sufficient fish to have given at least moderate catches had they shown the same tendency to migrate on to the banks in the summer as in earlier years. The real answer may possibly lie in a change in the main current system near the north Norwegian coast influencing the direction in which fish left the spawning grounds, rather than in the hydrography on the shelf itself.

THE WESTERN EDGE OF THE SPITSBERGEN SHELF, 1956

During the course of two cruises by the *Ernest Holt* in May-August 1956 it was possible to survey the distribution of fish along the western edge of the Bear Island Bank using the echo-survey method described by Cushing in Richardson *et al.* (1959). In this the ship proceeds at her cruising speed along a grid laid out over a wide area, the echoes from fish in the first fathom above the sea-bed are observed on a cathode ray tube, and the total signal from them over a unit distance is measured. By measuring the total signal obtained during trawl hauls and comparing

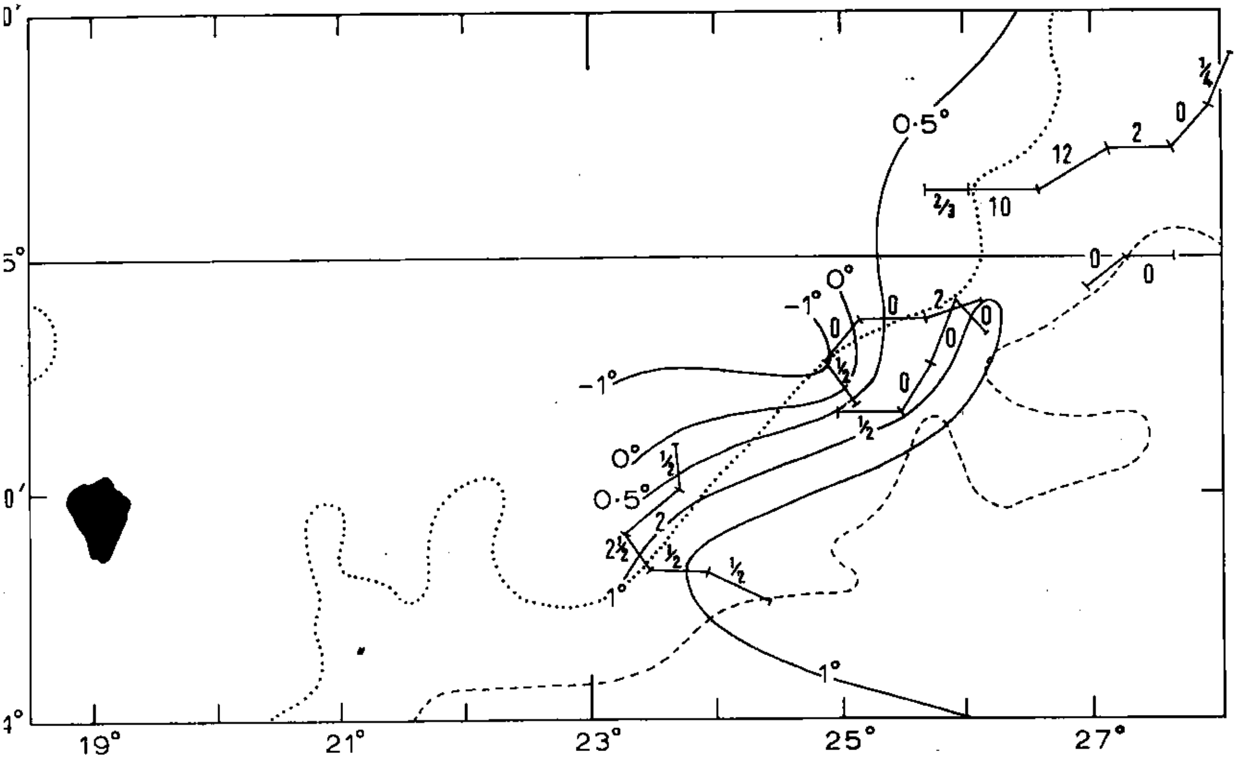


Fig. 13. Catches of cod and the distribution of bottom temperature east of Bear Island, 4-13 July 1953.

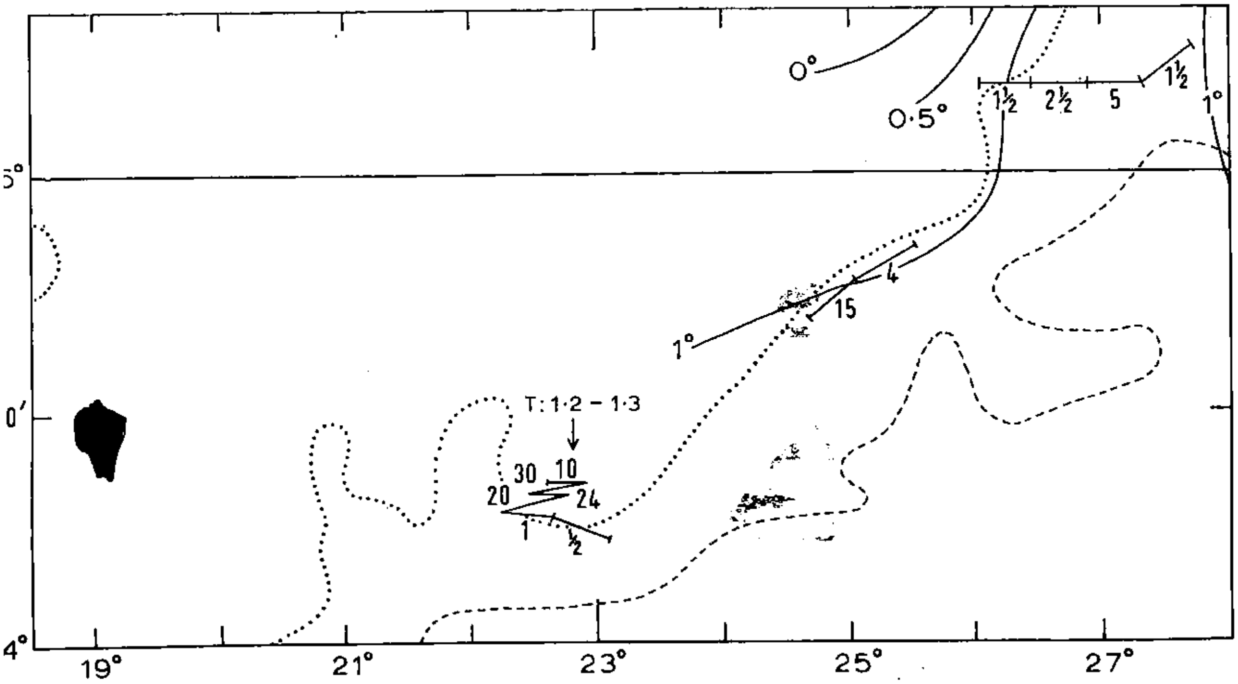


Fig. 14. Catches of cod and the distribution of bottom temperature east of Bear Island, 17-22 October 1953.

them with the catches expressed in baskets per hour it is possible to obtain a signal/baskets per hour relationship which can be used to estimate the catch over the whole area surveyed.

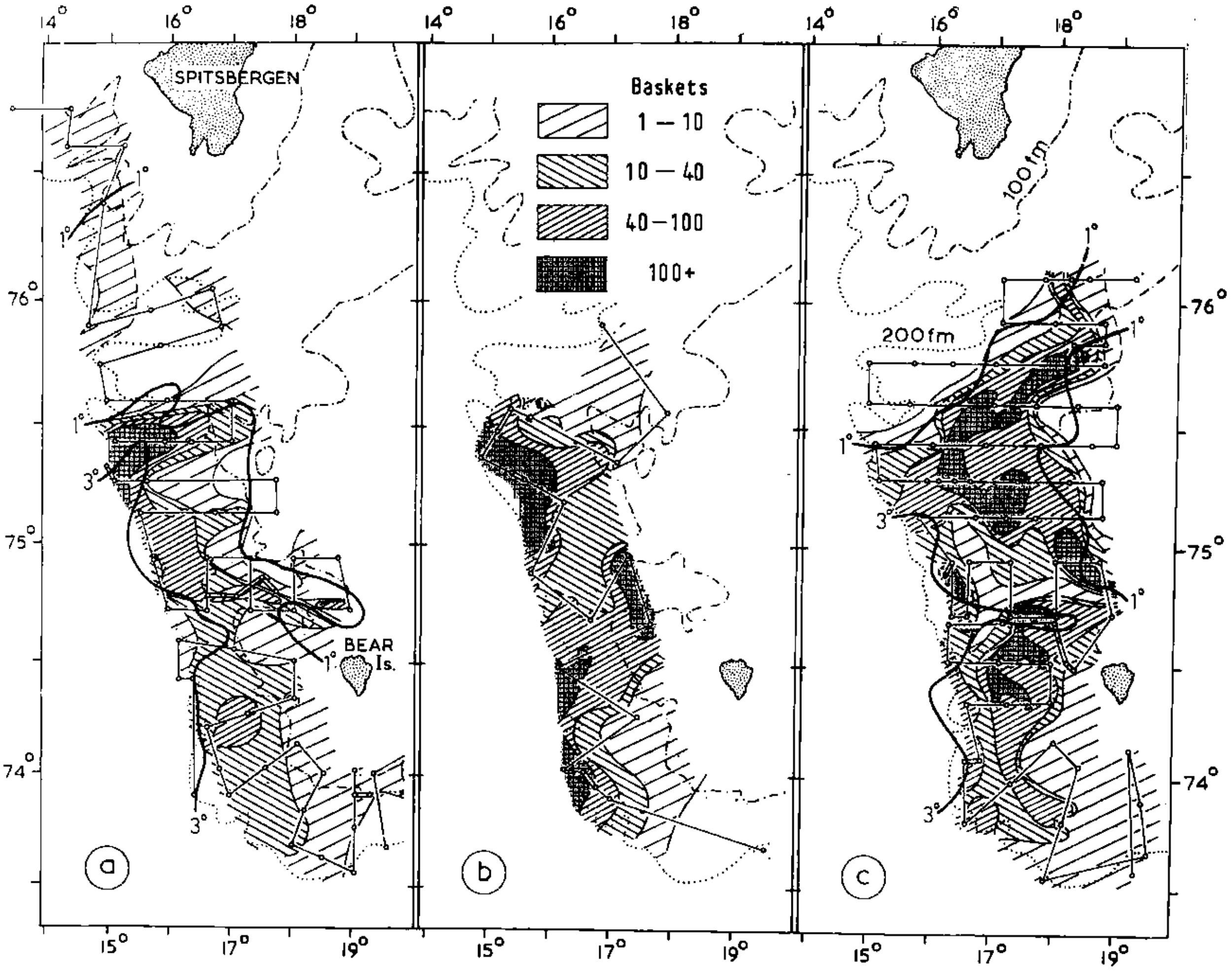


Fig. 15. Distribution of echo survey signals in the fathom above the bottom and the distribution of bottom temperature on the Spitsbergen Shelf.
(a) 29 May-4 June 1956.
(b) 4-6 June 1956.
(c) 11-17 June 1956.

The results obtained by using this technique during Cruise IV/1956 of *Ernest Holt* have already been described by Richardson *et al.* Their charts for the three surveys carried out along the western edge of the Bear Island Bank during the period 29 May-17 June are shown here as Fig. 15. On these charts the catch (baskets/hr) estimated from the total signal recorded during units of 15 min of steaming time (about 2½ miles) has been contoured. Caution is needed in interpreting the finer details of these contours since the fish echoes often occurred in patches separated by periods when few or no signals were recorded, even within a unit distance of ship's track; and with this degree of discontinuity the joining-up of contour levels between adjacent tracks of the grid may not always be fully justified. Nevertheless, the general picture of the fish distribuion and, in particular, its changes in time during the period May-August, are shown well by these cho-surveys. Several trawl hauls were made during the surveys which confirmed that for all practical purposes the fish responsible for the echoes were cod.

On the first survey, signals indicating a level of catch of over 10 baskets per hour were bserved along the whole of the western edge of the Bear Island Bank from south-west of Bear sland to the southern edge of the Storfjordrenna, but not beyond this trench. The heaviest conentrations, over 40 baskets per hour, were observed at the entrance to the Storfjordrenna, at the ntrance to the North-west Gully, and to the west of Bear Island. The bottom temperature distriutions on the first and third surveys are shown in Fig. 16 and it can be seen that the fish were ot limited by the 2°C isotherms, but that on the whole they were in water warmer than 1°C. urther, the heaviest concentration, at the entrance to the Storfjordrenna, was at a point where arm water was pushing into that gully, and the heavy concentration in the North-west Gully was lso in an area where an offshoot of the warm West Spitsbergen Current was pressing eastwards.

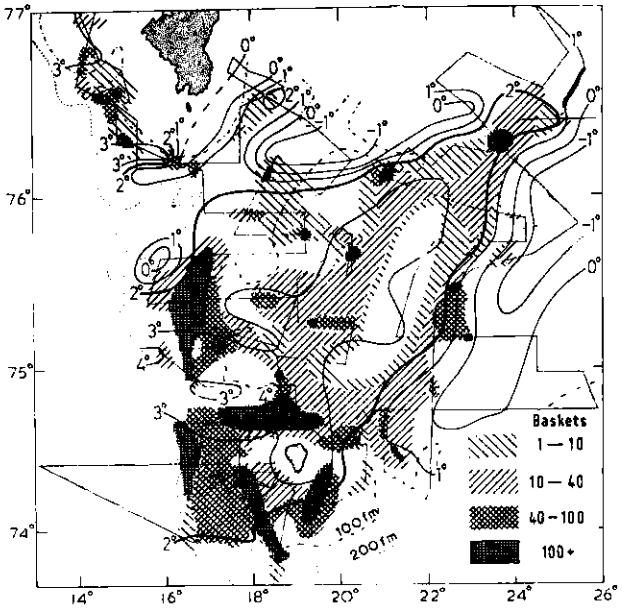


Fig. 16. Distribution of echo survey signals in the fathom above the bottom and the distribution of bottom temperature on the Spitsbergen Shelf.
24 July-15 August 1956.

The second and third surveys showed a rapid movement of the fish concentrations eastwards on to the shelf, particularly in the Storfjordrenna. On the third survey the concentrations were still in water warmer than 1°C, and there had been a marked extension of this water eastwards along the southern edge of the Storfjordrenna and in the region between this trench and the North-west Gully at the same time as the fish concentrations had moved eastwards. Although to some extent this movement of the fish can be interpreted as being a move from deep water into shallow, this could not have been the case in the Storfjordrenna, where the movement was parallel to the isobaths. Furthermore, Fig. 2 shows that between early April and the end of May 1956, there had been a marked increase in the strength of the West Spitsbergen Current: this increase normally occurs at this time of the year, but in 1956, by the end of May, the current had nearly twice its normal volume transport. Although this influx seems to have decreased subsequently and to have reached the normal level by the end of July, it is considered that the remarkable advance of both fish and warm water eastwards in the first half of June was associated with this surge in the current observed at the end of May.

It will be noted that many of the fish on this cruise were in water colder than 2°C. This is not in accord with the findings of Lee (1952): he found that on the comparable dates in 1949 and 1950 the cod to the west of Bear Island were on the whole in water warmer than 2°C, although in 1949 a few paying catches were taken in 1.5°C to 1.0°C. On the comparable dates in 1955, moreover, trawl hauls and an echo-survey in the area between the North-west Gully and the Storfjordrenna showed most of the fish to be in water warmer than 2°C. It would thus appear that along the western edge of the Spitsbergen Shelf the cod are in the warmer water at this season, but that the temperature of this water varies from year to year.

The results of the echo-survey and bottom temperature survey carried out during Cruise V/1956 in July-August are shown in Fig. 16. It can be seen that the advance of the fish and warm water eastwards had continued across the shelf and that the distribution of the fish was now limited remarkably closely by the 2°C isotherm. The heaviest concentrations, however, were still in the same position along the edge of the shelf as on the previous cruise.

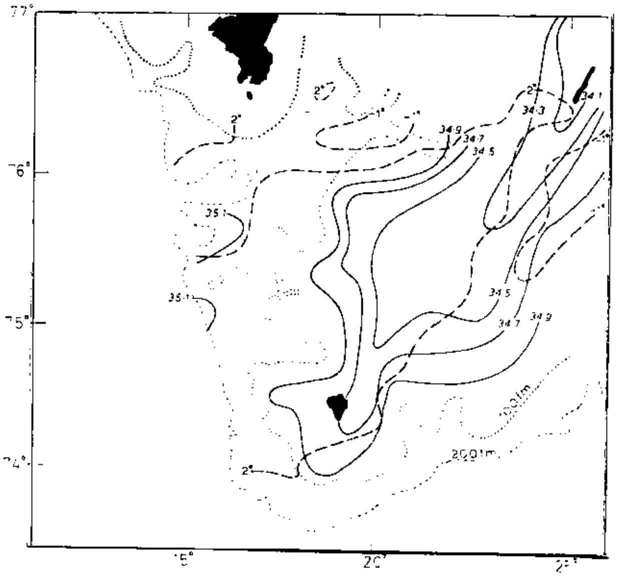


Fig. 17. Distribution of bottom salinity and bottom temperature on the Spitsbergen Shelf. 24 July-15 August,1956.

It might be thought that the advance of the fish and warm water eastwards was again due to the influx of the West Spitsbergen Current, but Fig. 2 shows that by the end of July this had decreased to its normal level. Further, bottom salinity samples were taken over a wide area on this cruise and the salinity distribution obtained is shown in Fig. 17. It can be seen that the axis of the low salinity water on the shelf, marking the Bear Island Current, lies to the westward of the axis of the low temperature water. If the increase in temperature on this part of the shelf had been due to the advection of Atlantic water one would not have expected this difference in position of the two tongues, and it is considered that summer surface heating is more likely to have been responsible for the rise in bottom temperature. Work carried out by us in 1953 shows that the influence of tidal mixing on the shallowest part of the bank is to prevent the formation of a thermocline and to carry heat right down to the sea-bed. In the deep area further eastward, however, a thermocline is formed and the bottom water remains cold. Thus, although in June the movement of the fish and warm water on to the shelf could be associated with a surge of the West Spitsbergen Current, by July-August some of the fish had advanced on to the shallower part of the bank into an area of water of Arctic origin warmed by summer heating.

DISCUSSION

Earlier publications, covering mainly the southern and western edges of the Spitsbergen Shelf (Lee, 1952; Graham *et al.,* 1954), established that as a general rule concentrations of cod were not found at bottom temperatures below 1.75°C. Exceptions to this rule were found in July-September on the eastern edge of the shelf between Bear Island and Hope Island (*i.e.,* including the area covered in this paper), when heavy concentrations were located in water as cold as -0.5°C in 1949 and lesser concentrations in 1950 and 1951. Drawing on additional evidence, including commercial fishing and echo-sounder records, Trout (1957) proposed a mechanism of cod distribution which placed less emphasis on temperature as a determining influence and more on the passive transport of fish in the northerly surge of the West Spitsbergen Current during the first half of the year. He coupled this with the proposition that the fish followed an intrinsic seasonal depth cycle, living deepest in the late winter and early spring and becoming more pelagic in habit in the summer in response to daylight radiance. The presence of fish in cold Arctic water in summer, he suggested, could have arisen by their movement downwards from warm surface water into cold bottom water rather than by horizontal migration across the boundary of the two water masses. On the other hand, the possibility that temperature was having a direct influence on the distribution of cod was strengthened by the studies of Woodhead and Woodhead (1959), who showed that except in the months of July to September certain physiological changes were found in those fish which were in water below about 2°C; in these three summer months, however, no corresponding changes were observed in fish in temperatures down to -0.5°C. As has been noted above, these are the only three months when major concentrations of fish have been found in cold water.

The results presented here lend added support to Trout's view of the importance of passive transport in a definable water mass. The echo-survey results of 1956 show more explicitly than had previously been possible, by trawling surveys, how the short-term movements of the main cod population on to the western edge of the Spitsbergen Shelf during early summer are closely associated with the surge of the Atlantic water of the West Spitsbergen Current, but also how later in the summer the spread of fish on to the shelf is made possible by *in situ* warming rather than by the movement of Atlantic water. In the opposite direction, the relatively sudden cascading of cold Arctic water down the southern slopes of the shelf during the spring of 1955 coincided with an equally sudden retreat of fish to deeper water. More generally, the main features of both the hydrography and fish distribution in the area seem on the whole to follow the seasonal and year-to-year variations in the strength of the West Spitsbergen Current as determined by measurement of its water transport.

From analysis of otolith structure and tagging results, Trout (1957) concluded that there was appreciable segregation between the fish on the eastern and western sides of the Spitsbergen Shelf. Those on the eastern side typically possessed a "split ring" otolith structure which Trout associated with their entry into cold water to feed in the summer. It is therefore of interest to find from the 1954 observations on the eastern edge of the shelf that the distribution of these fish, even when feeding, nevertheless coincided in a particularly striking way with sharp temperature gradients while these existed in the early and late periods of the year. Taking the results on both the eastern and western edges of the shelf as a whole, they agree in confirming earlier findings that a temperature a little below 2°C (1.5°C would seem a more precise figure) constitutes an effective limit to the distribution of cod for the greater part of the year.

The observations in the South-east Gullies region show that much of the seasonal depth cycle of cod deduced by Trout, mainly from records of the average depths of commercial fishing, is probably more a consequence of the seasonal depth change of the boundary between Atlantic and Arctic water than something intrinsic to the fish. This is evident from a comparison of the fish and temperature distributions in the exceptionally cold spring of 1953, the warm spring of 1954 and the changing spring of 1955. In 1953 the fish were concentrated at even greater depths than would be predicted by Trout's average curve; in 1954 they were very much shoaler; and in 1955 they moved from shoal to deep water. The boundary of the water masses varied correspondingly. This does not deny, however, Trout's thesis that the pelagic habit of cod in high summer (for which there is now added evidence from later echo-sounder records) is of significance in enabling fish to complete the final part of their "outward" migration in the warmer upper water layers, from which they may descend here and there into cold bottom water.

The influence of feeding and of the distribution of the food of cod has not hitherto emerged in any clear-cut way, and there is nothing in the evidence presented here to suggest that it is a major factor in determining the general distribution of cod. There are, however, the observations from South-east Gullies region that the presence of a restricted concentration of a preferred food (in this case young herring) may result in significant aggregation of cod on it within a region which is hydrographically tolerable but otherwise featureless; on the other hand, the widespread occurrence of a preferred food has little effect, as was the case with capelin in 1953. It is also clear that the preferred food can change with the hydrographic regime; as the Atlantic influence increased towards the end of 1953 so herring replaced capelin and it remained the preferred food in one locality through 1954 until the Atlantic influence decreased again.

There remains the biological problem of the precise mechanism which causes the cod to be localised - or, more strictly, to appear to be localised - for much of the time in a particular water mass. The three most plausible assumptions, acting separately or together, would seem to be

(a) that the fish are responding directly to the temperature gradient between the water masses by some directional behaviour mechanism

(b) that fish are responding to some difference between the water masses other than temperature, of which differential currents at their boundary seems the only likely feature

(c) that fish are not inhibited from crossing the boundary between the water masses and in fact do so, but die rapidly after entering cold water (except in the high summer), thus giving the impression of a positive behavioural response to the boundary.

Such evidence as there is seems mostly inconclusive in distinguishing between these, except perhaps that the last is unlikely to be a major factor in as much as dead fish have not to our knowledge been reported from cold water in this region, although there is abundant evidence from other areas that low temperatures can and do constitute a major cause of death of cod in certain circumstances (Woodhead and Woodhead, 1959). Disentangling the directional influences of temperature gradients and differential currents is particularly difficult from evidence of the kind presented here, since it follows hydrodynamically that the steeper the temperature gradient the more contrasting the currents are likely to be at the interface. Many of the observed temperature gradients are, in reality, so slight that it is difficult to imagine how fish could respond directionally to them. This may not have been the case at the boundary of the cold tongue in 1954 (Figs. 4-5). Here, the steepest temperature gradient, as judged from the spacing of the isotherms, was about 3°C in a distance of five miles. Accepting the experimental evidence of Bull (1952) that cod can detect a minimum temperature difference of 0.05°C, this means that a fish would have had to swim a distance of at least 150 m before it could detect a change in temperature. The true local temperature gradients may, of course, have been sharper than this, yet for such a structure to have remained localised and evidently stable for a period of several weeks there must have been strong lateral shearing between the water masses in the region of the steep temperature gradient, with the current flowing parallel to the isotherms. Fish in the region of the temperature gradient and in contact with the bottom are likely to have been facing predominantly into the current (whether actually progressing contranatantly or not is immaterial) and to have aligned themselves in a direction parallel to the boundary, and hence they were unlikely to cross it. Again when in the summer of 1956 *in situ* warming on the bank caused the temperature difference between the West Spitsbergen and Bear Island Currents to tend to disappear, fish evidently moved from one water mass to the other; but any current differential that may have previously existed is also likely to have decreased at the same time, and so the respective effects of temperature and current again cannot be disentangled. It would appear that an investigation is called for which analyses conditions around a cold tongue in great detail and which does this by using the echo-survey method together with techniques for measuring currents near the sea-bed and for the continuous recording of temperature against distance over the sea-bed.

REFERENCES

BROWN, W.W. and C. CHENG. 1946. Investigations into the food of the cod (*Gadus callarias* L.) off Bear Island, and of the cod and haddock (*G. aeglefinus* L.) off Iceland and the Murman coast. *Hull. Bull. Mar. Ecol.*, 3: 35-71.

BULL, H.O. 1952. An evaluation of our knowledge of fish behaviour in relation to hydrography. *Rapp. Cons. Explor. Mer*, 131: 8-23.

GRAHAM, M. *et al.* 1954. Report on research from the *Ernest Holt* into the fishery near Bear Island 1949 and 1950. *Fish. Invest., Lond.*, Ser. 2, 18 (3), 87 pp.

HILL, H.W. and A.J. LEE. 1958. The effect of wind on water transport in the region of the Bear Island fishery. *Proc. roy. Soc.*, (B), 148: 104-116.

LEE, A.J. 1952. The influence of hydrography on the Bear Island cod fishery. *Rapp. Cons. Explor. Mer*, 131: 74-102.

1961. Hydrographic conditions in the Barents Sea and Greenland Sea during the IGY compared with those in previous years. *Rapp. Cons. Explor. Mer*, 149: 41-43.

1962. The effect of the wind on water movements in the Norwegian and Greenland Seas. *Proc. Symp. Math.-Hydrodynam. Meth. Phys. Oceanogr., Sep. 1961*, Inst. Meereskunde Univ. Hamburg: 353-373.

RICHARDSON, I.D. *et al.* 1959. Echo sounding experiments in the Barents Sea. *Fish. Invest., Lond.*, Ser. 2, 22 (9), 57 pp.

TROUT, G.C. 1957. The Bear Island cod: migrations and movements. *Fish. Invest., Lond.*, Ser. 2, 21 (6), 51 pp.

WOODHEAD, P.M.J. 1964. Diurnal changes in trawl catches of fish. *Rapp. Cons. Explor. Mer*, 156 (in press).

WOODHEAD, P.M.J. and A.D. WOODHEAD. 1959. The effects of low temperatures on the physiology and distribution of the cod, (*Gadus morhua* L.) in the Barents Sea. *Proc. zool. Soc. Lond.*, 133: 181-199.

A-15

DATA ON THE DISTRIBUTION OF TUNA CONCENTRATIONS DURING THE FEEDING PERIOD IN THE TROPICAL ATLANTIC OCEAN[1]

By

V. L. Zharov[2]

ABSTRACT

The results of Soviet research fishing expeditions to the Gulf of Guinea and to the region off the northeastern coast of Brazil during 1959-63 are considered.

The distribution of tuna concentrations in both areas is determined first of all by the presence of frontal zones, either between water masses with different characteristics or between the surface waters of these regions and deep waters rising to the surface. Within such frontal zones waters with a high content of biogenic elements and most often characterized by low temperatures are found close to waters carrying a great supply of heat but poor in biogenic elements. Such a combination of high content of biogenic elements and a great supply of heat favours the development of organic life and results in the formation of areas of high biological productivity within the frontal zones. In their search for food, young fishes, many small fishes and large invertebrates (squids) and the tuna which follow them, tend to concentrate within these productive areas or in areas lying close to them. Thus the search for food is the main factor in the concentration of tuna in these areas of the tropical Atlantic Ocean.

Furthermore, in some regions within the frontal zones conditions exist which prevent the movement of some species of tuna in any direction. Factors limiting the movement of tuna include the horizontal and vertical location of the 20°C isotherm and the 35°/oo ishaline. The occurrence of waters with a temperature below 20° and a salinity below 35°/oo in the upper layers of the ocean acts as a barrier to tuna shoals and they concentrate near to the boundaries of these waters.

EDITORIAL NOTE:

As this paper deals with an area not strictly within the terms of reference of the ICNAF Environmental Symposium, Rome, 27 January-1 February 1964, only an abstract is published here. It was, however, presented in extenso at that symposium.

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[1] Originally Contribution No. A-11, ICNAF Environmental Symposium, Rome, 27 January-1 February 1964.

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A-16

INTERPRETATION OF FISH DISTRIBUTIONS IN RESPECT TO CURRENTS IN THE LIGHT OF AVAILABLE LABORATORY AND FIELD OBSERVATIONS[1]

By
T. Laevastu[2]

ABSTRACT

The existing knowledge of the response of fish to currents and the orientation and other behaviour of fish in currents is reviewed. The difficulties of observing and relating fish behaviour to currents are pointed out and it is suggested that these aspects be investigated through tests of pre-established hypotheses, several of which are established in this paper. The combined effects of currents and other environmental factors are described through examples from literature. A model of the behaviour of fish in respect to tidal currents is constructed. Some aspects of the seasonal migrations are analyzed in relation to current patterns. The possible effects of current boundaries on the aggregation and migrations of fish are described. These aspects of fish behaviour in currents which promise direct application in fish location and in practical fishery are emphasized.

INTRODUCTION

Several recent investigations tend to show that advection is the greatest component causing local changes of environmental properties in the sea. Fish can be expected to respond directly to those environmental changes caused by currents and, also, to respond directly to and orient in the current. Unfortunately, it is extremely difficult to observe directly the behaviour of fish in currents in the natural environment. Therefore, very few direct publications on the subject are available in literature. If one wants to clarify the interaction between fish behaviour and currents, one has to draw upon the knowledge from pertinent laboratory experiments, knowing that these experiments do not exactly reproduce complicated nature. A useful way to gain more insight on the influence of currents on fish is through testing of pre-established hypothetical models.

It could be expected that currents will affect the following aspects of fish behaviour:

1) Transport of fish eggs and larvae from spawning areas to nursery grounds and from nursery grounds to feeding grounds. Thus, any abnormality in this transport would affect the survival of a given year brood;

2) Currents might serve as the orienting means for the migration of adult fish;

3) Currents might affect the diurnal behaviour, especially in relation to tidal currents;

4) Currents, especially current boundaries might affect the distribution of adult fish, either directly or indirectly, through the aggregation of fish food or by determining other environmental boundaries;

5) Currents might affect the properties of the natural environment, thus determining the abundance and occurrence near the limits of the normal geographic distribution of given species.

The following summary deals with adult fish in relation to currents. It attempts to summarize the essentials of past investigations on the subject and to establish some hypothetical models of behaviour which need careful testing in nature before they can be accepted as valid.

The influence of currents on fish stocks is greatest in the egg and larval stages. Excellent investigations on this subject have been conducted by Walford (1938), Carruthers *et al.* (1951) (who also suggest the future approach for prediction of year-class strength from the wind current data), Rae (1957), Bishai (1960), Hela and Laevastu (1962). These aspects will not be discussed in this paper.

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[1] Originally Contribution No. A-2, ICNAF Environmental Symposium, Rome, 27 January-1 February 1964.

[2] University of Hawaii.

RESPONSE OF FISH TO CURRENTS

Bull (1952) found in his numerous, carefully designed laboratory experiments on the behaviour of fish in relation to hydrographic factors, no response of fish to the rate or direction of current flow and was unable to condition the fish to the current. Several other laboratory and field observations have shown that fish respond and react to currents and their changes in various ways. Elson (1939) found that a sudden increase in current strength and the amount of turbulence resulted in increased activity of speckled trout. In still water, the activity took the form of random wandering. The increased activity while in the current was manifested by movement upstream. Brawn (1960) observed that herring responded to real and apparent currents greater than 3 - 9 cm sec^{-1} by swimming upstream at a rate in excess of the current speed until the maximum swimming speed had nearly been reached. It is possible that there is a lower threshold value of current speed to which fish react and this threshold value may vary from species to species.

Aleev (1958) analyzed the adaption to movement and manoeuverability of fish. He has classified 25 species according to horizontal and vertical manoeuverability and the coefficient of resistance for rectilineal movement. It is obvious from his work that different species must react differently to currents, and it is not possible to generalize results obtained with a given species to all fish.

Most field and laboratory observations show that fish usually head to the current. It has been observed that a fish also heads to the current when it lets itself be carried along with the current. However, if the fish turns downstream in the current, it usually swims faster than the current. In weak currents, other directions and orientations can be observed.

It has been observed that fish are inactive in cold water and allow themselves to be carried along with the current (*e.g.*, herring during winter in the Norwegian Sea). It has also been found that when pelagic fish are feeding, they usually drift with the current (Bullen, 1912).

It can be noticed that the orientation of fish within the school and the movements of the schools of herring might be regulated by currents because in the net fishery for herring, the fish go into the net usually only from one side in a given night and only on rare occasion from both sides.

It has been further observed with fresh water fish that light plays a role in the orientation of fish to the current. Fish are observed to swim against the current in the light but drift with it in the dark. The behaviour of adult fish in respect to currents (as well as in respect to other environmental conditions) depends also on the physiological stage (*e.g.*, maturity stage) of the fish.

Some data on the observed and measured swimming and cruising speeds of fish have been summarized in Table 1. Swimming and cruising speeds obviously vary with the size of fish and also from species to species. Some observations also show that the swimming speed is greatly affected by the prevailing temperature. Brett *et al.* (1958) found that the optimum cruising speed of sockeye salmon was at 15°C and that of coho at 20°C. However, Blaxter and Dickson (1959) found no obvious correlation between the average maximum swimming speed and temperature. Blaxter and Dickson (1959) estimated that small fish (smaller than 30 cm in length) can swim about 10 body lengths per second, and the speed increases less above this body length than in the proportion mentioned.

It has been observed that fish cannot maintain the maximum speed for a long time and the cruising speeds are usually much lower than the maximum swimming speeds observed in the experiment. Some idea of the cruising speeds of fish can also be obtained from the pelagic trawling experiments. Schärfe (1959) found that the minimum speed required for the catching of sprat with a pelagic trawl was 2.5 knots, and for the catching of herring in the North Sea 3.5 knots. It can be tentatively concluded from various data that for small and medium size pelagic fish, the cruising speed is ca. 2.5 knots during the daytime and the day and night average is ca. 1.5 knots.

TABLE 1. SWIMMING AND CRUISING SPEEDS OF FISH

Species	Speed	Remarks	Author
	cm sec^{-1}		
Young sockeye and coho salmon	30-40	Maximum sustained speed	Brett, Hollands and Alderdice (1958)
Herring larvae	0.58-1.03	Critical velocity	Bishai (1960)
Herring	91	Maximum speed for 15.2 cm fish	Brawn (1960)
Herring	143	Maximum speed for 26.7 cm fish	Brawn (1960)
Cod (12 - 56 cm)	75-210	Maximum speed	Blaxter and Dickson (1959)
Herring (1 - 25 cm)	3-170	Maximum speed	
Mackerel (33 - 38 cm)	189-300	Maximum speed	
Plaice (6 - 25 cm)	6-129	Maximum speed	
Horse mackerel	5-55	Observed speeds; most frequent 25	Kawada, Tawara, and Yoshimuta (1958)

COMBINED EFFECTS OF CURRENTS AND OTHER ENVIRONMENTAL FACTORS ON FISH BEHAVIOUR

The behaviour of fish in relation to the environment might be, in most cases, a result of a combination of the influence of several environmental factors together. It is obvious to connect the diurnal behaviour with the diurnal change in light conditions which, when combined with currents (*e.g.*, tidal) can considerably affect the distribution of fish. Davidson (1949) reported experimental results which indicate that salmon swim during the day and rest on the bottom at night, whereas, eels burrow in the gravel in bright daylight, come out in the evening and translocate rapidly even at night when the salmon are resting. As already mentioned, it has been observed in fresh water fish that they swim actively against the current during the day, whereas, they drift with it during the night.

The temperature of the water can be expected to greatly affect the migrations and transport of fish by currents. It has been observed that in colder, near 0°C waters, fish are inactive and are carried with the current. This fact is assumed to affect the Norwegian herring migrations: Those herring aggregate in the cold water pocket east of Iceland during the early winter, and are assumed to be carried into this convergence area by a branch of the East Greenland Current. When these cold water pockets are cut off into the warmer Norwegian Current waters and sink, the fish come into the warm Norwegian Current waters and start their active migrations to the spawning grounds in the Norwegian coastal areas.

Trout (1957) described the migrations and movements of the Bear Island cod. This description illustrates the seasonal interactions between currents, light and seasonal migrations. The conclusions were as follows:

"Water movement is responsible for the changes in distribution of the Arcto-Norwegian cod.

Yet, this is only a secondary effect of their changing behaviour in respect to changing light conditions which results in their primary annual vertical migration and their annual depth range.

Winter, rheotactic, contranatant migration takes place on the bottom in the absence of light during the period of annual water transport maximum.

Summer, passive, or denatant migration takes place during the lower summer peak of water transport at which time the cod shoals are largely pelagic in response to light. They are, thus, capable of being displaced horizontally, relative to the bottom, by movement of the water mass containing them. Maximum horizontal displacement is not achieved because a portion of the shoal spends a part of each 24 hr on the bottom. All known geographical limits of fishing are well within this maximum distance. Variations in summer transport values will affect the limits reached by shoals from year to year. Therefore, distribution is the resultant of interaction of changing behaviour with the cycle of movement of the water masses in which the cod are found.

Normally, fish would tend to remain in their particular water mass, but transference from one water mass to another may take place as a result of changes in behaviour. In the absence of water movement, horizontal movement will be of limited extent, but the annual depth range would be expected to persist."

Fraser (1958) assumed that the diurnal migrations of fish and plankton also play their part in the transport of fish by currents, as for example, when the organisms are at the surface at night and are drifted in one direction, and in the daytime are returned by deeper currents running in the opposite direction.

The behaviour of fish in relation to light and currents might be valid also for other areas and species and merit testing with available distributional data. An analogous hypothetical behaviour pattern in relation to tidal currents is given in the section on these below.

LARGE SCALE TRANSPORT AS A FACTOR DETERMINING FISH DISTRIBUTION

It could be assumed that one of the main factors affecting the year to year variations of availability of fish in any given ground might be the prevailing currents, as affected by the year-to-year anomalies of winds; and that the same methods as suggested for the prediction of the brood-strength fluctuations (Carruthers, *et al.*, 1951) could also be used for the prediction of the availability of adult fish. Craig (1958) has shown that the availability of herring four years old and older in the Buchan pre-spawning fishery is related to the wind and temperature during the catching season. Obviously, the temperature can be greatly affected by the advection, and thus, the whole fishery might be directly related to currents which in turn are related to winds.

Based on the advection and temperature ranges, Craig (1958) devised a formula to predict the catches of herring in the Buchan fishing grounds. The main basis for such a prediction is the analysis of the anomalies of winds.

Fraser (1958) analyzed the influence of current transport of egg and larvae in the North Atlantic and the significance of this transport on the recruitment of given fish stocks, and found that some stocks are entirely dependent on broods from "downstream" spawning grounds.

The seasonal behaviour and migrations of fish might also be related to current patterns. The eggs and larvae are transported with the current from the spawning ground. At a certain stage of life, the fish have to begin swimming actively against the current to reach the spawning grounds again. This migration cycle may even be an annual one. Spawned fish, being weak after this process might be carried with the currents to the feeding grounds and must swim back later to the spawning grounds against the current, thus completing one cycle per year. This can be illustrated with the example of the Arcto-Norwegian cod which cover the whole of the Barents Sea and West Spitsbergen waters in their summer feeding migrations and come together to spawn in the early spring off the Lofoten Islands (Corlett, 1956). The current charts show that fish as well as larvae can be carried in the West Spitsbergen and North Cape Current as far as the Bear Island area. Thus, the products of the spawning in the West Fjord in spring are distributed over the feeding grounds of the western Barents Sea by autumn. This recurrent system and the spawning grounds in relation to it has been described by Lee (1952) and by Corlett (1959). A similar situation might exist in the Northwest Atlantic as well.

Lee (1961) has further analyzed the variation of the volume transport of the West Spitsbergen urrent and showed the dependence of this current on the development of the polar high pressure ystem. He has also suggested the possible process of cooling and anomalous advection in the area.

Rodewald (1960 *a,b,c,d*) has analyzed the fluctuations of the landings and availability of ifferent commercially important fish stocks in the Barents Sea, Labrador area, and Icelandic aters in relation to the anomalies of winds. All his results indicate that anomalous water transort caused by large scale variations of atmospheric pressure and winds determine the availability f a number of commercially important fish species, especially in northern waters where they are istributed close to the boundary of their normal range. By predicting the wind and pressure anomlies and the resulting anomalous currents, one would be able to predict the availability of fish n those fishing grounds. One of the biggest year to year fluctuations of the availability of elagic fish is that of the California sardine. This fluctuation has been described as being due o changes in the current system (Cal.Coop. Oc. Fish. Invest., 1953). It is assumed that a strong ountercurrent in the spring and early summer would affect the northward migration and physical ransport of sardines. If the countercurrent remains strong throughout the year, the southward eturn against the current would impede the fish, and therefore, the sardines would reach the pawning grounds later in the year. The heavy countercurrent along the coast also causes the emperatures in the inshore areas to be higher than average. Thus, if it is the cooling of the ater due to the onset of winter that causes the sardines to migrate southward, the beginning of he migration would be delayed. Further, the abundance of California sardines may be influenced y the transport of egg and larvae.

A preliminary study of the boundaries of ichthyofaunal regions of the world in relation to urrents indicates that sharp changes of fauna occur where the permanent currents along the coasts re strong, exceeding one knot. The species inhabiting the downcurrent waters have especially harp distributional boundaries in the Agulhas, Kuroshio, and Florida currents. Currents weaker han the above mentioned might well establish distributional boundaries of less mobile species uch as flatfish.

FISH IN RELATION TO TIDAL CURRENTS

One of the first to describe the possible relation between herring catches and tides was ester (1938) who discovered an inverse relation between the tidal difference and herring catches n the British Columbia waters. His explanation was:

"At present, therefore, it would seem that the most plausible explanation of why herring are ore available in the Swanson Channel fishery during the first and third quarters of the moon and ess available during the new and full moon lies in the effect of tides on the movements of hering."

Tester further assumed that strong tidal currents affect the transport of herring to and from arious areas. The interaction between diurnal behaviour and strong tidal currents might affect he transport of any fish. Assume that a fish species spends the day on or close to the bottom and ises into the water mass during the evening. Assume also that strong diurnal tides prevail in a iven locality. In these conditions, the fish are expected to keep a given position on the bottom uring the day, but are most probably carried along with the tidal currents during the night. In he case of diurnal tides, the ebbing current dominates during the night for about two weeks. The ish may be transported in one direction during this period and carried back again during the next wo week period.

Jones (1957) studied the movements of herring shoals in relation to tidal currents in the North ea. His conclusions were:

"Echo surveys carried out in the Calais region in December 1955 show that herring shoals move n the same direction as the tidal currents. It is most likely that these observations were made n herring which had not yet spawned.

It was not possible to come to any definite conclusion as to whether the fish were stemming he current, swimming with it, or being carried along passively.

One set of results suggested that the herring were stemming the current at a swimming speed f 1 to 2 knots although they were being carried along the ground."

There are several fishing methods which rely on tidal currents. One, most peculiar, is the so-called bag net fishery off Bombay where the fish are carried by strong tidal currents into big, anchored bag nets. It seems that the fish stem the current but are transported with it, being relatively sluggish in the low oxygen content water on the Bombay continental shelf.

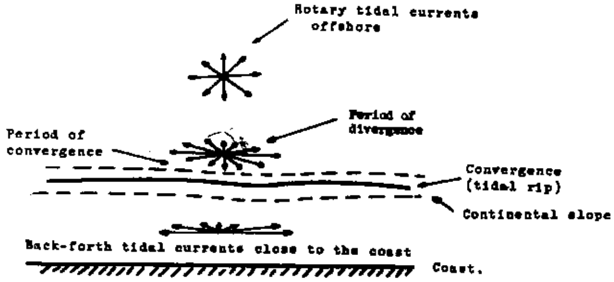

Fig. 1. Scheme of coupling of coastal back-forth and offshore rotary tides.

The present author has observed the aggregation of fish (nehus, dolphins, sharks, and other species) along the island slopes of the Sandwich Islands where a convergence is caused by the prevailing tidal currents. The scheme of this convergence is shown in Fig. 1. It is possible that smaller fish and other fish food are aggregated on this current boundary by the tidal currents and bigger fish aggregate there actively for feeding purposes. Some of these problems are examined in the next section.

EFFECTS OF CURRENT BOUNDARIES ON THE DISTRIBUTION OF FISH

Zusser (1958) described the theory that commercial aggregation of fish usually occurs in the centers of the eddies of currents where fish rest. His explanation points to the fact that the fish usually stem the current and need occasional rest.

Orton (1937), Redfield (1939, 1941) and Laevastu (1962) have shown, at least partly, that the retention and accumulation of plankton, fish egg, and larvae occur in the centers of anticyclonic eddies on the northern hemisphere. This aggregation might also be connected with (*e.g.*, through feeding) the aggregation of adult fish in the current eddies. Local eddies are caused by the morphology of the coast and configuration of the bottom. Therefore, local knowledge of the details of the currents would play an important role in the locating of fishable concentrations of fish, if the fish distribution is affected by eddies.

The current convergences cause a "mechanical" aggregation of forage organisms and also small fish. This hypothetical mechanism of concentration has been described by the present author (Laevastu, 1962). For a long time, Japanese tuna fishermen have made practical use of this knowledge to locate concentrations of pelagic tunas. The convergence between cold and warm currents are found to be especially rich. Here, in addition to the transport, high basic organic production may play an additional role. The convergences usually change positions during the year in medium and high latitudes. The Japanese salmon fishery in the Bering Sea follows the movement of the eastern convergence of Oyashio towards the northwest during the salmon fishing season. The bulk of the largest catches of pelagic salmon are obtained at the convergence.

Uda (1936) stated that the 'saury' *(Cololabris saira)* stays in the areas between the boundaries of the Kuroshio and Oyashio Currents, and always migrated toward the maximum gradient of surface temperature. According to Uda (1952) the best areas for pelagic fishery in general are the convergences of currents.

The relation between convergences and fish aggregation might not be a simple statistical one. Three hypothetical conditions must be recognized in this relation.

1) The converging currents might be weak, below the threshold value for orientation of fish. Zooplankton is slowly accumulated at the convergence and the aggregation of fish might still occur on prey. Because of this the convergence might act as an environmental boundary.

2) The converging currents might be of medium strength. Fish orient to the current and aggregate at the "upcurrent" end of the convergence. Slight accumulation of zooplankton occurs.

3) The converging currents might be strong. Fish head the current and are carried along with t. Fish aggregation at the "downcurrent" end of the convergence is possible. Because of the trong current no aggregation of zooplankton occurs.

Several hypotheses on the effects of currents need testing with observational data, the obaining of which requires at times the help of experienced fishermen.

REFERENCES

ALEEV, I.G. 1958. Prisposovlenie k dvizheniiu i povorotlibost ryb (Adaption to movement and maneuverability of fish). *C.R. Acad. Sci., USSR,* 120: 510-513.

BISHAI, H.M. 1960. The effect of water currents on the survival and distribution of fish larvae. *J. Cons. int. Explor. Mer.,* 25(2): 134-146.

BLAXTER, J.H.S. and W. DICKSON. 1959. How fast can fish swim? *Scot. Fish. Bull.,* 12: 14-18.

1959. Observations on the swimming speeds of fish. *J. Cons. int. Explor. Mer.,* 24(3): 472-479.

BRAWN, V.M. 1960. Underwater television observations of the swimming speed and behaviour of captive herring. *J. Fish. Res. Bd. Canada,* 17(5): 689-698.

BRETT, J.R., M. HOLLANDS and D.F. ALDERDICE. 1958. The effect of temperature on the cruising speed of young sockeye and coho salmon. *J. Fish. Res. Bd. Canada,* 15: 587-605.

BULL, H.O. 1952. An evaluation of our knowledge of fish behaviour in relation to hydrography. *Rapp. Cons. Explor. Mer.,* 131: 8-23.

BULLEN, G.F. 1912. Some notes on the feeding habits of mackerel and certain clupeoids in the English Channel. *J. Mar. biol. Ass. U.K.,* 9: 394-403.

CALIFORNIA COOPERATIVE OCEANIC FISHERIES INVESTIGATIONS. 1953. Progress Report 1952-53. Sacramento State Printer, 44 pp.

CARRUTHERS, J.N., A.L. LAWFORD and V.F.C. VELEY. 1959. Fishery hydrography: Brood-strength fluctuations in various North Sea fish with suggested methods of prediction. *Kieler Meeresforsch.,* 8(1): 5-15.

CORLETT, J. 1958. Distribution of larval cod in the Western Barents Sea. *Spec. Publ. int. Comm. Northw. Atlant. Fish.,* No. 1,pp.281-288.

CRAIG, R.E. 1952. The Scottish programme of herring hydrography, 1951. *Rapp. Cons. Explor. Mer.,* 131: 108-110.

1958. Dependence of catches on temperature and wind in the Buchan pre-spawning fishery. *ICES, C.M. 1958 Herring Comm. No. 43* (mimeo).

DAVIDSON, V.M. 1949. Salmon and eel movement in constant circular current. *J. Fish. Res. Bd. Canada,* 7: 432-448.

ELSON, P.H. 1939. Effects of currents on the movement of speckled trout. *J. Fish. Res. Bd. Canada,* 4(5): 491-499.

FRASER, J.H. 1958. The drift of the planktonic stages of fish in the Northeast Atlantic and its possible significance to the stock of commercial fish. *Spec. Publ. int. Comm. Northw. Atlant. Fish.,* No. 1, pp. 289-310.

HELA, I. and T. LAEVASTU. 1962. Fisheries hydrography. Fishing News (Books) Ltd., London, 132 pp.

JONES, F.R.H. 1957. Movements of herring shoals in relation to tidal current. *J. Cons. int. Explor. Mer.,* 22: 322-328.

KAWADA, S., Y. TAWARA and C. YOSHIMUTA. 1958. An attempt for determining the swimming speed of fish schools by the fish finder — Preliminary report. *Bull. Jap. Soc. sci. Fish,* 24: 1-4.

LAEVASTU, T. 1960. Factors affecting the temperature of the surface layer of the sea. *Soc. Sci. Fenn., Comm. Phys.-Math.,* 21(1): 136 pp.

1962. The adequacy of plankton sampling. *Rapp. Cons. Explor. Mer.,* 153: 66-73.

LEE, A. 1961. Hydrographic conditions in the Barents Sea and Greenland Sea during the IGY compared with those in previous years. *Rapp. Cons. Explor. Mer.,* 149: 40-43.

MEYER, A. and M. RODEWALD. 1960. Ist die Grösse der Fischfänge vor Labrador von der atmosphärischen Zirkulation abhängig? *Hansa,* 97(12/13): 669-670.

ORTON, J.H. 1937. Some inter-relations between bivalve spatfall, hydrography and fisheries. *Nature, Lond.,* 140: 505.

RAE, K. M. 1957. A relationship between wind, plankton distribution and haddock brood strength. *Bull. Mar. Ecol.,* 4(38): 247-269.

REDFIELD, A.C., 1939. The history of a population of *Limacina retroversa* during its drift across the gulf of Maine. *Biol. Bull., Woods Hole,* 86: 26-47.

1941. The effect of the circulation of water on the distribution of the Calanoid community in the Gulf of Maine. *Biol. Bull., Woods Hole,* 80: 86-110.

RODEWALD, M. 1960*a*. Bestandsschwankungen des Rotbarsches vor Südlabrador und die atmosphärische Zirkulation im Nordwest-Atlantik. *Hansa,* 97(6/7): 365-367.

1960*b*. Die jüngsten Wassertemperature-und Fischpendelungen in der Barentsee als Folge von Schwankungen der Luft-Kirkulation. *Hansa,* 97(8/9): 481-482.

1960*c*. Die extreme 1958 und 1950 des nordatlantischen Rotbarsch-Jahrgangs: atmosphärisch ausgelöst? *Hansa,* 97(18): 933-934.

1960*d*. Seelach-Wanderungen unter dem Gesichtspunkt der Änderung des Grosswetterlage. *Hansa,* 97(19/20): 1017-1018.

SCHÄRFE, J. 1959. Report on the one-boat midwater-trawling experiments in the North Sea in December 1958 and February-March 1959. *FAO/59/11/9452.*

TESTER, A.L. 1938. Herring, the tide and the moon. *Progr. Rep. biol. Sta., Nanaimo and Prince Rupert,* 38: 10-14.

TROUT, G.C. 1957. The Bear Island Cod: Migrations and movements. *Fish. Invest., Lond.* Ser. 2(31)(6) 51 pp.

WALFORD, L.A. 1938. Effect of current on distribution and survival of the egg and larvae of the haddock *(Melanogrammus aeglefinus)* on Georges Bank. *Fish. Bull., U.S. Bureau of Fish.,* 49(29): 73 pp.

ZUSSER, S.G. 1958. A contribution to the study of fish behaviour. *IPFC Symp. on Fish Behaviour, Colombo* (mimeo).

A-17

FISH MIGRATION AND WATER CURRENTS

By

F.R. Harden Jones[1]

ABSTRACT

The relations between fish migration and water currents are presented with reference to a heoretical framework linking gyrals, production and fish movement. The terms denatant and contra- atant are discussed and suggestions are made as to the biological significance of migration and oming. The conditions under which fish react to water currents and the nature of the response rovide the basis of making a distinction between migration on the open sea and migration on the ontinental shelf. In the open sea oceanic currents are important in the surface waters and fish hould be carried passively with them. Seasonal or diurnal vertical movements would allow fish to ove into a counter-current or into faster or slower water. A comparison is made between fish and ocusts. Passive drift could enable the fish to be carried into areas of high production (upwell- ng zones, polar fronts) and the problem then becomes that of the control of the timing mechanism hich ensures that the fish leaves and joins the gyral, or the counter-current, at the appropriate oment. On the continental shelf tidal currents are often more important than oceanic currents. n shallow water complications arise as the combination of changing tidal current and diurnal ver- ical migration allows a complex interaction between passive drift and orientated movement by isual or tactile contact with the bottom. A model is presented to study the horizontal displace- ents resulting from such an interaction in the case of Downs herring migrating down the Southern ight of the North Sea in the autumn. The model, based on tidal data and what is known of the ehaviour of the herring, shows that the fish are carried to the south towards their spawning rounds. Reversing this line of approach predictions are made of currents based on knowledge of he movements of fish. Counter-currents should be present to carry the European eel to the Sargasso, he Arcto-Norwegian cod to Lofoten, and the south-west Greenland cod to Iceland. Reference is made o Sund's reports of a deep south-going current off the Norwegian coast carrying cod from Andenes o Lofoten.

INTRODUCTION

Fish migrations are thought to conform to the pattern shown diagramatically in Fig. 1. The arvae drift from the spawning ground to the nursery ground. From the nursery ground the juveniles ecruit to the adult stock. The adults migrate to the spawning ground and return later as spent ish to the feeding ground. These movements are, in general terms, related to the water currents. he drift of the larvae is downstream and with the current. The adult spawning migration is against he current, and that of the spent fish with the current. From the association between the move- ent of the spawning fish and that of the water current it is often inferred that the latter pro- ides a directional clue during migration. As this hypothesis appears to be widely accepted, the elation between fish migration and water currents will be considered more closely.

A THEORETICAL FRAMEWORK

A pelagic fish, with pelagic eggs and larvae, living within a region covered by an oceanic ddy or gyral, and carried passively within the system, is essentially a planktonic organism, how- ver strong a swimmer it may be. In marine tropical waters it is not unreasonable to suppose that he environmental conditions would be favourable for the development and survival of eggs and lar- ae at all seasons of the year and throughout the whole region covered by the eddy. Production in ropical waters is probably continuous, and perhaps even a steady state process (Cushing, 1959), nd food, if available at all, should always be present in sufficient quantities for the larvae. gg production could be continuous as Quasim (1955) suggests. Eggs, larvae, young and adult fish ould be found together, but possibly at different depths, and the species would have a continuous istribution throughout the region of the eddy, as shown diagramatically in Fig. 2A. This pattern ay be characteristic of tropical oceanic species, and under these conditions the pelagic fish has o biological need for a definite spawning area or season. Young fish that are carried out of, or

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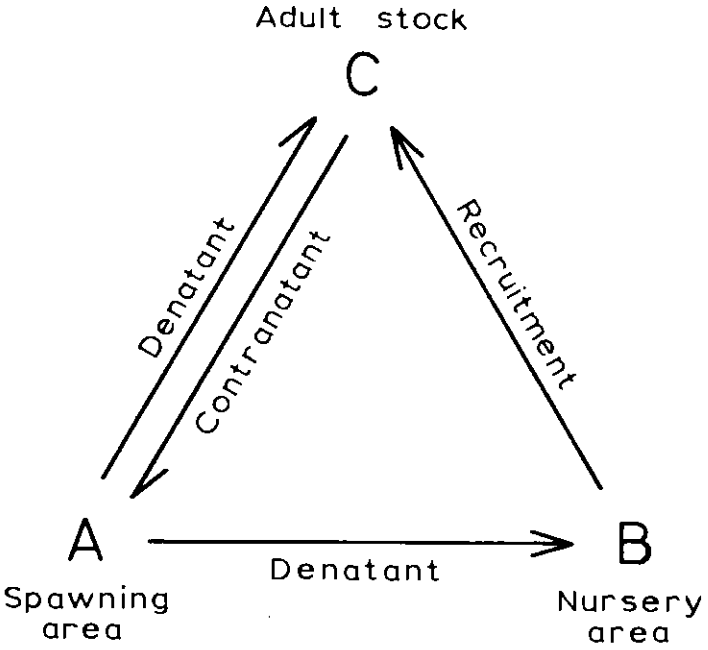

Fig. 1. A simple diagram to illustrate the general pattern of fish migrations.

escape from, the system would, so far as reproduction is concerned, be waste material. But if the eddy system extends from the tropics into temperate or arctic water there would be environmental differences within the region covered by the gyral. The water may change its character as regards temperature and salinity, so that while the older fish may be able to live anywhere within the system, the younger stages could not do so and spawning would only be successful within a limited area. In temperate and arctic waters the production cycle differs from that found in tropical waters. Food is unlikely to be available in more or less equal quantities throughout the year. If the young are to survive the adults must spawn, not only at the right place, but also at the right time. There must be an annual cycle of activity in the gonads and, as shown in Fig. 2B, egg production will be limited to a particular season. The distribution of the species becomes discontinuous and it can only survive as a passive, planktonic organism if the processes of growth and maturation are geared to the circulation time of the eddy so that sufficient numbers of mature and ripe adults are brought into the spawning area at the right time. If the adults take to the bottom, or leave the gyral for a time (Fig. 2C), they could still reach the spawning area by rejoining the system later. But there may be an environmental barrier, such as temperature, which prevents the mature fish completing the circuit, or the gyral itself may be broken by some geographical barrier (Fig. 2D). Under these conditions the adults must return to the spawning ground in the opposite direction to the current in which the eggs and larvae were carried.

DENATANT AND CONTRANATANT MOVEMENTS

Meek (1915) introduced these terms. Denatant means swimming, or drifting, with the current; contranatant means swimming against the current. Thus one would speak of the denatant migration of the pelagic eggs and larvae, and the contranatant migration of the adults towards the spawning area. Now it is important to be clear as to what water current the adults are supposed to migrate against. The biological significance of the migration of the ripening fish is that it is in the opposite direction to the current which carries the eggs and larvae away from the spawning area.

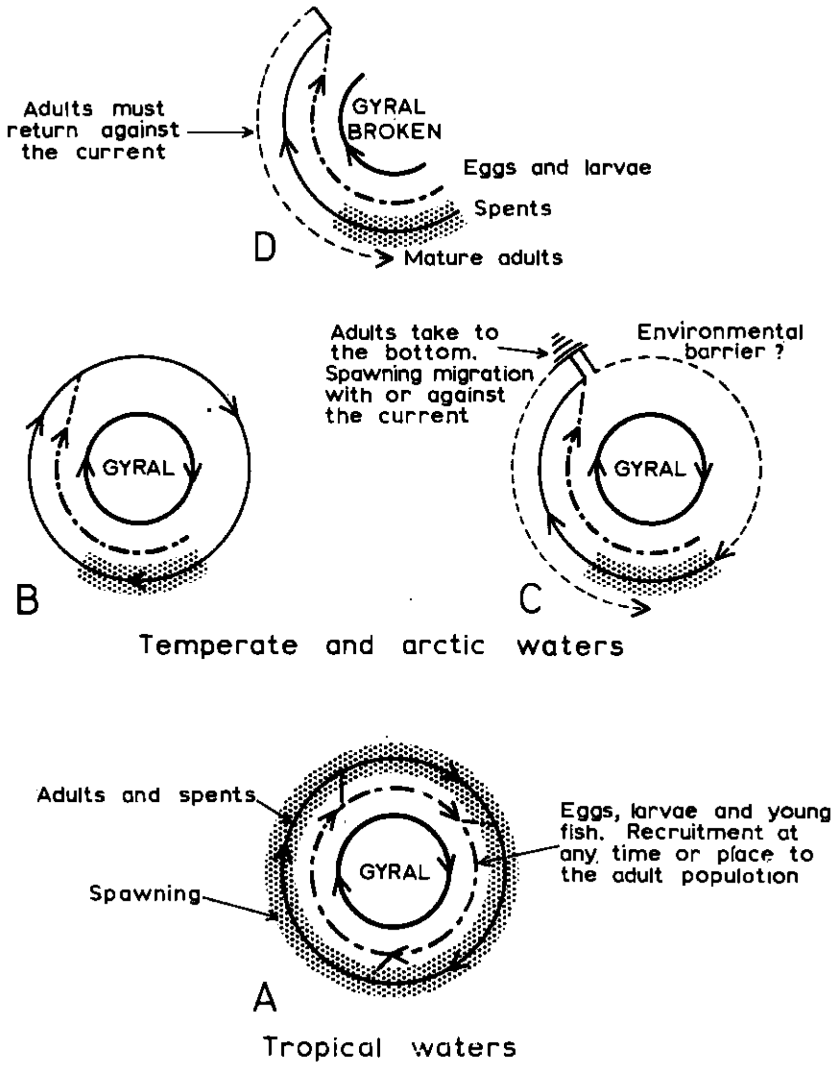

Fig. 2. The relation between oceanic gyrals, production, spawning and fish migration in different water masses. A. Gyral restricted to tropical waters; production and spawning continuous. Gyral extends into temperate and arctic waters. B. Production and spawning restricted, gyral complete. C. Production and spawning restricted, gyral complete, but adults may become demersal or there may be an environmental barrier which prevents them completing the circuit. D. Production and spawning restricted, gyral broken.

ıt this does not mean that the adults always have to swim against a current, that is, upstream,) spawn. In the sea, and even in fjords or lakes, there may be the possibility that the adults, lving in deeper water than the younger stages, are moving with the stream in a counter-current ving below that in which the eggs and larvae are carried in the opposite direction. I think that ıch a migration should be thought of as contranatant even if the adults are swimming, or even rifting passively, in a counter-current towards the spawning area: one of the points of Meek's erminology is that it recognises the biological relationship between the migration of eggs and larvae on the one hand, and that of the adults on the other. It does not follow that there is a causal relationship between the direction of the water currents and the movements of the fish. "Contranatant" is a useful description. There is a danger in that a description of a phenomenon can so easily become accepted as its explanation and there may be confusion if a migration which is obviously contranatant in the biological sense (cod migrating south to Lofoten; herring migrating down the Southern Bight of the North Sea) turns out to depend on some other environmental factor, or on another behaviour pattern.

BIOLOGICAL SIGNIFICANCE OF MIGRATION AND HOMING

The biological significance of migration and of homing follows from the theoretical relationships between migration patterns and water currents. In the temperate latitudes, or in a restricted environment, there may not be enough food on the spawning or nursery grounds to maintain the immature and mature members of a large population. So it may be an advantage to an expanding stock to have separate spawning, nursery and feeding areas. Migration could then be regarded as an adaptation towards abundance. Taking Gerking's (1959) definition of homing as the return to "a place formerly occupied instead of going to other equally probable places", there is something to be gained by a species whose adults return to spawn in the area where they themselves survived. A fish might spawn along the length of a coastline, or in half a dozen tributaries of one river system. At any one part of the coast, or in any one tributary, conditions might be particularly favourable for the survival of eggs and larvae. A return of the survivors to the parent spawning area, or ground, provides a means by which the good conditions may be exploited. It is worth remembering that good survival from a particular area, or ground, could be a consequence of local environmental conditions, or because the site stands upstream to a favourable nursery ground onto which the larvae drift. Homing could be a disadvantage if fish persisted in returning to spawn to an area or ground where the conditions had become unfavourable to the survival of eggs but not to the act of spawning. Frost (1963) cites the disappearance of charr (*Salvelinus willughbii*) from Ullswater (English Lake District) as a case where this might have happened. The only biological insurance against this is a satisfactory level of "straying" and a multiplicity of spawning grounds, whose contribution to the population would change as environmental conditions varied. Fish would do well to follow the proverb and not put all their eggs in one basket.

THE REACTION OF FISH TO WATER CURRENTS

Experimental work in the laboratory has shown that fish will react to a water current only when they can detect their displacement through visual or tactile clues. In the dark, or when blinded, fish that are in midwater drift passively with the current. Observations made at sea tend to confirm those from the laboratory. Midwater shoals drift with the tide; only shoals close to or on the bottom have been found to stem the current (Jones, 1962).

The normal response to a water current is to head upstream and swim against the flow. Thresholds for an orientated response are low, 5-10 cm/sec for a displacement of the background simulating the optical stimuli produced by a water current (Jones, 1963). The thresholds for a water current detected by tactile stimuli are probably 2-3 times higher. I have found that fish react kinetically to the optical stimuli equivalent to a water current, swimming faster as the background speed increases. But the relation between the speed of the fish and the moving background shows that they would gain ground at water currents equivalent to speeds less than 1 fish length/second, but lose ground when swimming against faster currents. The herring was an exception to this rule, and always gained ground up to background speeds equivalent to currents of 3-4 fish lengths/second, its maximum cruising speed.

MIGRATION IN THE OPEN SEA

In the upper waters of the open sea, down to about 400 m, water movement will be predominantly under the influence of the wind-driven surface currents. As laboratory results show that fish out of sight or out of touch of the bottom drift with the current, I think we should face these facts and admit the possibility that fish in the open sea may behave in the same way. Changes in horizontal distribution could be achieved through seasonal or diurnal vertical movements, the fish being carried in water layers moving at different speeds or in different directions. Hardy (1953) has discussed these possibilities. Under such circumstances the fish could be thought of as being carri on what has been called a hydrographic escalator (Jones, 1961). I would suggest that the migration patterns of at least three species (sockeye salmon in the Alaska Gyral; Atlantic herring in the Norwegian Sea, northern and central North Sea; and the European eel, returning to the Sargasso in a eep counter-current, or the Canary current) are more consistent with the hypothesis of an overall ovement with the current than against it. Only detailed investigations comprising simultaneous bservations of the movements of the fish, and water current measurements at the depth at which hey are swimming, will give us the speed of one relative to the other. Sophisticated sonar techiques, such as sector scanning (Jones and McCartney, 1962), would be the research tools to use for his job.

It is of interest to note that the movements of desert locust swarms are essentially downwind nd Rainey (1951) has pointed out that the winds lead to zones of convergent surface wind-flow, here there is a net ascent of air and heavy precipitation. These are the areas where conditions f moisture and vegetation are suitable for breeding. There is, perhaps, a parallel here with ishes which could ride the oceanic currents to areas of upwelling or to the polar fronts, and eturn to the spawning grounds on the counter-current, or the other limb of the gyral. The problem ere is the control system which ensures that the fish leaves and joins the gyral at the appropriate ime. It is possible that an innate releasing mechanism is involved, triggered by a simple sign timulus (Creutzberg's (1961) work with elvers), the stimulus level to which the fish responds being nder hormonal control.

MIGRATION ON THE CONTINENTAL SHELF

On the shelf tidal currents become important and in certain shallow water areas must be the redominant source of water movement. The situation is further complicated by diurnal vertical igrations which may bring the fish on to or close enough to the bottom during the day to obtain ne tactile or visual clue essential for orientation to the current. So the combination of chaning tidal current, and diurnal vertical migration would permit a complex interaction between pasive drift and orientated movement. It is of some interest to consider, by means of a model, the orizontal displacements which could follow from such an interaction. An analysis has been made or the Downs herring on their migration down the Southern Bight of the North Sea to the Channel pawning ground (Jones, 1961), but as the details have not been published, they will be given here.

THE MIGRATION MODEL

The Downs Herring

The overall migration pattern for this stock is fairly well known. The larvae drift with the esidual current from the Channel spawning grounds to the nursery grounds which lie along the oastal regions of the Southern Bight south of 52°N to the west, but extending beyond Texel and nto the German Bight to the east. From these coastal grounds the young fish move offshore so nat the centre of the distribution of the I-group usually lies south-east of the Dogger, near the lay Deep. From this area II-group fish move west and north to recruit to the feeding fisheries ff the north-east coast of England, and then, as maturing fish, migrate south to enter the East nglian fishery in October, and spawn on the Channel grounds in December. The spent fish move orth, and some reach the northern North Sea the following summer. Cushing (1955, Fig. 5) figures ne migration route of this stock.

Parameters of the Model

The model only deals with a small part of one leg of the migration and the following assumtions are made and procedures followed:

A 25 cm herring starts at a position 53°N 27.5'N, 2°46.0'E (Admiralty Tidal Station B12) to ne east of the Indefatigable Banks at sunset on 1 October 1961 (Fig. 3).

The times of sunset and sunrise are those given in a nautical almanac for the appropriate day.

Between sunset and sunrise it is assumed that the herring loses tactile and visual contact with ne bottom and drifts passively with the tidal stream.

Between sunrise and sunset the herring regains visual contact with the bottom, orientates to ace upstream and swims against the tide at a speed 1.4 times that of the current. The multiplier .4 is based on laboratory experiments relating the swimming speed of small herring to that of a oving background simulating the optical stimuli produced by a water current. The average tidal urrent in the surface waters at Station B12 is about 1.5 knots (75 cm/sec). Profiles in the

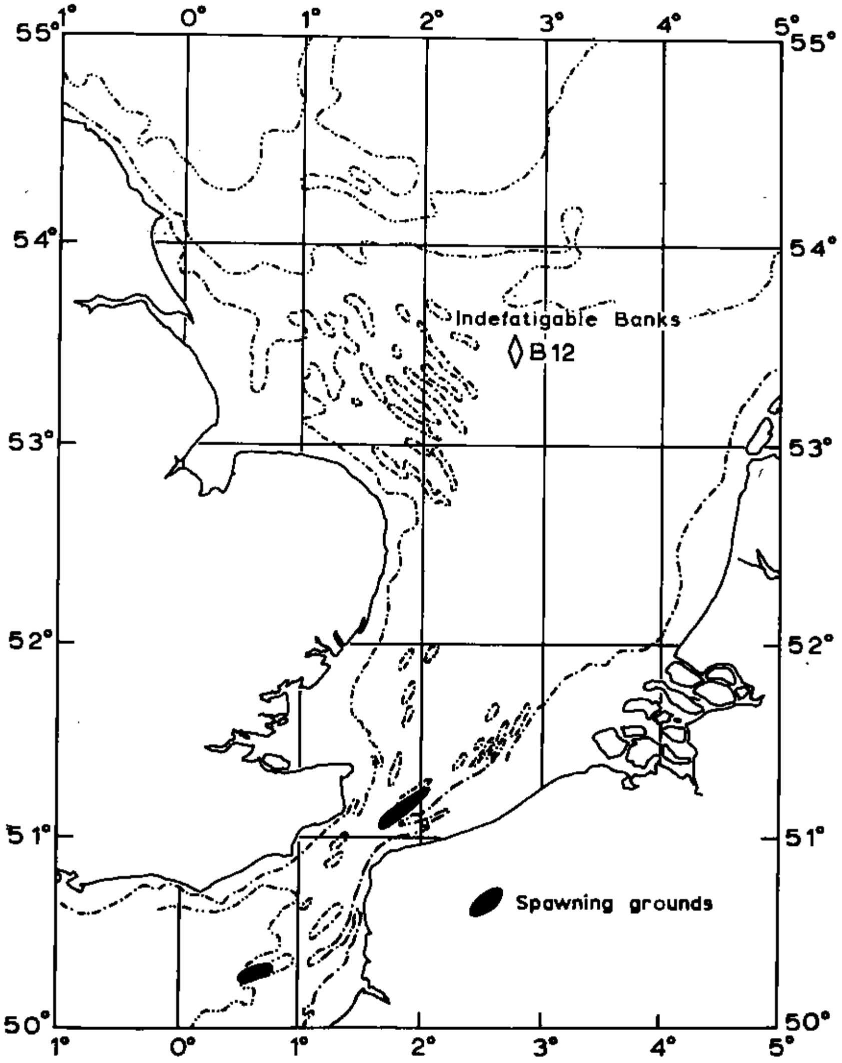

Fig. 3. The position of Admiralty Tidal Station B12. Spawning grounds of the Downs herring are shown.

Southern Bight have shown that the water current 5m from the bottom is approximately two thirds of the surface speed giving, at B12, a speed of 1 knot (50 cm/sec), equivalent to 2 fish lengths per second for the 25 cm fish in the model. The laboratory experiments showed that herring gained ground by a factor of 1.4 at background speeds equivalent to a water current of 2 fish lengths/second.

The Results of the Model

The results of the model are shown in Fig. 4, where the noon positions of the fish are shown from 2 October to 1 November 1961. The course made good during the night (passive drift) is shown by the thick lines, that made good during the day (1.4 against the tide) by the thin lines. Inspection of this figure shows that there are two periods when the fish makes ground to the south, between 4-10 October and 19-24 October, the periods of new and full moons and the spring tides. It may be significant that these are the times when the catch per effort in the East Anglian drift net fishery is highest (Bolster, 1962).

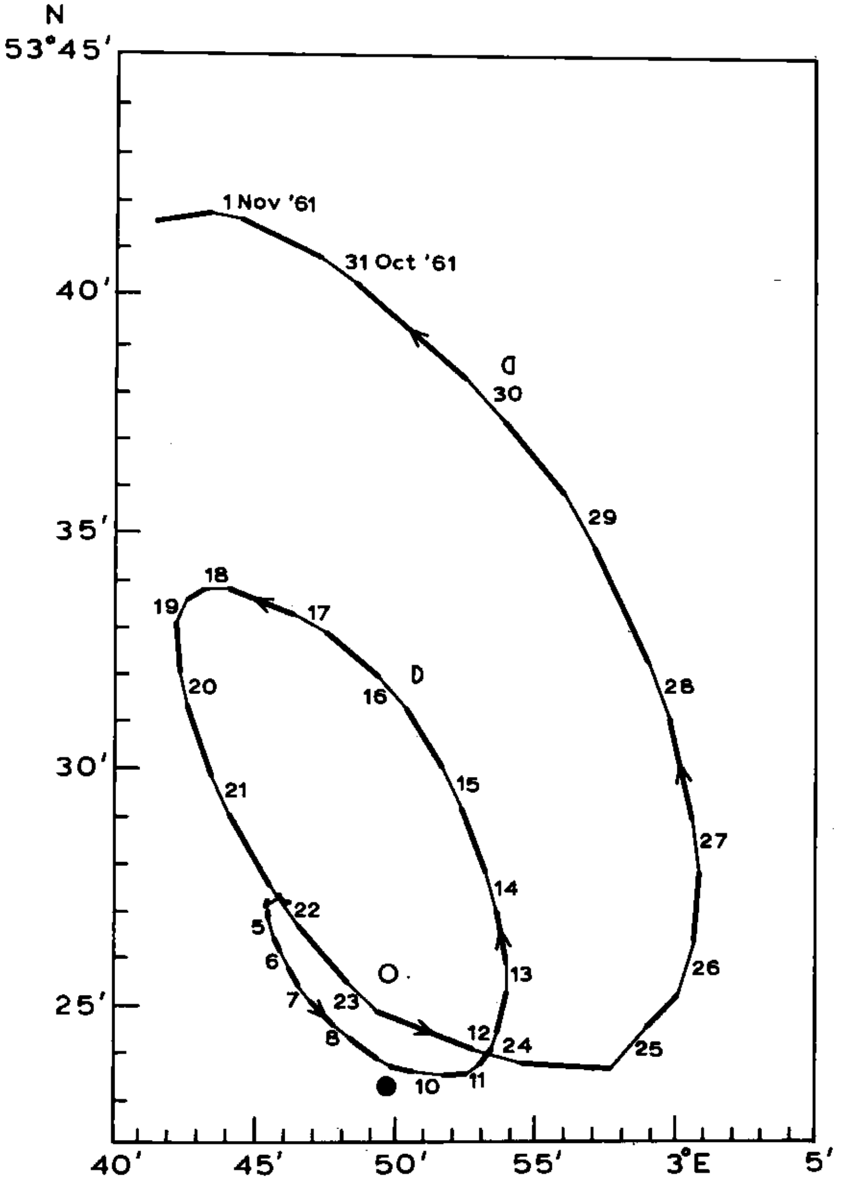

Fig. 4. The migration model: noon positions of the herring which left Station B12 at sunset on 1 October 1961, drifting with the tide during the night (thick line), swimming against the tide during the day (thin line). For further explanation see text.

The semi-lunar periodicity in the south-going movement suggests that if a fish arrives at tation B12 on certain days it might get into a "tidal-fishway" and make rapid progress southwards. igure 5 shows the noon position on 25 October of fish that arrived at Station B12 at sunset each ay from 2-24 October inclusive. This figure was derived from Fig. 4 in the following way. The ourse and distance made good between any day from 2-24 October and 25 October was given by the line oining the sunset position on the first day to the noon position on the 25 October. The course nd distance run were then transferred to B12. It is clear that fish that arrive at B12 between

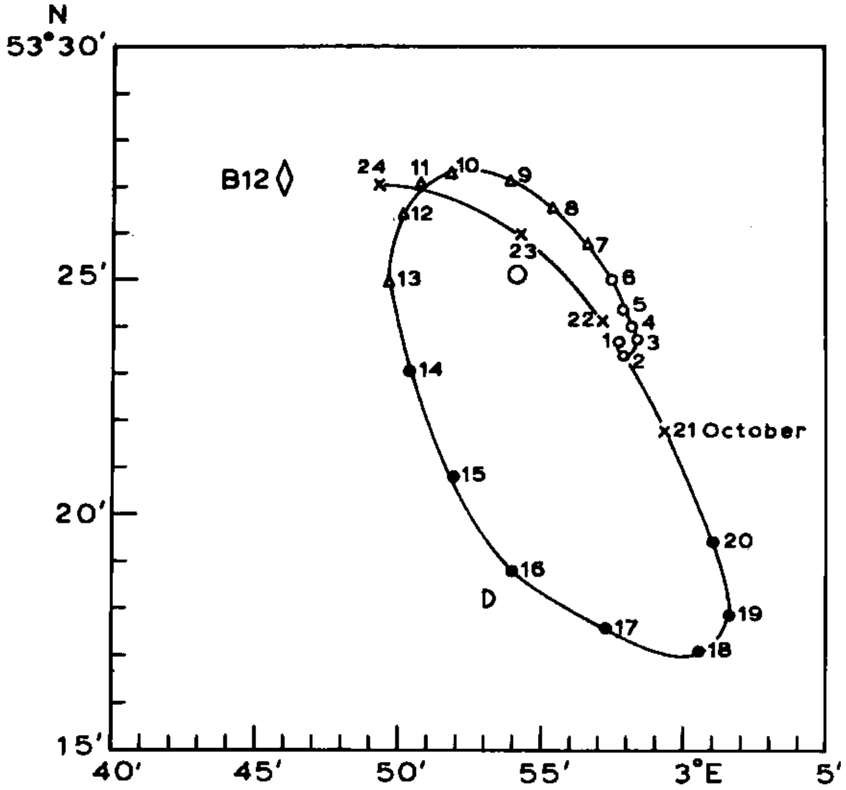

Fig. 5. The migration model: positions at noon on 25 October 1961 of fish leaving Station B12 at sunset, 1-24 October inclusive. For further explanation see text.

15-21 October move rapidly southwards if they drift passively with the tide by night and swim against it by day. The model does provide a mechanism for a south-going migration based on assumptions that are consistent with our knowledge of the behaviour of the fish.

The Residual Current

No allowance has been made for the residual current at B12, which flows eastwards across the axis of the tidal stream at a velocity of about 1.5 miles/day. The residual is unlikely to have any significant effect on the southward movement of the fish, even if it were flowing along the line of the tidal stream. During the night the fish would be carried north, but it would gain ground south during the day. If day and night were of equal length there would be a net gain south of (1.5 x 1.4) - 1.5 = 0.6 miles/day to add to the noon positions plotted in Fig. 4. But during October and at a latitude of 52°N, the ratio of day/night hours is close to 1:1.3 so the ground gained during the day is almost entirely lost by the extra drift at night. The effect of the residual has therefore been ignored.

Further Study of the Model

The apparent success of the model should not be pressed too far. While the calculations do offer a basis for a prediction of the distribution of the recovery of tagged fish, or movements of the fishery, they only relate to one tidal station and the extrapolation of the data relating to this single point has probably been carried too far. When the fish has moved a few miles from Station B12 its movements should be calculated using tidal data relating to its new position, and so on down the Southern Bight. These calculations require the services of a computer and this is eing considered. Other models of migration (drift by day and by night, drift by night and holding round by day, swimming south day and night with and against the tide etc.) should also be examined.

It would be very interesting if there was a "tidal-fishway" which could carry the herring rom the feeding area to the spawning ground. To get them back again does not present the same roblem. A change in behaviour to light, so that they stayed in midwater and never made visual ontact with the bottom, would allow the spent fish to drift north-east with the residual current.

CURRENT PREDICTIONS FROM FISH MIGRATIONS

Let us reverse this line of thought and try to predict the presence of currents from what is nown of the migration of fish. The European eel is an abvious example. European eels leave fresh ater in November-December and spawn in February-March, but it is not known whether they take a ew months or one of two years over the migration. There should be a deep counter current which ould take the mature fish back from the continental shelf to the Sargasso Sea in 3, 15 or even 27 onths. There is some evidence to show that deep counter-currents are present in the eastern tlantic (Stommel, 1958; Lappo, 1963).

Migrations of the Arcto-Norwegian and south-west Greenland cod should also be considered. I uggest that there may be a deep counter-current carrying the mature fish from the Bear Island area o Lofoten, and from West Greenland to Iceland. This is not a new hypothesis so far as the Arcto-orwegian cod are concerned, and I want to draw attention to Sund's (1932; 1938; 1939) much earlier uggestion. Sund was clearly of the opinion that the cod were carried to Lofoten, at least from ndenes, on a south-going current at a depth of 300-700 m on the edge of the shelf, at a velocity f about 7 km a day. We have not heard very much about Sund's hypothesis or about this current. s there a counter-current running along the Norwegian coast? And if there is, where does it come rom, and where does it go? Could it carry the cod as Sund said?

ACKNOWLEDGEMENT

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REFERENCES

BOLSTER, G.C. 1962. The influence of wind and tide on the catch by drift nets in the East Anglian herring fishery 1952-56. *J. Cons. int. Explor. Mer,* 27: 150-61.

CREUTZBERG, F. 1961. On the orientation of migrating elvers (*Anguilla vulgaris* Turt.) in a tidal area. *Ned. J. Sea Res.,* 1: 257-338.

CUSHING, D.H. 1955. On the autumn-spawned herring races in the North Sea. *J. Cons. int. Explor. Mer,* 21: 44-60.

1959. The seasonal variation in oceanic production as a problem in population dynamics. *J. Cons. int. Explor. Mer,* 24: 455-64.

FROST, W.E. 1963. The homing of charr *Salvelinus willughbii* (Günther) in Windermere. *Anim. Behav.,* 11: 74-82.

GERKING, S.D. 1959. The restricted movement of fish populations. *Biol. Rev.,* 34: 221-42.

HARDY, A.C. 1953. Some problems of pelagic life, in *Essays in Marine Biology,* ed. by S.M. Marshall and A.P. Orr. Oliver and Boyd, Edinb. p. 144, 101-21.

JONES, F.R. HARDEN. 1961. The migration of fish. *Biology hum. affairs.* 26: 31-39.

1962. Further observations on the movements of herring (*Clupea harengus* L.) shoals in relation to the tidal current. *J. Cons. int. Explor. Mer,* 27: 52-76.

1963. The reaction of fish to moving backgrounds. *J. Exp. Biol.,* 40: 437-46.

JONES, F.R. HARDEN and B.S. McCARTNEY. 1962. The use of electronic sector-scanning sonar for following the movements of fish shoals: sea-trials on R.R.S. *Discovery 11. J. Cons. int. Explor. Mer,* 27: 141-49.

LAPPO, S.S. 1963. On the deep currents in the northern part of the Atlantic Ocean. (In Russian) *Okeanologiya,* Moscow, 3: 808-13.

MEEK, A. 1915. Migrations in the sea. *Nature, Lond.,* 95: 231.

QUASIM, S.Z. 1955. Time and duration of the spawning season in some marine teleosts in relation to their distribution. *J. Cons. int. Explor. Mer,* 21: 144-55.

RAINEY, R.C. 1951. Weather and the movements of locust swarms: a new hypothesis. *Nature, Lond.,* 168: 1057-60.

STOMMEL, H. 1958. The Gulf Stream. Univ. Calif. Press and Cambridge Univ. Press. 202 p. 160-172.

SUND, O. 1932. On the German and Norwegian observations on the cod in 1931. *Rapp. Cons. Explor. Mer,* 81: 151-56.

1938. The cod and the sea 1937 - cod tagging experiments. *Fiskeridir. Skr. Havundersøk.,* 5: (7) 10-11 and 47-48.

1939. The stock of cod in 1938. *Fiskeridir. Skr. Havundersøk.,* 6: (1) 21-22.

A-18

EFFECTS OF LIGHT UPON BEHAVIOUR AND DISTRIBUTION OF DEMERSAL FISHES OF THE NORTH ATLANTIC[1]

By

P.M.J. Woodhead[2]

CONTENTS

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[1] Originally Contribution No. A-15, ICNAF Environmental Symposium, Rome 27 January-1 February 1964.

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SUMMARY

1. Data concerning the structure, function and performance of the fish eye are considered in relation to the problems of vision in the demersal environment.

2. Some laboratory observations on the reactions of demersal fish to light changes are reviewed and particular attention is drawn to diurnal patterns of behaviour changes by day and night. It is concluded that these patterns are frequently endogenous cycles which are environmentally timed, although they may be suppressed or modified under experimental conditions. The diurnal patterns of behaviour are frequently complex.

3. Diurnal changes in behaviour in demersal fish frequently result in changes in their rates of capture by trawls. In some cases this seems to be due to vertical migration of the fish.

4. It is suggested that many "demersal" species may spend considerable periods in midwater, and some evidence of this for flatfishes, haddock, redfish, whiting, hake, coalfish and cod is reviewed.

5. Changes in vertical distribution may be associated with feeding in some species but not in others, and it is suggested that vertical movements away from the sea-bed may be part of the specific behaviour patterns of different fish. The patterns may vary with the size or condition of the fish.

6. Changes in vertical distribution in relation to light may expose fish to differences in the action of currents, or even to different current systems. These changes must have fundamental effects upon the horizontal distribution of the fish. Some examples are considered and it is suggested that diurnal vertical migration may form an integral part of the distribution mechanism of many demersal fish.

INTRODUCTION

Against the relative physical and chemical uniformity of the seas over considerable areas, submarine light shows almost continuous cyclical changes in quality and intensity, both diurnally and seasonally; light also changes rapidly with increasing depth. It is therefore not surprising that light has a fundamental role in determining fish behaviour. The modes by which light may affect the fish are complex; its intensity, angular distribution, polarization and spectral composition may all exert direct effects upon behaviour and physiology. These properties of submarine light all vary with depth and with the time of day, and in some cases their rate of change may also be important. The diurnal changes of day and night (including the duration of daylight and the quantity of light energy received per day), monthly lunar changes, and the annual light cycles may all be of considerable physiological importance to fish.

I do not intend to discuss all of these many diverse effects of light upon fish, but will consider only those aspects which appear to be of significance in influencing the distribution of demersal fishes of the North Atlantic. Even in this more restricted field, the relationships of light to the behaviour and physiology of the demersal fish are by no means simple. (Certain effects of light upon seasonal changes in the physiology of cod are discussed elsewhere (Woodhead and Woodhead, this symposium)).

LIGHT IN THE SEA

Absorption and scattering in seawater both rapidly reduce the light from the surface. In coastal waters light is reduced to 1% of its surface value in 15-30 m, whereas for continental slope waters this reduction is achieved in 40-60 m, and at about 100 m in clear oceanic water (Clarke, 1954). Within a single area there may be considerable seasonal variations in transparency which may have greater effects upon subsurface illumination than the seasonal changes in surface radiation; thus Clarke (1938) showed that although the total solar radiation at the surface per day off the Massachusetts coast was about four times greater in summer than in winter, at a depth of 30 m the total radiation was 10,000 times greater in May, with high incident light and high transparency, than in December when both incident light and transparency were low.

In coastal waters maximum transparency is in the yellow-greens (500-600 mμ) whereas in clear oceanic waters maximum transparency is in the blue part of the spectrum (400-500 mμ). With increasing depth the composition of the light changes as the spectrum narrows to the most penetrating wavelengths. Towards both ends of the spectrum extinction is more rapid than in the middle, and at depths of more than 100 m blue light predominates (Jerlov, 1951).

In the sea directionality of light is maintained to considerable depths, light flux from above being about a hundred times greater than light scattered from below (Clarke and Denton, 1962). However, in clear weather the direction of maximum light intensity will be at an angle of obliquity to the vertical, related to the altitude and azimuth of the sun. In the relatively clear waters of the English Channel Atkins and Poole (1959) found that the average angle of obliquity remained about the same down to 70 m; Tyler and Preisendorfer (1962) have given extensive tables for the estimation of radiance distribution in lake water under different weather conditions. In the sea, light is also linearly polarised, and Ivanoff and Waterman (1958) have shown that, in clear water, although the polarization decreases rapidly in the surface layers, after that the rate of decrease is slow and submarine polarization extends towards the limit of the photic zone. The pattern of polarization is dependent upon the sun's position in the sky and changes during the day. Waterman (1958) has suggested that these changes may still be appreciable at 200 m and could provide a form of compass for orientating horizontal migrations. The possibilities of orientated movements by fish well below the surface, in relation to the sun, guided either by the direction of maximum light radiance or by submarine polarization patterns, cannot therefore be dismissed. It is possible that the claims of some North Sea fishermen that in the early mornings in spring the best trawl catches of plaice are to be made by towing towards the sun may have their basis in such orientated movements by the fish. However, too little is known of such behaviour in demersal fish for this fascinating subject to be pursued further here.

The qualities of light in the sea are discussed in greater detail by Blaxter (this Symposium p.647).

THE EYE

In discussing the reactions of fish to light it is necessary to consider the properties of the receptor organs. The principal light receptors in demersal fishes are the eyes. Although the pineal organ and the mid-brain have also been shown to be light-sensitive in some freshwater fishes (Scharrer, 1928; Breder and Rasquin, 1947, 1950), it seems unlikely that they play an important part in the behaviour of the adult fish considered here, principally because their sensitivity is low, and because the top of the head is frequently too thick or opaque to allow the penetration of the weak light present at the depths in which the fish live. Dermal photoreceptors have also been shown in a few fishes, but none were found in the marine fishes examined by Parker (1909).

All fish do not have the same sensitivity to light, nor is their vision equally good. It could not therefore be expected that the eye would be the same, even for all fish living within the same demersal environment. In fact the eyes show many diverse modifications and adaptations to the mode of life of particular species. Aspects of vision and photoreception in fishes have recently been reviewed by Nicol (1963) from the viewpoint of physiological function and by Rochon-Duvigneaud (1958) for general aspects of the fish eye.

1: Visual pigments and retinal structure

The scotopic visual pigments of marine fish have generally been shown to be adapted to the type of light occurring in the region in which they live. The eyes of the coastal and surface-living fishes have rhodopsin pigments absorbing maximally in the yellow-greens at about 500 mμ, whereas conger eels (*Conger conger*) and deep-sea fishes have chrysopsins in which the maximum absorption occurs in the blues, about 485 mμ, greatest sensitivity corresponding to the wavelengths of greatest penetration (Munz, 1958 *a* and *b*: Denton and Warren, 1957). The visual pigments from the coalfish (*Pollachius virens*), plaice (*Pleuronectes platessa*), gurnards (*Trigla lucerna*) and spurdogs (*Squalus acanthias*) have absorption peaks at 500 mμ (Nicol, 1960).

Coastal teleosts usually have duplex retinae in which the cones are frequently large and well spread; double cones and occasionally triple cones also occur in many species; there is usually a well developed pigment epithelium. Pure rod retinae are found in deep-sea teleosts and in the majority of elasmobranchs (though the retinae of *Mustelus* and *Myliobatis* are duplex). High-cone retinae are generally found in fish feeding in light and possessing good vision, whereas numerous large rods are associated with life at low illumination. Visual acuity might be expected to increase with the numbers of cones per unit area of retina, but in the eyes of nocturnal and deep-sea fish acuity is actually sacrificed for high light sensitivity, many rods communicating through secondary neurones with single nerve fibres. Wunder (1925, 1926, 1936) has described these relationships in detail for freshwater fish, and it might be expected that they would also apply to marine fish. High rod densities occur in the retinae of some elasmobranchs; in *Chimaera* there are 100,000 per sq mm of retinal surface, and 30,000 per sq mm in *Acanthias*. However, in the specialised eyes of deep-sea fishes extremely high densities of up to 25 million rods per sq mm have been reported (Brett, 1957).

Engström (1961) has described the arrangement and structure of cones in gadoid fishes, and Ali and Hanyu (1963) have reported on the retinal structure for several species caught in moderately deep Atlantic waters. Cod (*G. morhua*), sea poachers (*Aspidophorodes menopterygius*) and a sculpin (*Triglops ommatistuus*) had a well developed pigment epithelium and many cones and conducting elements, suggesting good vision; *Lycodes* sp. and redfish (*Sebastes marinus*) had a less well developed pigment epithelium, numerous rods and fewer conducting elements, presumably no longer adapted to vision at high intensities. Pure rod retinae for low light vision occurred in the silver smelt (*Argentina silus*) and rat-fish (*Macrourus bairdi*), in which form perception is probably of little importance. Comparing specimens of *Sebastes marinus marinus* and the sub-species *S. m. mentella*, caught at the same depth in *S.m. mentella* the retina had larger rods and smaller cones than in *S. m. marinus*, and in this respect it is interesting that *S.m. mentella* has a relatively larger eye, both differences suggesting intraspecific visual adaptations to the deeper habitat of this form (Templeman, 1959). It is of interest that within the sub-species *S.m. mentella*, a specimen from 549 m had shorter cones and larger rods than a specimen from 275 m, differences which would better fit the deeper-living fish for life at lower light intensities (Hanyu and Ali, 1962). Obviously further investigations would be required to confirm these results, but they raise the interesting possibility that there may be a number of different physiological forms, or ecotypes, within the species, each specialised to fit a particular depth-range, perhaps with little vertical interchange.

2: Light sensitivity

Although the absolute light threshold of the fish eye has not been measured, Nicol (1963) concludes that many fish are equally as sensitive as man. The eyes of marine fish frequently have a number of properties tending to increase their sensitivity; there is usually a relatively large pupil, the rods in the retina are long, and the retinal pigment density is high, so that up to 75% of the incident blue-green light may be absorbed compared with 30% absorption in the human eye. (Denton (1959) has calculated that in the specialized eyes of deep-sea fishes absorption may exceed 90%). It is therefore likely that the absolute light threshold in many demersal fish will be lower than in man; Denton and Warren (1957) have suggested that for some deep-sea fishes this gain in sensitivity may be as high as 100 times that of man (indeed the eyes of deep-sea fishes are believed to be the most sensitive in existence).

On this basis, light from the surface could probably be detected by demersal fish at an intensity of 10^{-8} μ W/cm^2, which is similar to Harden Jones' (1958) estimate of 10^{-7} m.c. Clarke and Denton (1962) have calculated figures for the depths of penetration of sunlight and moonlight into seas with different rates of light absorption, in relation to the visual thresholds of fish and man (calculated for light from a broad field of illumination). Their results for the limits of detectable light, together with those estimated from absorption data given by other authors, are summarised in Table 1.

TABLE 1. CALCULATED APPROXIMATE DEPTHS OF PENETRATION OF SUNLIGHT AND MOONLIGHT INTO VARIOUS SEAS IN RELATION TO MINIMUM INTENSITY FOR VISION IN FISH.

Sea	Sunlight	Moonlight	Author
Turbid harbours or estuaries	20 m	-	Clarke and Denton, 1962
Southern North Sea (53°N 2°E)	120 m	65 m	P.O.Johnson (unpublished observations)
Baltic Sea) English Channel)	200 m	100 m	Clarke, 1954
Barents Sea	500 m	250 m	Trout, 1957
Clearest oceanic water	900 m	500 m	Clarke and Denton, 1962

3: Underwater vision and visual acuity

The problems of underwater vision are complex (Duntley, 1962), but, in general, visibility in water is restricted by light scattering (much as fog reduces visibility on land), and by heavy absorption, which is much greater than in air; both properties profoundly affect visual range. The visibility of objects thus depends not only upon the intensity of the residual image-forming light reaching the eye but also upon the degree of diffusion of the image, and upon the radiance from the scattering of ambient light in the sea along the line of vision. The relationship of the amount of image-forming light reaching the eye, to the ambient radiance, is dependent upon the scattering properties of the water and independent of light intensity, so that above a critical visual threshold underwater visibility would be expected to be constant over a wide range of intensities; this has been confirmed by direct measurements made from a submarine (Sokolov, 1961).

In the fish eye the spherical lens is almost completely free of spherical and chromatic aberration (Pumphrey, 1961), so that good retinal images could be formed. The cornea is of the same refractive index as the sea water and plays no part in forming the image.

Acuity is governed partly by the concentration of cones in the retina and the number of ganglia supporting them, but in demersal fishes with duplex retinae the cones tend to be large and well spread and there is rarely a fovea in fish. For these reasons, and because scattering of light in water will also limit precise vision, the image perceived is probably poor compared with that in many terrestrial vertebrates. However, the retinal elements are not evenly distributed and in particular areas of the retina there may be differentiation; thus cones predominate in the upper half of the eye of the bottom-feeding dragonet (*Callionymus lyra*), which is appropriate to downward vision. Similarly, although the cones in the genus *Gadus* radiate outwards from the centre of the eye in a regular pattern, there may be differences in visual cell density, concentration frequently occurring in the temporal plane of the retina, as in the pollock (*P. pollachius*) (Engström, 1961).

As the light intensity rises above the absolute visual threshold, visual acuity increases very quickly, and fish can probably begin to discriminate surrounding objects at intensities only a few times greater than the threshold (Clarke and Denton, 1962); that is at depths which would be only short distances above the depths given in Table 1 as the limits for detection of sunlight and moonlight. Nicol (1963) states that, due to the high sensitivity of the eye, a fish at 100 m could perceive objects from sunrise to sunset on the darkest winter day (latitude 50°N) in coastal waters with an absorption coefficient of about 0.13 (*i.e.* English Channel or Baltic Sea).

DIURNAL CYCLES OF ACTIVITY

Diurnal cycles of activity have been described for a large number of species of fish, generally based on observation of fish living in aquarium tanks. Observations on a large number of marine and freshwater fish living in the aquarium of the Zoological Society of London were reported by Boulenger (1929) who found that elasmobranchs and most marine teleosts, including the flatfishes, were more active at night than by day, or at least were equally active at both times. However, the gurnards (*Trigla hirundo* and *T. gurnardus*) rested on the bottom at night, and four species of wrasse were observed to be lying on their sides at the bottom at night. Other species including the grey mullet (*Mugil cephalus*) and the sea breams (*Pagella centrodontus* and *Pagrus pagrus*) floated quiescent at night just above the bottom, while others including the sea bass (*Morone labrax*) were found resting just beneath the surface at night. Breder (1959) also gives a number of examples of differential diurnal behaviour patterns. Obviously there may be considerable diversity in the type of activity cycles exhibited by different species.

A few attempts at more quantitative analysis of the activity patterns of fish have been made. Harder and Hempel (1954) studied the activity of flatfish in an experimental tank containing only seawater; plaice and soles exhibited considerable nocturnal activity and were quiescent by day, although flounders were active in the apparatus at all times of day and night. Kruuk (1963) and Woodhead (1963*a*) have also described sole as being nocturnally active in aquaria, but lying wholly or partly buried in sand at the bottom of the aquarium during the day; deGroot (1963) and Woodhead (1960) have made somewhat similar observations on the behaviour of the plaice, which frequently swam freely off the bottom at night. Both Kruuk and deGroot drew attention to the close resemblances between the behaviour of the flatfish in the laboratory and their postulated behaviour in the sea, as reflected in the catches of trawlers.

The author has made observations on the activity of 30 cm to 80 cm cod in a large concrete tank (4 m x 6 m x 1 cm). Twenty to thirty cod kept in the tank showed slow swimming activity under diffuse daylight illumination of about 500-1000 m.c. at the water surface. They tended to swim together in loose groups of four or five fish, often stopping or milling very slowly. At night activity increased by several times, the cod swimming constantly back and forth across the bottom of the tank, each fish moving independently. It was remarkable that diffuse illumination by a fluorescent light giving about 1 m.c. at the water surface did not appear to interfere with this pattern of nocturnal swimming activity if it was switched on.

Laboratory studies are of considerable interest and importance in demonstrating the contrasting activity patterns which may occur in different species, but some caution should be exercised in the interpretation of such behaviour as "normal", since its relationship to the behaviour of the fish in the sea may be less direct than would at first appear. Thus Bregnballe (1961) showed that flounders (*P. flesus*) swam actively both by night and by day in an aquarium containing only seawater, as had also been observed by Harder and Hempel (1954), but when sand was placed on the bottom of the tank the flounders were active only at night and lay buried during the day. Perhaps the clearest demonstrations of effects of experimental design on diurnal activity were the experiments of Harden Jones (1956) with minnows (*Phoxinus laevis*); in an open glass aquarium the minnows were very active by day and inactive at night, but when a very simple shelter was provided for the fish their pattern of activity was completely reversed - they sheltered, inactive, during the day, and were nocturnally active. Similarly minnows swimming in a tank covered by a light gradient showed marked changes in their behaviour patterns above and below an intensity of about 0.2 m.c. (Woodhead, 1956). If ecological parallels are to be drawn from laboratory studies of marine fish, the animals should not be submitted to higher daylight intensities than they might normally encounter in their lives in the sea; thus deGroot (1963) was able to show that the degree of activity of plaice during daytime was to some extent dependent upon the lighting of the experimental tanks.

It seems likely that most of these diurnal changes in locomotory behaviour are timed by the light-dark cycle. They might be regarded as forms of photo-kinesis (Fraenkel and Gunn, 1940); such kineses have been demonstrated in a number of freshwater fish (Shaw, Escobar and Baldwin, 1938; Schlagel and Breder, 1947; Harden Jones, 1955; Woodhead, 1957) and in the marine larvae of the herring (*Clupea harengus*), *Blennius ocellaris* and *Lepadogaster microcephalus* (Woodhead and Woodhead, 1955, 1962). This suggestion gains some support from experiments in which continuous light has inhibited movement or continuous darkness has allowed persistent activity. However, there is frequently an endogenous component to such rhythmic activities (Brown, 1958; Harker, 1958); thus Kruuk (1963) was able to suppress the diurnal activity cycle of soles by keeping them in continuous light, but when they were kept in darkness for two days the normal periodicity of activity was maintained - although a fairly high level of activity occurred throughout the day it was still at a lower level than at night, when peak activity was recorded. In similar experiments, in which plaice were kept in artificial light during the night, Harder and Hempel (1954) were able to reduce nocturnal activity but did not achieve complete suppression; similarly deGroot (1963) observed little reduction of nocturnal activity in plaice kept at a low level of artificial light. It has also been reported that a 24-hr rhythm of activity persisted in goldfish (*Carassius auratus*) kept in continuous light (Spencer, 1939).

Strong evidence of a precise internal rhythm or "biological clock" was provided by freshwater fishes which were trained to use the sun as a directional reference. They were able to compensate for the daily movement of the sun, remaining orientated in the trained direction during the course of the day (Hasler and Schwassmann, 1960; Braemer and Schwassmann, 1963).

Behaviour in relation to light has been shown to change diurnally in a few species. Breder (1959) gave some evidence for *Gambusia* sp; and Kawamoto and Konishi (1955) showed a definite diurnal rhythm in the "light-seeking" responses of *Girella punctata* and *Rudarius ercodes* to an artificial light in a dark-room. Bluegills (*Lepomis macrochirus*) which have been kept in darkness have a well defined light-shock reaction when exposed to a bright light, and Davis (1962) has clearly shown a regular daily rhythm in the intensity, or duration, of this reaction to a constant stimulus. Such behavioural changes could imply central variations in the responsiveness of the fish, but could also be due to changes in the sensitivity of the eye itself. In fact there is some evidence that the eye is not a consistent receptor organ throughout the day; thus rhythmic movements of the cones and pigment epithelium of the retina have been shown to persist in catfish kept in constant darkness (Welsh and Osborne, 1937; Arey and Mundt, 1941). Similar experiments made on goldfish kept in constant darkness also showed that the condition of retinal dark adaptation, with cones and pigment expanded, was more extreme at night than during the hours of daylight (Wigger, 1941). Tamura (1957) found that even when illuminated at low light intensities the retinae of the sea bass (*Lateolabrax japonicus*) and the carp (*Cyprinnus carpio*) tended to a condition of stronger dark adaptation before midnight than after midnight, suggesting retinal responses to cyclical changes occurring within the fish.

It is concluded that there are probably endogenous 24-hr cycles of physiological and locomotor activity in many fish, more strongly expressed in some species than in others; thus Gompel (1937) found evidence for the presence of a persistent rhythm of oxygen consumption in plaice (*Pleuronectes platessa*) and turbot (*Rhombus maximus*). Normally these endogenous cycles will tend to "anticipate" the start of the daylight or night periods, but will be environmentally timed and reinforced by the changes in light intensity at dusk and dawn. Laboratory experiments with continuous light or darkness, which may partially or completely inhibit the normal expression of such rhythms, or cause the phase to drift, in no way refute their presence.

In considering such cyclical changes in diurnal behaviour it is important to make the distinction that although light may exert important orientating and kinetic influences directly upon the fish, as would appear to occur in herring shoals whose migration to the upper waters at dusk has been related to an optimum light intensity (Postuma, 1957; Chestnoy, 1961), light changes at dusk or dawn may also be important in simply releasing a pattern of behaviour which is then largely "self-steering" and independent of further changes in illumination. The diurnal cycles of behaviour in fish are usually complex, and swimming activity may be associated with feeding, vertical migration, changes in aggressiveness, dispersion or aggregation of shoals, etc. The duration and level of activity are by no means constant in any phase, and the periods of swimming have frequently been found to achieve maxima both at dusk, when light intensities are falling, and at dawn, when they are increasing again.

DIURNAL BEHAVIOURAL CHANGES IN THE SEA AND CHANGES IN CATCHES BY FISHING GEAR

In the sea the diurnal rhythms of swimming activity are frequently associated with feeding. Thus Kruuk (1963) showed that soles fed during their period of nocturnal activity. Plaice and flounders are largely visual feeders on benthic animals, and some feeding may go on generally during the day, but the main feeding periods occur at twilight and also coincide with the activity peaks at dusk and dawn (Franz, 1910; Jones, N., 1952; Hempel, 1956; Bregnballe, 1961; deGroot, 1963). In the sea, plaice and flounders do not appear to feed much during the middle of the night, and in aquaria they have frequently been found to swim freely well off the bottom at night (Harder and Hempel, 1954; Woodhead, 1960; Bregnballe, 1961; deGroot, 1963).

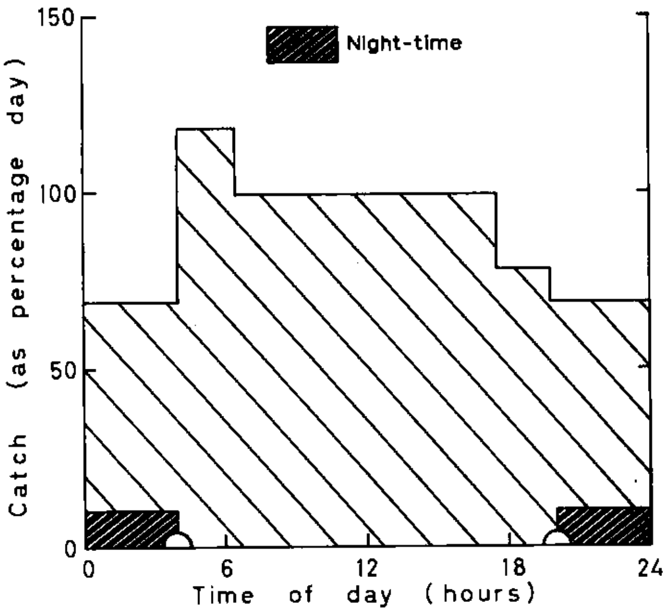


Fig. 1. Diurnal pattern of trawl capture of plaice in the southern North Sea, Haddock Bank (from Woodhead, 1960).

Such marked changes in the behaviour of demersal fish would be expected to be reflected in their catches by fishing gear; thus soles are caught in sea-bed gill-nets during their periods of nocturnal activity (Møller Christensen, 1960), and the marked diurnal changes typical of trawl catches of soles have been well established (Boerema and Stam, 1962; Boerema, 1963; Woodhead, 1963*b*). It has been suggested that soles are largely able to avoid trawl capture during the day when lying inactive, buried in sand, but become more vulnerable when moving over the sea-bed searching for food during their nocturnal period of activity (Kruuk, 1963; Woodhead, 1963*b*). Diurnal variations in trawl catches of plaice have also been described in offshore regions; the catch of large plaice frequently falls at night (Woodhead, 1960; deGroot, 1963) (Fig.1), and Woodhead has suggested that this fall may be partly due to a decrease in availability as fish leave the sea-bed to swim in midwater, behaviour which has been observed in large aquarium tanks. Paradoxically the trawl catches of plaice, and of flounders, in very shallow inshore areas are greatest at night. Bregnballe (1961) has pointed out that this may be partly explained by the inshore migration of fish from deeper water at night. However, in such shallow waters as Kysing Fjord (1 m) the vertical range of the fish could not be much greater than the headline height of the trawl and there would be little change in availability. Furthermore, in shallow waters flatfish would probably be more vulnerable to trawling when swimming freely within the depth of operation of the trawl than when buried in the sea-bed, and under these conditions higher catches could be expected at night.

Although such attempts to account for diurnal changes in catches of fish in terms of cyclical changes in their locomotory and feeding activities, particularly in relation to vertical migrations, may meet with limited success, in fact it is seldom possible to differentiate completely between the innate behaviour patterns of the fish and the changes in their reactions to the fishing gear by day and night. Detailed analyses of diurnal changes in the composition of trawl catches of fish show that they may be complex, showing many variations during a 24-hr cycle (Woodhead, 1963*b*). Diurnal changes in innate behaviour patterns may reduce the numbers of fish available for capture by the gear, particularly when associated with vertical migration, but they may also increase the vulnerability of those fish remaining within the effective zone of operation of the trawl. The catching efficiency of the fishing gear would also be expected to change by day and night. Thus the direct avoidance of trawls by those fish within their zone of operation is probably decreased at night, but the herding effect, believed to be produced by the trawl-doors and bridles, may also be reduced or made ineffective when these parts of the gear cannot be seen by the fish (Blaxter, Parrish and Dickson, 1963).

Although it is not possible to provide direct evidence for the vertical migration of fishes on the basis of the diurnal changes occurring in the catches of bottom trawls, nevertheless such catch changes are not to be completely disregarded and may provide supplementary evidence if they have occurred at the same time as other indications of fish departing from or returning to the sea-bed.

VERTICAL DISTRIBUTION

There is considerable evidence that many fish considered as demersal species, largely because they are normally caught in trawls on the sea-bed, in fact regularly assume a pelagic habit, swimming freely in midwater and frequently feeding there. Cases where fisheries have been developed to catch demersal species in midwater provide strong evidence of their pelagic habit. But in other instances it may be argued that the capture of small numbers of particular species well above the sea-bed, or at the surface, may be based upon chance encounters not typical of the population as a whole; for example, whiting are very frequently caught at night in herring drift-nets, but large numbers are seldom caught on any occasion. However, here it can equally be asserted that the herring drift-net may be unsuited to the efficient capture of whiting, just as salmon are not usually taken at sea in surface-floating longshore herring nets, although they certainly swim at the surface at night and can be caught there with the appropriate trammel gear.

Perhaps the best example of an apparently completely demersal fish periodically assuming the pelagic habit on an unsuspected scale is provided by the sole. Although soles have occasionally been reported swimming at the surface (Verwey, 1960; Møller Christensen, 1962), the recent report of de Veen (1963) has shown this behaviour to be a widespread and regular phenomenon amongst North Sea soles prior to spawning; indeed, at that time, the soles may leave the sea-bed in sufficient numbers at night that the normally marked diurnal pattern of trawl capture is reversed, the night catches being less than during the day.

Some evidence for commoner demersal fish leaving the sea-bed is now considered, although a comprehensive review is not attempted.

1: Cod (*Gadus morhua*)

There are many reports of cod in midwater or near the surface of the sea. Bigelow and Schroeder (1953) described cod being caught by gaff at the surface in the Gulf of Maine, and in Holsteinborg Deep, Greenland, a commercial fishery was established using pelagic longlines (Rasmussen, 1953, 1954). Cod have been caught near the surface in gill nets over depths of more than 1000 m (Hjort, 1914; Konstantinov, 1958), and Jensen and Hansen (1931) have reported Greenland cod pursuing capelin (*Mallotus villosus*) close to the surface; similar reports have been made for the Barents Sea (Zatsepin and Petrova, 1939). In the North Sea, cod have frequently been caught in mid-water trawls used from research vessels of this laboratory (unpublished observations) and by commercial pair-trawlers (Harden Jones, 1962).

One of the first successful uses of the echo-sounder to locate fish (Sund, 1935) showed large shoals of cod above the bottom in the Norwegian Vestfjord, and echo-sounders have since frequently

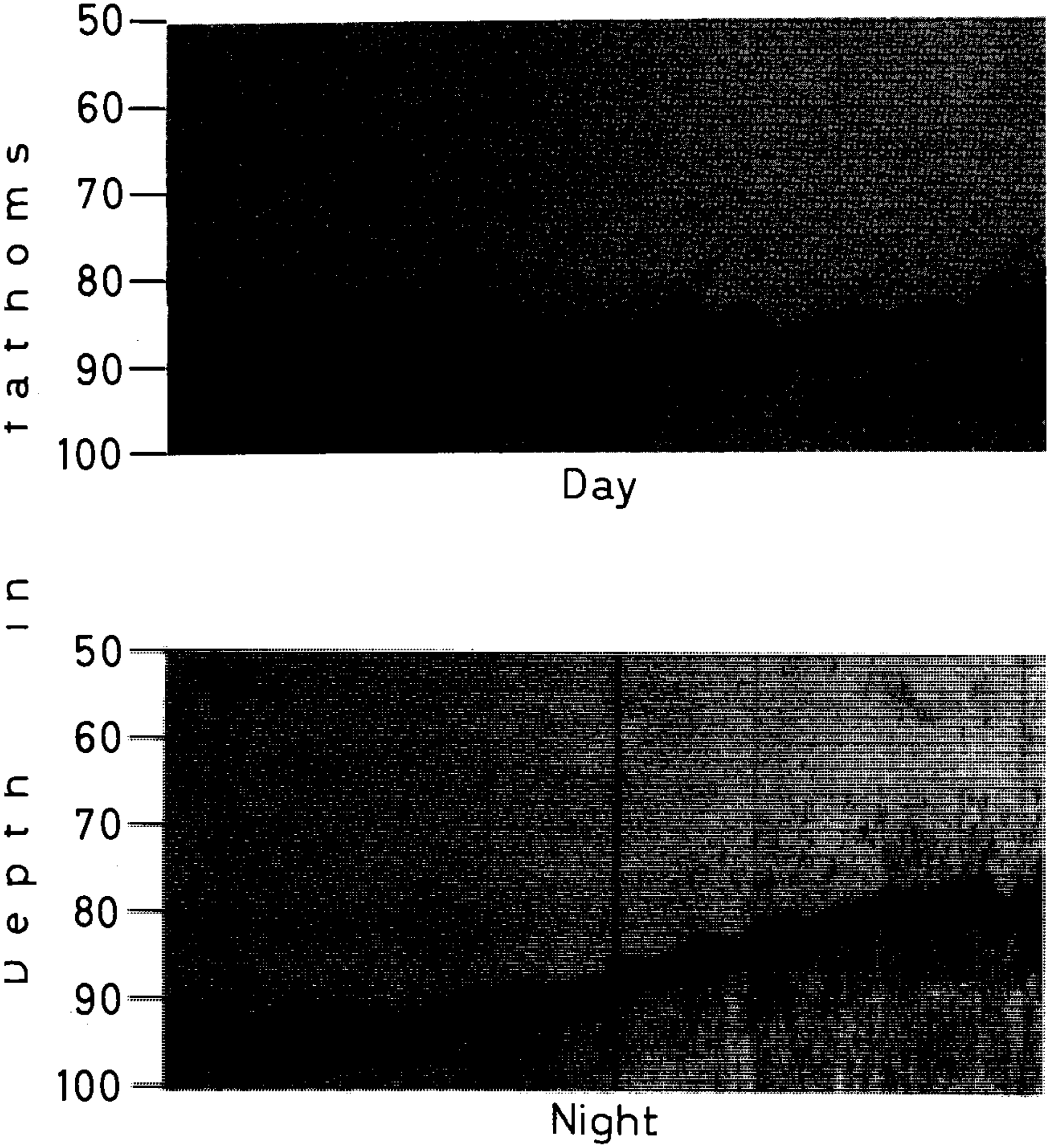


Fig. 2. Echo-recordings of cod on the Norwegian coastal banks, outside the Lofoten Islands, showing dispersion into midwater at night (ship steaming at 10 knots).

shown cod well above the sea-bed, particularly in the Barents Sea (Saetersdal, 1955; Midttun and Saetersdal, 1956; Trout, 1957; Konstantinov, 1958; Richardson *et al.*, 1959). The fish have sometimes been restricted to a relatively narrow range of depth (Ellis, 1956) and at other times have been spread over a range of perhaps 100 m - 200 m.

Possibly because cod have been observed over such a wide depth range, there have been few accounts of diurnal changes in vertical distribution in relation to day and night. The most complete series of echo-sounder records over a period of day and night was collected by Ellis (1956) in September in the Barents Sea on board a Hull trawler fishing around two dahn buoys; although the cod showed marked changes in shoaling behaviour, there was no obvious variation in the catch; however, this observation may not have been significant since it was apparent from the echo-records that the bulk of the cod were off the bottom throughout the period. Compact shoals at 100 fathoms in daylight dispersed at sunset and reformed at sunrise; during the night there was some evidence of vertical migration although its extent was not greater than 30 fathoms.

Echo-grams of cod inside the Vestfjord spawning grounds also showed dispersion of shoals at night and aggregation by day, some of these shoals staying in midwater by day but others returning to the sea-bed (Saetersdal and Hylen, 1959). During trawling on the north Norwegian coastal banks in winter with the research vessel *Ernest Holt* the author has frequently observed the vertical movement of cod shoals from the sea-bed at the onset of night, and this has been accompanied by a fall in the average catch of cod to about 50% of the daytime average; echo-recordings of the formation of cod shoals in this area by day and night are shown in Fig. 2. From this figure it can be seen that at night the cod dispersed into midwater over a range of 70 m or more. Konstantinov (1958) also reported diurnal changes in the catches of cod made by Russian trawlers during the spring and autumn in the Barents Sea; he associated these changes with cod leaving the sea-bed at night and presented echo-recordings of the cod shoals breaking up to disperse into midwater at night. In Scottish waters cod catches have also been found to decrease at night as cod were seen to leave the bottom, and some cod were also sighted at the surface at night (Parrish, Blaxter and Hall, 1963). Brunel (this symposium p. 439) described some interesting fishing experiments for cod with a split trawl, and with gill nets fished simultaneously on the bottom and just above it.

It would seem that, at least in distant northern waters, cod may spend considerable periods swimming pelagically both by day and night. As light intensities fall at dusk there is a dispersion of the cod shoals; if fish are on the sea-bed by day many of them rise into midwater at dusk and this diurnal dispersion is accompanied by a decrease in the catches of bottom trawls.

2: Coalfish (*Pollachius virens*)

Coalfish may have a pelagic distribution over deep waters and have frequently been caught near the surface in purse seines off Iceland and in the Norwegian fjords.

Clearly defined vertical migrations at night of more than 100 m have been shown by Schmidt (1955) in a remarkable series of echo-recordings. The coalfish left the sea-bed as a number of large shoals at dusk and there appeared to be some tendency to disperse into smaller shoals; however, in the middle of the night the fish had formed an almost continuous layer of midwater shoals some 10 m - 20 m deep. At dawn they returned to the neighbourhood of the sea-bed, once again forming numerous compact shoals. At Svinøy Bank, off the western coast of Norway, the present author has also made observations on the behaviour of large mature coalfish which were about to spawn; at dusk similar migrations were made of up to 100 m from the sea-bed, but at Svinøy Bank there was a greater tendency to disperse during the night and a midwater layer, as had been found by Schmidt at Iceland, was not recorded; the fish returned to the sea-bed at dawn.

Trawl catches of coalfish frequently show marked diurnal variations; on the northern Norwegian coastal banks the average night catch is about half the day catch (Woodhead, 1963*a*); but the situation may not be simple. Wagner (1959) has observed diurnal variations in the size of the fish caught, and Schmidt states that, both off Iceland and at Norway, although the greatest numbers of large fish were caught during the daytime, most small fish were caught at night.

3: Hake (*Merluccius merluccius*)

Although the hake is believed to make extensive vertical migration in pursuit of its prey, there seems to be surprisingly little published evidence of such behaviour. Hickling (1935) reported that at night Breton fishermen set pelagic long lines for hake about 30 m from the surface;

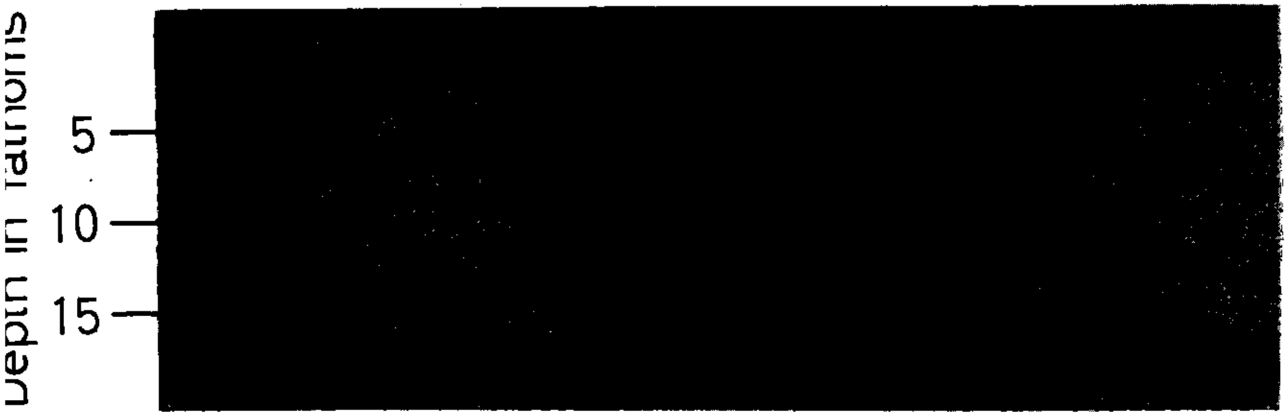
ake were also reported to be caught in large numbers in trammel nets set at the surface for salmon, nd mackerel drifters also catch small hake in their nets near the sea-surface. They have been aught at night within a few metres of the surface in midwater Engels trawls fished by research essels (H.A. Cole, *personal communication*).

There are marked diurnal changes in otter trawl catches of hake, the night catches frequently eing so small that commercial trawlers may stop fishing (Hickling, 1927, 1933). Hickling considred that the fall in catch was certainly due to the hake leaving the sea-bed and pointed out that he diurnal effect extended over a wide range of depths, the diminished catches being as notable n deep waters of 600 m as in shallower water, so that it was unlikely that the behaviour was dirctly related to the depth of an optimum light intensity; it would seem more likely that the change n light initiated an innate cycle of nocturnal migration. He suggested that when the hake were eeding at night they probably dispersed over all the water levels. There is some evidence of diferential vertical migration with size in hake, the day to night catch ratio being higher for smaler fish (Hickling, 1933).

: Whiting (*Gadus merlangus*)

It has already been mentioned that whiting are frequently caught in small numbers at night in erring drift nets fishing in the surface waters; longshore herring nets, which fish right up to he sea surface, frequently catch whiting in the top metre. It seems that the whiting are dispered at night since they are normally caught singly in drift nets, not in patches as might be exected if they were in shoals.

Blaxter and Parrish (1958) reported that in Loch Striven, Scotland, whiting moved down from he surface waters at dawn to a daytime depth of about 50 m, and they calculated that the light inensity at that depth was 0.17 lux. At night, by using electric artificial lights of different trengths, Blaxter and Parrish were able to alter the depth of whiting aggregations, over a range of rom 5 m to 18 m. They showed that the depth of the aggregations was related to the intensity of he lights, the fish remaining at a general "optimum" intensity range of 0.06 to 0.22 lux; that was t about the same intensity as at their normal daytime depth, suggesting that the whiting had ineed an optimum light intensity.



ig. 3. Echo-recordings of numerous single whiting in midwater at night, Southern Bight of North Sea (ship at anchor with slow tide running past).

In the Southern Bight of the North Sea, the author has observed the diurnal behaviour of hiting shoals in a depth of 18 fathom (unpublished observations); the shoals rose in the water at usk and then the fish dispersed to spread singly throughout the water column at night (Fig. 3). t dawn the fish sank down and reformed small shoals which went down to, or on to, the sea-bed. he fish were maturing adults; examination of their guts showed them to be empty, so that the verical migrations were not obviously related to feeding movements.

In view of these observations it might be expected that the trawl catches of whiting would decrease at night but, rather surprisingly, Parrish, Blaxter and Hall (1963) reported, fairly consistently, better catches of whiting during darkness in Scottish waters. In the southern North Sea it is common to catch large numbers of whiting well above the sea-bed at night with mid-water trawls, used both by research vessels and by commercial pair-trawlers (Harden Jones, 1962).

5: Haddock (*Gadus aeglefinus*)

Haddock are generally considered to be more closely associated with the sea-bed than many of the other gadoids of commercial interest, but there are a few records of haddock being caught in midwater. Zatsepin (reported by Konstantinov, 1958) observed that, in the Barents Sea, haddock (like cod) may follow the capelin close to the surface. Trout (1962) caught large haddock in a midwater trawl about 120 m above the sea-bed, and Saetersdal has caught haddock on pelagic line in the Barents Sea (reported by Trout, 1962); Hjort (1914) also took a few haddock in surface nets over water of more than 1,000 m depth. Blacker (unpublished, reported by Trout, 1962) has obtained photographs of juvenile haddock in the surface waters of the Barents Sea.

Trawl catches of haddock in the Barents Sea have been reported as being greater by day than at night and this has been interpreted as an effect of the fish rising into midwater (Bückmann, 1931: Konstantinov, 1958). Similar results were obtained when fishing with the *Ernest Holt* on Skolpen Bank in late November, and analysis of the catches also led the author (Woodhead, 1961, 1963*a*) to conclude that the low night catches (28% of mean day catch) were probably due to a change in availability as large numbers of smaller haddock left the sea-bed. Fish echo traces were seen leaving the sea-bed at dusk, but since cod were also present in the area no conclusions could be drawn about the identity of the traces, although the cod catches showed no significant variation. On this bank the greatest diurnal changes occurred in the smaller fish, little change being recorded in the diurnal catches of the largest haddock. The changes were not associated with feeding, since the smallest fish were feeding almost exclusively on benthic animals (echinoderms polychaetes and anemones) whilst the food of the larger haddock was increasingly of planktonic origin (*Beroe*, amphipods, *Tomopteris*) (Table 2)*; only 2% of fish were recorded as having a mixture of planktonic and benthic food in their stomachs.

TABLE 2. DIURNAL CHANGES IN CATCH OF HADDOCK, AND FEEDING CHANGES IN RELATION TO THE SIZE OF FISH.

Length (cm)	$\frac{\text{Mean night catch}}{\text{Mean day catch}} \times 100$	Planktonic food %	Benthic food %
20-29	17	0	100
30-39	11	12	88
40-49	26	27	73
50-59	44	46	54
60-69	60	54	46
70+	75	65	35

Since the apparent changes in vertical distribution were unrelated to feeding, it was thought that they might be characteristic behaviour patterns of the species which tended to change with size. This may be taking too simple a view, since although daytime catches of haddock are also greatest on the Norwegian coastal banks (Woodhead, 1963*b*), at the Faeroes Islands the greatest catches of haddock are made at night (Jones, R., 1956), and in Scottish waters Parrish *et al.*(1963) obtained very variable results at different times or localities.

6: Redfish (*Sebastes marinus*)

Like the hake the redfish is a pelagic feeder and there are very marked diurnal changes in their catches in trawls. The daytime catches are almost invariably greatest and in some fisheries these changes may be so great that trawling becomes unprofitable at night (Steele, 1957; Konstantinov and Scherbino, 1958; Templeman, 1959; von Seydlitz, 1962). It seems that these

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* In the paper of Woodhead (1961) the changes in feeding were described in the text, but in a tabulation of the analysis the captions were unfortunately transposed. The correct results are given in Table 2.

arked diurnal changes in catch are due to vertical migration by the redfish, since the fall in rawl catches has been linked with echo-records of the movement of redfish shoals from the bottom t dusk (Konstantinov and Scherbino, 1958; Templeman, 1959); Templeman reported that the shoals ad been observed to disperse during the night, though the migrations of 300 m described by onstantinov and Scherbino did not result in the dispersion of shoals of large redfish observed t Flemish Cap.

The vertical movements of redfish have also been approached from a physiological standpoint; n the basis of nitrogen analyses from the gas bladder of redfish caught at 200 m, Scholander *et al.* 1951) suggested that the fish had made migrations of up to at least 80 m during the night; howver, later work (Scholander and Van Dam, 1953) on some apparently bottom-living species gave ather similar results, and the earlier results were considered inconclusive.

: Flatfishes

There are generally few reports of flatfish swimming near the surface, at least in deep waters. he sole seems to be rather exceptional in that periodically numbers of soles may be reported as wimming along in the surface layer in the North Sea (deVeen, 1963); this behaviour seems to be ssociated with the spawning migration and occurs on dark moonless nights.

Most of the data concerning the vertical movements of flatfish have come from midwater trawing. In the southern North Sea plaice and dabs are very frequently caught in midwater at night Woodhead, 1960; Harden Jones, 1962; unpublished observations on research vessels). Soles are selom caught well off the bottom, despite their surface-swimming on particular occasions. Hartley 1940) mentions flounders being sometimes taken in surface drift nets in the Tamar estuary and hey have also been taken at night with midwater trawls in the southern North Sea.

It is difficult to assess laboratory observations of flatfish swimming in midwater at night, ince the aquaria normally apply severe restrictions to both the vertical and horizontal movements f the fish; however, swimming activity may persist for considerable periods. Using a circular rough for experiments, Bregnballe (1961) recorded average speeds of about 900 m per hour in 26 cm lounders, and one flounder swam 5 km during the course of a night.

In offshore regions of the southern North Sea trawl catches of plaice tend to decrease at night, nd it has been suggested that this may be due to a change in availability as plaice leave the seaed (Woodhead, 1960; de Groot, 1963; as discussed above). However, Parrish, Blaxter and Hall (1963) ound that in the northern North Sea plaice catches were generally greater at night; as yet these ifferences cannot be explained.

ADAPTIVE SIGNIFICANCE OF VERTICAL MIGRATION

In many pelagic fish, such as the herring and anchovy, feeding generally occurs at twilight ear the surface, and Zusser (1958) has suggested that daily vertical migration is of advantage o the fish in changing their environment and choice of food by "scanning" a range of depths twice aily. This might also apply to hake and coalfish which feed on other fish and on plankton in midater. Yet many other demersal species which feed mainly at the sea-bed, such as plaice, flounders nd possibly haddock, show evidence of adopting basically similar diurnal behaviour patterns, freuently involving movement of the fish away from the sea-bed. Examination of the stomach contents f such fish has frequently shown that they feed little, if at all, when swimming clear of the botom at night. In these species the adaptive value of leaving the sea-bed is not immediately so bvious, since it imposes a restriction on the feeding period; nevertheless this behaviour appears o be widespread, although it may show some variations seasonally or with the size and condition of he fish. The possible role of vertical migrations as part of distribution mechanisms of particular pecies is now considered.

Diurnal changes in the behaviour patterns of demersal fish, which take the fish away from senory contact with the sea-bed, must expose the fish to changes in the actions of water currents, and ay well lead to their passive displacement; in some cases the extent of their vertical migrations ay take the fish into different current systems from those at the sea-bed. Very little is known of he reactions of fish to steady linear currents once they have lost tactile and visual contact with he sea-bed, or some external reference point (for discussion see Harden Jones, 1958). However, obervations on the behaviour of blind fish well clear of the bottom in a steady stream of water have hown that their swimming is unorientated by the current, the fish being carried passibely along in

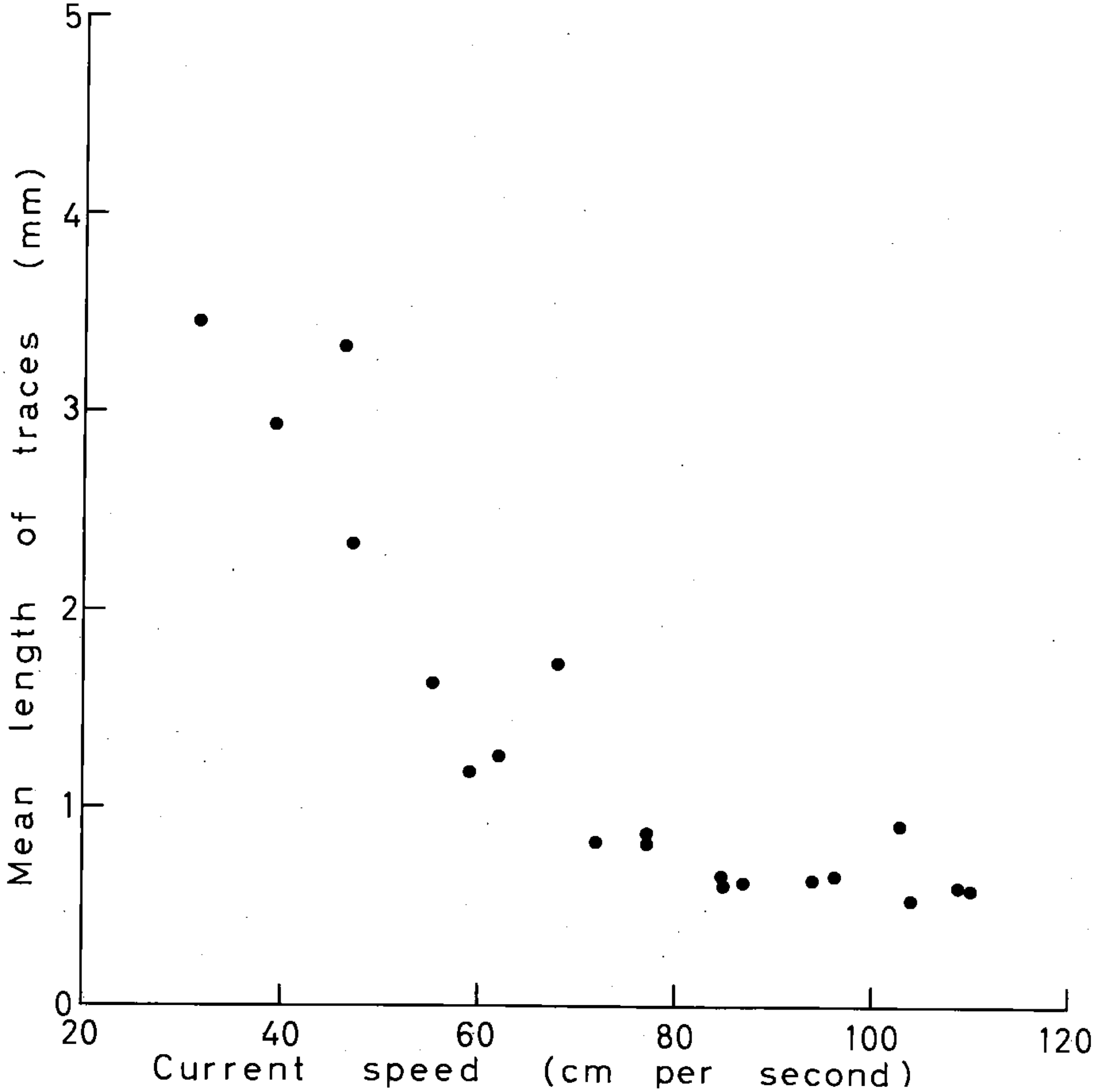

Fig. 4. Mean length of echo-recordings from whiting, in relation to the speed of the tidal current, for one quarter of a tidal cycle. The size of the traces has been corrected for the depth at which the fish occurred.

the water (Lyon, 1904, 1909; Dijkgraaf, 1933). If this also happened with marine fish, once they had lost contact with the bottom, their duurnal vertical migrations could exert considerable effects upon their horizontal displacment.

An example of this form of passive displacement at night was provided by observations on the behaviour of whiting made during a recent cruise of the research vessel *Clione* in the Southern Bight of the North Sea. The ship lay at anchor in a tidal stream in an area in which the echo-sounders recorded numerous small fleck or comet echo-traces, typical of single fish (Richardson *et al.*, 1959), in midwater. The tidal speed was measured with two Kelvin Hughes Direct Reading Current Meters, suspended at 8 m and 20 m. It was observed that, as the current speed decreased, the echo-traces recorded from the fish become progressively longer as they passed more slowly beneath the ship. It was concluded that the fish were being carried along passively in the current, but this was checked by measuring the size of the echo-traces recorded within the depth range 8 m - 26 m, and comparing their mean sizes with the simultaneously measured mean current speed. The results are shown graphically in Fig. 4, in which it can be seen that the relationship wss curvilinear. From the results it would appear that the fish were being carried rapidly past the ship at fast current speeds. If this had also been the case at low speeds the relationship should have been hyperbolic, but the considerable increase in mean trace size at low speeds suggested that the fish were then partly stemming the tide. Although the fish may have been using the ship as an external reference point for orientation against the tidal current at low speeds (though the seawater was very turbid and the ship's lights were obliterated, except for the minimum required for navigational purposes, so that visual clues were small), it was apparent from the form of the relationship in Fig. 4 that for most of the observation time the speed at which fish were passing the ship was directly related to the tidal speed, and it seems probable that they were largely being carried passively in the tidal current. The fish were identified by fishing with an Engels midwater trawl immediately after the tidal observations had been made; the catch was mainly whiting 29-49 cm long (215 fish), with 17 pilchards and 1 herring, 5 codling of 40-60 cm, and 6 flatfish. After daybreak the fish were observed to form small shoals which later returned to the sea-bed.

Transport of fish by water currents after they have left the bottom has been suggested by a number of authors as a mechanism for carrying out directional migration (*e.g.* Trout, 1957; Fraser, 1956; Harden Jones, 1961; Stieve, 1961), although little direct evidence has been obtained until recently. Harden Jones (1957 and 1962) showed that at night in the Southern Bight of the North Sea midwater herring shoals moved in the direction of the tidal current, though it was not possible to say whether the movements were due to passive drift; herring shoals in contact with the sea-bed were able to maintain their position by stemming the tides. Vertical migrations from the sea-bed may coincide with a particular phase of the tide, and Verway (1958 and 1960) has suggested that the migration of elvers, shrimps, and possibly soles may be achieved by passive transport during special phases of the tidal cycle. This suggestion has been amply confirmed for elvers by the experiments of Creuztberg (1959, 1961), and the recent report of deVeen (1963) on the surface swimming of soles suggests that passive transport during particular parts of the tidal period may indeed help these fish to achieve directional migrations. If such methods of migration exist in some fish of limited swimming ability, there seems to be no reason *a priori* why similar behaviour should not apply, at least in part, to better-swimming species; indeed, Harden Jones (1961) suggests that by making judicious use of systems of currents and counter-currents, fish may be able to achieve most of their migratory movements by passive transport mechanisms.

It is concluded that diurnal changes in behaviour patterns in relation to light are widespread in fish; frequently these cyclic patterns involve changes in the vertical distribution of the fish. In some species vertical migrations are obviously related to feeding activities, but in other species there appears to be little direct relationship. Changes in the vertical distribution of demersal fish may expose them to differences in the action of currents, and in some cases may take them into current systems other than those at the sea-bed. Essentially, the transport of the fish in such currents must have considerable effects upon their horizontal distribution. Diurnal vertical migration may therefore be considered as an integral part of the distribution mechanism of demersal fish. It may be that future research will show that some fish are able to make orientated movements with or against the currents, or at compass bearings to them, even when swimming well away from the sea-bed; nevertheless the direct effects of water transport will still be important, since the overall movements of the fish with respect to the sea-bed will be the resultant of the swimming movements of the fish and the movement of the water.

At present there is surprisingly little published information on the vertical movements of demersal fish, mainly due to problems of sampling the fish in midwater. Quantitative information on the vertical distribution of demersal species is now required, and valuable results are likely to come from the development of effective and easily applied midwater trawling techniques.

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REFERENCES

ALI, M.A. and I. HANYU. 1963. A comparative study of retinal structure in fishes from moderately deep waters of the North-west Atlantic. *Canad. J. Zool.*, 41: 225-241.

AREY, L.B. and G.H. MUNDT. 1941. A persistent diurnal rhythm in visual cones. *Anat. Rec.*, 79: 5-11.

ATKINS, W.R.G. and H.H. POOLE. 1959. Cube photometer measurements of the angular distribution of submarine daylight and of the total submarine illumination. *J. Cons. int. Explor. Mer*, 24: 327-336.

BIGELOW, H.B. and W.C. SCHROEDER, 1953. Fishes of the Gulf of Maine. *Fish. Bull.*, U.S., 53, (74): 1-577.

BLAXTER, J.H.S. 1964. Effect of change of light intensity on fish. *This symposium Contribution No. F-2.*

BLAXTER, J.H.S. and B.B. PARRISH. 1958. The effect of artificial lights on fish and other marine organisms at sea. *Mar. Res. Scot.*, 2: 1-24.

BLAXTER, J.H.S., B.B. PARRISH and W. DICKSON. 1963. The importance of vision in the reactions of fish to driftnets and trawls. *F.A.O. 2nd World Fish. Gear Congr.*, Lond., Paper 69: 1-18.

BOEREMA, L.K. and A.B. STAM. 1952. A preliminary note on the sole in the Dutch coastal area. *I.C.E.S. 1952, North Sea Committee*, 1-3.

BOEREMA, L.K. 1963. Some effects of diurnal variation in the catches upon estimates of abundance of plaice and sole. *I.C.E.S. 1963, Symposium on the measurement of abundance of fish stocks.* No. 22, pp. 1-7.

BOULENGER, E.G. 1929. Observations on the nocturnal behaviour of certain inhabitants of the Society's aquarium. *Proc. zool. Soc., Lond.*, pp. 359-362.

BRAEMER, W. and H.O. SCHWASSMAN. 1963. Vom rhythmus der sonnen orientierung am Aquator (beifischen). *Ergebn. Biol.*, 26: 182-202.

BREDER, C.M. 1959. Studies on social grouping fishes. *Bull. Amer. Mus. nat. Hist.*, 117 (6): 397-481.

BREDER, C.M. and P. RASQUIN, 1947. Comparative studies in the light sensitivity of blind characins from a series of Mexican caves. *Bull. Amer. Mus. nat. Hist.*, 89 (5): 319-352.

BREDER, C.M. and P. RASQUIN. 1950. A preliminary report on the role of the pineal organ in the control of pigment cells and light reactions in recent teleost fishes. *Science*, 111: 10-12.

BREGNBALLE, F. 1961. Plaice and flounder as consumers of the microscopic bottom fauna. *Medd. Komm. Havunders., Kbh.*, N.S., 3 (6): 133-182.

BRETT, J.R. 1957. in *The Physiology of Fishes.* Chapter II, pt. 1. The Eye Acadamic Press Inc., New York, *Ed.* M.E. Brown.

BROWN, F.A.,Jr. 1958. Studies of the timing mechanisms of daily, tidal and lunar periodicities in organisms. *In Perspectives in Marine Biology, Ed.* A.A. Buzzati Traverso, Univ. of California Press.

BRUNEL, P. 1964. Food as a factor or indicator of vertical migrations of cod in the Western Gulf of St. Lawrence. *This Symposium Contribution No. C-2.*

BÜCKMANN, A. 1931. Fischfang im Barentsmeer. Mitt. Dtsch. Seefisch.-verein., 47 (1): 4-13.

CHESTNOY, V.N. 1961. Vertical migrations of herring and the methods of their utilization in the fishing practice. *Ryb. Khoz.* 37 (6): 53-57 (In Russian).

CLARKE, G.L. 1938. Seasonal changes in the intensity of submarine illumination off Woods Hole. *Ecology*, 19: 89-106.

Elements of Ecology. 1954. Chapter 6. Light. John Wiley, New York, and Chapman and Hall, London.

CLARKE, G.L. and E.J. DENTON. 1962. Light and animal life. *In: The Sea. Ed.* M.N. Hill, 1: Chap.10, 456-468. John Wiley, New York and London.

CREUTZBERG, F. 1959. Discrimination between ebb and flood tide by migrating elvers (*Anguilla vulgaris* Turt.) by means of olfactory perception. *Nature*, Lond., 184: 1961-2.

1962. On the orientation of migrating elvers (*Anguilla vulgaris* Turt.) in a tidal area. *Ned. J. Sea Res.* 1, (3): 257-338.

DAVIS, R.E. 1961. Daily rhythm in the reaction of fish to light. *Science*, 137: 430-432.

DENTON, E.J. and F.J. WARREN. 1957. The photosensitive pigments in the retinae of deep-sea fish. *J. mar. biol. Ass. U.K.* 36: 651-662.

DENTON, E.J. 1959. The contributions of the orientated photosensitive and other molecules to the absorption of whole retina. *Proc. roy. Soc., (B)* 150: 78-94.

DIJKGRAAF, S. 1933. Untersuchungen über die Funktion der Seitenorgane an Fischen. *Z. vergl. Physiol.*, 20: 162-214.

DUNTLEY, S.Q. 1962. Underwater visibility. *In: The Sea., Ed.* M.N. Hill, 1: Chap. 9. 452-455. John Wiley, New York and London.

ELLIS, G.H. 1956. Observations on the shoaling behaviour of cod (*Gadus callarias*) in deep water, relative to daylight. *J. mar. biol. Ass. U.K.*, 35: 415-417.

ENGSTRÖM, K. 1961. Cone types and cone arrangements in the retina of some gadoids. *Acta. zool.*, Stockh., 42: 227-243.

FRAENKEL, G.S. and D.L. GUNN, 1940. *The orientation of animals.* Oxford University Press.

FRANZ, V. 1910. Über die Ernahrungsweise einiger Nordsee fische imbesonders der Scholle. *Wiss. Meeres. Unt. abt. Helgoland, NF* 9: 197-216.

FRASER, J.H. 1956. The drift of the planktonic stages of fish in the North East Atlantic and its possible significance to the stocks of commercial fish. *Spec. Publ. int. Comm. Northw. Atlant. Fish.*, No. 1, pp. 289-310.

GOMPEL, M. 1937. Recherches sur la consommation d'oxygene de quelques animaux aquatiques littoraux. *C.R. Acad.* Sci., Paris, 205: 816.

de GROOT, S.J. 1963. Diurnal activity and feeding habits of plaice. *I.C.E.S. 1963.* Near N. Seas Committee, Paper 11: 1-4.

HANYU, I. and M.A. ALI. 1962. Intra-sub-specific variation in retinal structure in *Sebastes marinus mentella*. *Nature*, Lond., 196: 554-555.

HARDER, W. and G. HEMPEL. 1954. Studien zur Tagesperiodik det Aktivität von Fischen. 1. Versuche an Plattfischen. *Kurz. Mitt. Inst. Fischbiol.* Univ. Hamb., Nr. 5: 22-31.

HARKER, J.E. 1958. Diurnal rhythms in the animal kingdom. *Biol. Rev. 33: 1-52.*

HARTLEY, P.H.T. 1940. The Saltash tuck-net fishery and the ecology of some estuarine fishes. *J. mar. biol. Ass., U.K.,* 24: 1-68.

HASLER, A.D. and H.O. Schwassmann. 1960. Sun orientation of fish of different latitudes. *Cold Spring Harbor Symp. Quant. Biol.* 25: 429-441.

HEMPEL, G. 1956. Studien zur Tagesperiodik der Aktivität von Fischen. II. Die Nahrungsaufnahme der Scholle. *Mitt. Inst. Fischbiol.* Univ. Hamburg, 6: 22-37.

HICKLING, C.F. 1927. The natural history of the hake. Pts. I and II. *Fish. Invest.* Lond., Ser. 2, 10 (2): 1-100.

1933. The natural history of the hake. Pt. IV. *Ibid.*, Ser. 2, 13 (2): 1-120.

1935. *The hake and the hake fishery.* (Buckland Lectures for 1934. Edward Arnold: Lond: 1-142.

HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe reviewed in the light of biological research. *Rapp. Cons. Explor. Mer*, 20: 3-227.

IVANOFF, A. and I.H. WATERMAN. 1958. Factors, mainly depth and wavelength, affecting the degree of underwater light polarization. *J. Mar. Res.* 16: 283-307.

JERLOV, N.G. 1951. Optical studies of ocean waters. *Rep. Swed. Deep-Sea Exped.*, 3 (1): 1-60.

JENSEN, A.S. and P.M. HANSEN. 1931. Investigations on the Greenland cod (*Gadus callarias* L.) *Rapp. Cons. Explor. Mer*, 72(1): 1-41.

JONES, F.R. HARDEN. 1955. Photo-Kinesis in the ammocoete larva of the brook lamprey. *J. exp. Biol.*, 32: 492-503.

1956. The behaviour of minnows in relation to light intensity. *J. exp. Biol.*, 33, (2): 271-281.

1957. Movements of herring shoals in relation to the tidal current. *J. Cons. int. Explor. Mer*, 22: 322-28.

1958. Reactions of fish to stimuli. *F.A.O. Indo-Pacific Council*, 8th Session, (3): 18-28.

1961. Fish migration: passive drift or orientated movement? *Anim. Behav.* 9, (3 and 4): 239.

1962. Further observations on the movements of herring (*Clupea harengus* L.) shoals in relation to the tidal current. *J. Cons. int. Explor. Mer*, 27: 52-76.

JONES, N.S. 1952. The bottom fauna and the food of the flatfish off the Cumberland coast. *J. Anim. Ecol.*, 21: 182-205.

JONES, R. 1956. A discussion of some limitations of the trawl as a sampling instrument. *Rapp. Cons. Explor. Mer*, 140 (1): 44-7.

KAWAMOTO, N.Y. and J. KONISHI. Diurnal rhythm in phototaxis of fish. *Rep. Fac. Fish. Univ. Mie.*, 2: 7-17.

KONSTANTINOV, K.G. 1958. Diurnal vertical migrations of the cod and haddock. *Trans. Int. Mar. Fish. USSR*, 36: 62-82.

KONSTANTINOV, K.G. and M.N. SCHERBINO. 1958. Diurnal vertical migrations of redfish. *Rybnoye Khozyaistvo*, No. 10: 11-13 (In Russian).

KRUUK, H. 1963. Diurnal periodicity in the activity of the common sole. *Solea vulgaris* Quensel. *Netherlands J. Sea. Res*; 2: 1-28.

LYON, E.P. 1904. On rheotropism. Rheotropism in fishes. *Amer. J. Physiol.*, 12: 149-161.

1909. On rheotropism. Rheotropism of fish blinded in one eye. *Amer. J. Physiol.*, 24: 244-251.

MIDTTUN, L., and G. SAETERSDAL. 1956. Rapport on tokt med *G. O. Sars* til Barentshavet 14/3-26/4 1956. *Fiskets Gang* Nr. 19: 275-7.

MØLLER CHRISTENSEN, J. 1960. The stock of soles (*Solea solea*) and the sole fishery on the Danish North Sea coast. *Medd. Komm. Havunders*. Ser. Fisk., 3, (2): 19-53.

1962. In report of the working group on sole. *I.C.E.S. 1962, Near Northern Seas Committee*. Paper 92. 28-29.

MUNZ, F.W. 1958*a*. The photosensitive retinal pigments of fishes from relatively turbid coastal waters. *J. gen. Physiol.* 42: 445-449.

1958*b*. Photosensitive pigments from the retinae of certain deep sea fishes. *J. Physiol.* 140: 220-235.

NICOL, J.A.C. 1960. *The biology of marine animals*. Sir Isaac Pitman and Sons Ltd., London. 305-365.

1963. Some aspects of photoreception and vision in fishes. Advances in Marine Biology, 1: 171-208.

PARKER, G.H. 1909. The integumentary nerves of fishes as photoreceptors and their significance for the origin of the vertebrate eyes. *Amer. J. Physiol.*, 25: 77-80.

PARRISH, B.B., J.H.S. BLAXTER and W.B. HALL. 1963. Diurnal variations in size and composition of trawl catches. *I.C.E.S. 1963, Symposium on the measurement of abundance of fish stocks*, No. 34: 1-12.

POSTUMA, K.H. 1957. The vertical migration of feeding herring in relation to light and vertical temperature gradient. I.C.E.S. 1957 Herring Committee. 1-7.

PUMPHREY, R.J. 1961. Concerning Vision. *In: The Cell and the Organism.* Essays presented to Sir James Grey, Cambridge Univ. Press., 193-208.

RAE, B.B. 1957. A preliminary account of the turbot in Scottish waters. *Scot. Fish Bull.* 8: 10-12.

RASMUSSEN, B. 1953. Norwegian fisheries investigations in 1952. *Annls. biol.*, Copenh. 9: 52-56.

1954. On the Norwegian pelagic long-line fishery in the Holsteinborg Deep- 1953. *Internat. Comm. Northwest Atlantic Fisheries, Ann. Proc.*, 4: 40-45.

RICHARDSON, I.D., D.H. CUSHING, F.R.H. JONES, R.J.H. BEVERTON and R.W. BLACKER 1959. Echo sounding experiments in the Barents Sea. *Fish. Invest. Lond.*, Ser. 2, 22(9): 1-57.

ROCHON-DUVIGNEAUD, A. 1958*a*. L'oeil et la vision. *In:* "Traite de Zoologie". *Ed.* Grasse, P.-P. 13, Fasc. 2, 1099-1142, Masson, Paris.

SAETERSDAL, G. 1955. Torsk med. *G.O. Sars* til Barentshavet 22/7 til 10/8 1955. *Fiskets Gang.* Nr. 38: 497-8.

SAETERSDAL, G. and A. HYLEN. 1959. Skreiundersøkelsene og skreifisket i 1959. *Fisken og Havet* 1: 1-20.

SHAW, R.J., R.A. ESCOBAR, and F.M. BALDWIN. The influence of temperature and illumination on the locomotor activity of *Carassius auratus*. *Ecology*, 19: 343-345.

SCHARRER, E. Die Lichtempfindlichkeit blinder Elritzen (Untersuchungen über das Zwischenhirn der Fische I) *Z. vergl. Physiol.*, 7: 1-38.

SCHLAGEL, S.R. and C.M. BREDER, Jr. 1947. A study of the oxygen consumption of blind and eyed cave characins in light and in darkness. *Zoologica*, N.Y., 32: 17-27.

SCHMIDT, U. 1955. Beiträge zur Biologie des Köhlers (*Gadus virens* L.) in den isländfischen Gewässern. *Ber. Dtsch. Komm. Meeresforsch.*, 14: 46-82.

SCHOLANDER, P.F., C.L. CLAFF, C.T. TENG, and V. WALTERS. 1951. Nitrogen tension in the swim bladder of marine fishes in relation to the depth. *Biol. Bull.*, Woods Hole, 101 (2): 178-193.

SCHOLANDER, P.F. and L. VAN DAM. 1953. Composition of the swimbladder gas in deep sea fishes. *Biol. Bull.*, Woods Hole, 104 (1): 75-86.

SEYDLITZ, H. von. 1962. Untersuchungen über die Tagesperiodiztät des *Rotbarsches marinus*, auf Grund von Fanganalysen. *Kurz. Mitt. Inst. Fisch. Biol. Univ. Hamb.* No. 12: 27-36.

SHAW, R.J., R.H. ESCOBAR, and F.M. BALDWIN. The influence of temperature and illumination on the locomotor activity of *Carassius auratus*. *Ecology*, 19: 343-5.

SOKOLOV, O.A. 1961. Underwater visual observations during the fifth voyage of the submarine *Severyanka*. *Okeanologlia*, 4: 757-61. (In Russian).

SPENCER, W.P. 1939. Diurnal activity rhythms in freshwater fishes. *Ohio J. Sci.*, 39: 119-32.

STEELE, D.H. 1957. The redfish (*Sebastes marinus* L.) in the western Gulf of St. Lawrence. *J. Fish. Res. Bd. Canada*, 14 (6): 899-924.

STIEVE, H. 1961. Sinnesphysiologische Betrachtungen über die Orientierung der Meerestiere bei ihren Wanderungen. *Helg. Wiss. Meer.* 8 (1): 153-165.

SUND, O. 1935. Echo-sounding in fishery research. *Nature*, Lond., 135: 953.

TAMURA, T. 1957. On the relation between the intensity of illumination and the shifting of cones in the fish retina. *Bull. Jap. Soc. sci. Fish.*, 22: 742-6.

TEMPLEMAN, W.F. 1959. Redfish distribution in the North Atlantic. *Fish. Res. Bd. Canada*, Bull 120: 1-173.

TROUT, G.C. 1957. The Bear Island cod migrations and movements. *Fish. Invest. Lond.*, Ser. 2, 21 (6): 1-51.

1962. Specific seasonal density changes in cod and haddock populations. *I.C.E.S. 1962, Comp. Fish Comm.* No. 24. 1-5.

TYLER, J.E. and R.W. PREISENDORFER. 1962. Light. 8. In: *"The Sea"*. *Ed.* M.N. Hill. 1: Chap. 8, 394-451. John Wiley, New York and London.

DE VEEN, J.F. 1963. On the phenomenon of soles swimming near the surface of the sea. *I.C.E.S. 1963. Near N. Seas Committee,* No. 56: 1-4.

VERWEY, J. 1958. Orientation in migrating marine animals and a comparison with that of other migrants. *Arch. neerl. Zool.,* 13: Suppl. 1, 418-445.

1960. Über die Orientierung wandern der Meerestiere. *Helgol. Wiss. Meeresunters,* 7: 51-58.

WAGNER, G. 1959. Untersuchungen über die Tagesperiodizität der Nahrungsaufnahme bei *Pollachius virens* L. *Kurz. Mitt. Inst. Fish. Biol., Univ. Hamb.,* No. 9: 61-103.

WATERMAN, T.H. 1958. Polarized light and plankton navigation. *In: Perspectives in marine biology. Ed.* A. A. Buzzati Taverso, Univ. of California Press. 428-450.

WELSH, J.H. and C.M. OSBORNE. 1937. Diurnal changes in the retina of the catfish, *Ameiurus nebulosus. J. comp. Neurol.,* 66: 349-59.

WIGGER, H. 1941. Diskontinuität und Tagesrhythmik in der Dunkelwanderung retinaler Elemente. *Z. vergl. Physiol.,* 28: 421-427.

WOODHEAD, P.M.J. and A.D. WOODHEAD. 1955. Reactions of herring larvae to light: a mechanism of vertical migration. *Nature, Lond.,* 176: 349-350.

WOODHEAD, P.M.J. 1956. The behaviour of minnows (*Phoxinus phoxinus* L.) in a light gradient. *J. exp. Biol.,* 33, (2): 257-270.

1957. Reactions of salmonid larvae to light. *J. exp. Biol.,* 34: 402-416.

1960. Diurnal variations in the trawl catches of plaice. *I.C.E.S. 1960, Comp. Fish. Comm.* No. 158. 1-3.

1961. Diurnal variations in trawl catches of haddock. *I.C.E.S. 1960, Comp. Fish. Comm.* No. 71. 1-4.

1963*a*. A change in the normal diurnal pattern of capture of soles during the severe winter of 1963. *I.C.E.S. 1963, Symposium on the measurement of abundance of fish stocks.* No. 19: 1-3.

1963*b*. Diurnal changes in trawl catches of fishes. *I.C.E.S. 1963, Symposium on the measurement of abundance of fish stocks.* No. 18: 1-18.

WOODHEAD, P.M.J. and A.D. WOODHEAD. 1962. Reactions of marine fish larvae to light in relation to vertical migration. *Lecture delivered to Plymouth meeting of Soc. Exp. Biol. 17th July 1962.*

WUNDER, W. 1925. Physiologische und vergleichend anatomische untersuchungen an der Knochenfischnetzhaut. *Z. vergl. Physiol.,* 3: 1-61.

1926. Über den Bau der netzhaut bei Süsswasserfischen, die in grosser tiefe leben (Coregonen, Tiefseesaibling). *Z. vergl. Physiol.,* 4: 26-36.

1936. Physiologie der Süsswasserfische Mitteleuropas. Handb. Binnenfisch. Mitteleurop., 2B, Stuttgart: 1-340.

ZATSEPIN, V.J. and N.S. PETROVA. 1939. The feeding of the cod in the south part of the Barents Sea. *Trans. Knipovich Polar Sci. Inst. Sea-Fish. and Oceanogr.,* 5: 1-169.

ZUSSER, S.G. 1958. A study of the causes of diurnal vertical migration in fishes. *Ikht. Kom. Akad. Nauk. S.S.S.R.* No. 8: 115-120.

SECTION

B

B-1

THE RELATIONSHIP BETWEEN THE DISTRIBUTION OF *SEBASTES* LARVAE, ZOOPLANKTON AND TEMPERATURE IN THE IRMINGER SEA

By

Jakob Magnússon[1] and Ingvar Hallgrímsson[1]

ABSTRACT

This contribution is based on material collected from the upper 50 m of the sea with Helgoland larvae nets and Icelandic High Speed Samplers at 178 stations during a cruise in May 1961 covering the Irminger Sea south to 60°N and east to 24°W.

Charts showing the station grid and the distribution and abundance of redfish larvae are presented. *Sebastes* larvae were found in most of the oceanic region of the survey area. The main concentrations were observed along the western slope of the Reykjanes Ridge in two main zones, one corresponding with the area bounded by the 1,000 and 2,000 m depth contours and the other mainly outside the area of the 2,000 m contour. Generally, the density zones and tongues ran in a south-north direction.

Fairly large quantities of zooplankton were found. The volume distribution was also characterized by marked zones of high density extending into the area from south and east creating a very uneven horizontal distribution of the zooplankton. This distribution is believed to be closely related to the complex current system.

A chart showing the temperature distribution at a depth of 20 m is presented. A close connection was established between the abundance of larval redfish and certain isotherms.

Although it was not possible to show a detailed correspondence between zooplankton abundance and the isotherms at 20 m, it was evident that the isolines for the zooplankton volume mainly followed the same general direction as the isotherms.

Generally, there was a good agreement between the abundance of redfish larvae and zooplankton density in the oceanic area. The larval abundance did not always coincide with high zooplankton volume. But in such cases a high percentage frequency of *Calanus finmarchicus* was found, this species being the most dominant one in the whole oceanic area (varying from 72% to 99% of the total zooplankton numbers). Thus, a good correlation existed between the abundance of larvae and *Calanus finmarchicus*. No such correlation was found with *Spiratella retroversa*. The percentage frequency of these two species is presented in charts. The results of this cruise have been compared with the results of cruises in 1962 and 1963. In 1961 and 1962, a great abundance of redfish larvae corresponded with a high standing stock of zooplankton. In 1963 there were relatively low numbers of larvae and the stock of zooplankton was low.

From these results, and assuming that year-class strength is determined during the larval phase, it is expected that the 1963 year class of redfish from this area will be a relatively poor one.

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B-2

ON THE ANALYSIS OF VARIATION IN THE PLANKTON, THE ENVIRONMENT AND THE FISHERIES

By

J.M. Colebrook[1]

INTRODUCTION

One of the objectives of marine biology is the detection of relationships between the plankton, he hydrographic environment and the fisheries with a view to determining control mechanisms and stablishing prediction equations. Irrespective of the form of these relationships, the planktoloist's immediate problem is the same: how to measure and express the variations in the plankton in uch a way as to facilitate comparisons with variables obtained from hydrographical and fisheries tudies.

The purpose of this paper is to describe an approach to this problem based on the Continuous lankton Recorder survey of the North Sea and the North Atlantic. Plankton Recorders are towed by erchant ships and weather ships along a number of standard routes which are sampled (at a depth of 0 m) once in each month. The instrument has been described by Hardy (1939), the methods of analysis y Rae (1952) and Colebrook (1960) and the characteristics of the samples and the survey by Glover 1962). Fig. 1*a* shows the routes in operation in 1963 (supported by H.M. Treasury from the Development Fund and by contract N62558-3612 between the Scottish Marine Biological Association and the nited States Department of the Navy, Office of Naval Research).

The survey of the western North Atlantic, including the ICNAF area, has been developed during he past two years and there is insufficient material from this area, as yet, for analyses of the ind described in this paper. These are based on the survey of the eastern North Atlantic and the orth Sea during the period 1948 to 1962. However, the intention here is to demonstrate possible ethods of analysing dats of this kind rather than to draw conclusions about any particular area.

The basic data consists of counts of species in samples at intervals of 20 nautical miles along he standard routes. On the average 150 samples have been collected in each month for the last 15 ears (up to 1962) and about 50 species occur regularly in the samples: this amounts to well over million observations. Each species shows geographical, seasonal and annual variations in abunance and clearly this situation is far too complicated to be compared, as it stands, with variations n hydrography and fisheries: it is necessary to simplify the situation in some way.

Glover (1957) and Glover *et al.*(1961) used year to year fluctuations in the abundance of zoolankton species as an estimate of annual variations in the plankton of the herring fishing grounds ff the east coast of Scotland. They found that the variations were related to water movements and o fluctuations in the success of the fishery. A more important result, in the present context, was hat groups of species were detected showing similar annual fluctuations of abundance. This sugests the possibility of deriving quantitative estimates, integrated by species, representing the nnual fluctuations in the abundance of the plankton as a whole. What would be required, in this ase, is a variable or a small number of variables giving the maximum discrimination between years nd including the variability of all the species in the plankton. Williamson (1961 and in press) erived such variables and used them to demonstrate quantitative relations between herring mortality nd distribution, hydrography and the fluctuations in abundance of the plankton. There is no reason hy the same principle should not apply to other aspects of plankton fluctuation such as seasonal nd geographical variations. This suggests the need for new methods of classifying the variations in he plankton as a whole. One possible system is that used in analysis of variance. The variability f the standing stock of the plankton as sampled by the Continuous Plankton Recorder can be repreented as a five dimensional variable, with standing stock as the variate, the other co-ordinates eing species, areas, months and years. The variability included in this system can be classified

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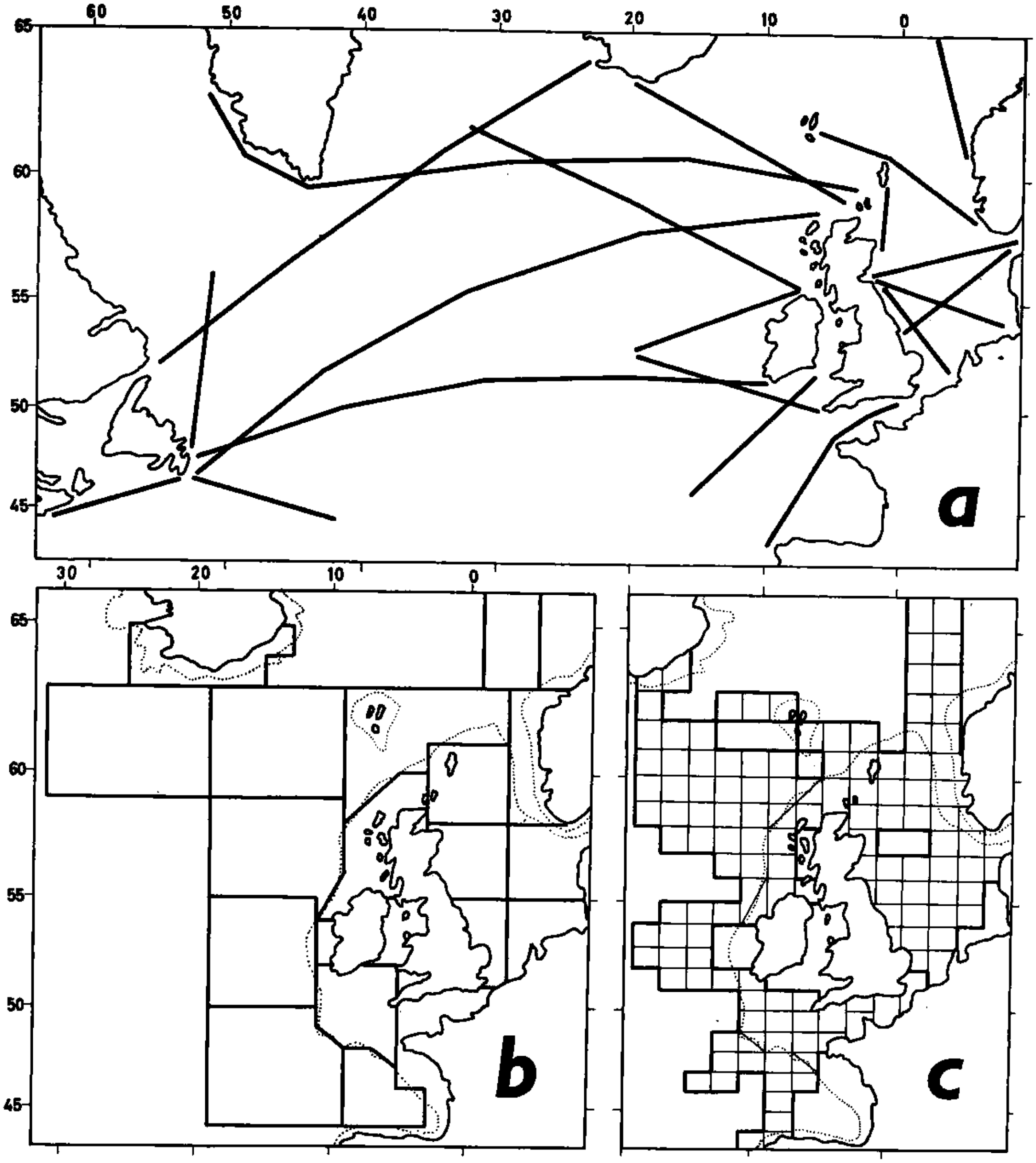


Fig. 1. (*a*) A chart showing the routes included in the Continuous Plankton Recorder survey in 1963.

(*b*) A chart showing the standard large area subdivision of the survey.

(*c*) A chart showing the subdivision of the Northeast Atlantic and the North Sea covering the area which has been sampled continuously since 1948. Each rectangle is 1° lat x 2° long: subdivided where necessary to give a boundary following the edge of the continental shelf.

s a four factor analysis of variance as shown in Table 1. Each source contains the variability easured along the included co-ordinates with the variability due to the other factors eliminated y averaging and also with the variability due to lower order sources involving the factors, if any, ubtracted. Thus, the source, species-areas, contains information about the geographical distri-utions of species with data for all years and months averaged and with the differences in abundance etween species and the variations in the overall abundance in the various areas eliminated.

The object of this classification is to divide the total variability of the standing stock of he plankton into a number of independent parts. Associated with each part is its degrees of free-lom (the values shown in Table 1 are based on expressions of the data in the form described below). he sum of these degrees of freedom is the same as that of the original variable so this classifi-ation, as it stands, does not constitute any simplification of the system. In order to achieve he required simplification it is necessary to find out first of all whether any of the sources of ariation can be ignored. This can be done by carrying out the analysis of variance and expressing he variability included in each source as a proportion of the total. Any source which is small in elation to the others can be ignored without any great loss of information. For the remainder, it s necessary to find methods of representing the variation of each source, or of groups of sources ncluding the same factors, by means of a variable or variables with a smaller number of degrees of reedom.

TABLE 1. CLASSIFICATION OF VARIATION OF THE STANDING STOCK OF 22 SPECIES OF PLANKTON IN THE 17 STANDARD AREAS SHOWN IN FIG. 1*b* DURING THE PERIOD 1948-1962.

	Degrees of freedom
Species	21
Areas	16
Months	11
Years	14
Species - Areas	336
Species - Months	231
Species - Years	294
Areas - Months	176
Areas - Years	224
Months - Years	154
Species - Areas - Months	3696
Species - Areas - Years	4704
Species - Months - Years	3234
Areas - Months - Years	2464
Species - Areas - Month - Years	51744

The final object, therefore, is to represent a large proportion of the variability of the standing stock of the plankton by variables with relatively small total degrees of freedom. This objective has not yet been achieved in the analysis of the data from the Continuous Plankton Recorder survey but successful analyses have been done on several of the sources of variation. Some of these are described in the following sections of this paper; more detailed accounts of each analysis are being prepared for publication.

METHODS OF ANALYSIS

1. Presentation of Data.

The first problem in the representation of variability is the selection of suitable units and methods of presentation. This is a matter of compromise between the requirements of the analytical methods and the limitations of the original data. The calendar month and year have been used as the time units and a system of areas was selected dividing the survey into rectangles of 1° lat x 2° long (Fig. 1*c*). For many purposes a less detailed sub-division is convenient and a system of larger areas (Fig. 1*b*) was devised with the intention of dividing the survey into as small a number of areas as possible without introducing too great a loss of variability and also giving areas corresponding as closely as possible with those in general use for the presentation of fishery and hydrographic data. The variate, standing stock, is represented by the logarithmic transformation (in the form $y = \log [x + 1]$ of the original sample counts: all subsequent analyses are carried out using the transformed values.

Ideally the taxonomic unit should be a biologically self-contained population with its own characteristic parameters of reproduction, growth and mortality, which can be treated as being dynamically independent (Glover, 1961). In practice, the species is usually the smallest unit that can be identified and sometimes it is necessary to resort to larger taxonomic units or to groups of species to avoid spending an undue amount of time identifying the organisms. Judging from the results so far, it appears that most species represent ecologically homogeneous populations, within the context of the Recorder survey, but several cases of ecological differentiation within a species have been described by Colebrook and Robinson (1963).

Most of the analyses which have been carried out so far are based on data for the copepods and the gastropods *Clione* and *Spiratella*. The other major groups in the zooplankton are not identified to species during the routine counts and the phytoplankton has been omitted from most of the analyses because, up to 1958, the counting method that was used did not yield suitable data.

2. Classification and Analysis of Variance

Table 2 gives the results of an analysis of variance with the variability due to years excluded. The analysis was based on the monthly means of 22 species, averaged for the years 1948 to 1961 in the standard areas shown in Fig. 1*b*. The results are expressed as percentages of the total sum of squares and the degrees of freedom are given. It can be seen that by far the largest single source of variation is species with 43.4%; this merely reflects the fact that some species are more abundant than others and is of no particular interest in considering relationships with the environment. The second column in the table shows the percentage of the total sum of squares with species excluded. It is clear that the only source of variation that could be ignored with little loss of information is areas-months. In practice, however it was found convenient to include this source with species-areas months in a single analysis; similarly it was found convenient to include months with species-months and areas with species-areas.

TABLE 2. ANALYSIS OF VARIANCE FOR 22 SPECIES IN THE 17 STANDARD AREAS SHOWN IN FIG. 1*b* BASED ON LONG-TERM AVERAGES FOR THE PERIOD 1948-1962.

	% Sum of Squares		Degrees of Freedom
Species	43.4		21
Areas	5.2	9.2	16
Months	12.7	22.4	11
Species - Areas	11.8	20.8	336
Species - Months	13.5	23.8	231
Areas - Months	2.5	4.4	176
Species-Areas-Months	11.0	19.4	1344

3. The Variability due to Areas and Species-Areas.

The 2° x 1° rectangles (Fig. 1*c*) were used as the area units in this analysis and 22 species were included. The first step was to eliminate the variability involving the sources months and years by averaging; the resulting means were written as a two-dimensional matrix with each column referring to a rectangle and each row to a species. Each row of the matrix represented the mean geographical distribution of a species. Each row was expressed in standard measure, with a mean of zero and unit variance, by applying the transformation $t_{ij} = (m_{ij} - \overline{m}_i)/s_i$ to each row where $\overline{m}_i$ is the mean of the observations of species i and s_i is the standard deviation. This procedure is equivalent to subtracting the variability due to species in analysis of variance. The resulting standardized matrix contained only the variability due to areas and species-areas, *i.e.* the pattern of variation of the geographical distributions of the different species.

A principal component analysis was applied to this matrix. The object of component analysis, as used here, is to select variables, which are linear functions of the geographical distributions of all the species included in the analysis, in such a way that the distributions may be represented by a smaller number of variables known as components. The first component is a representation of all the geographical distributions, selected so as to have the greatest possible variance. The second component is uncorrelated with the first and it has the greatest possible variance in relation

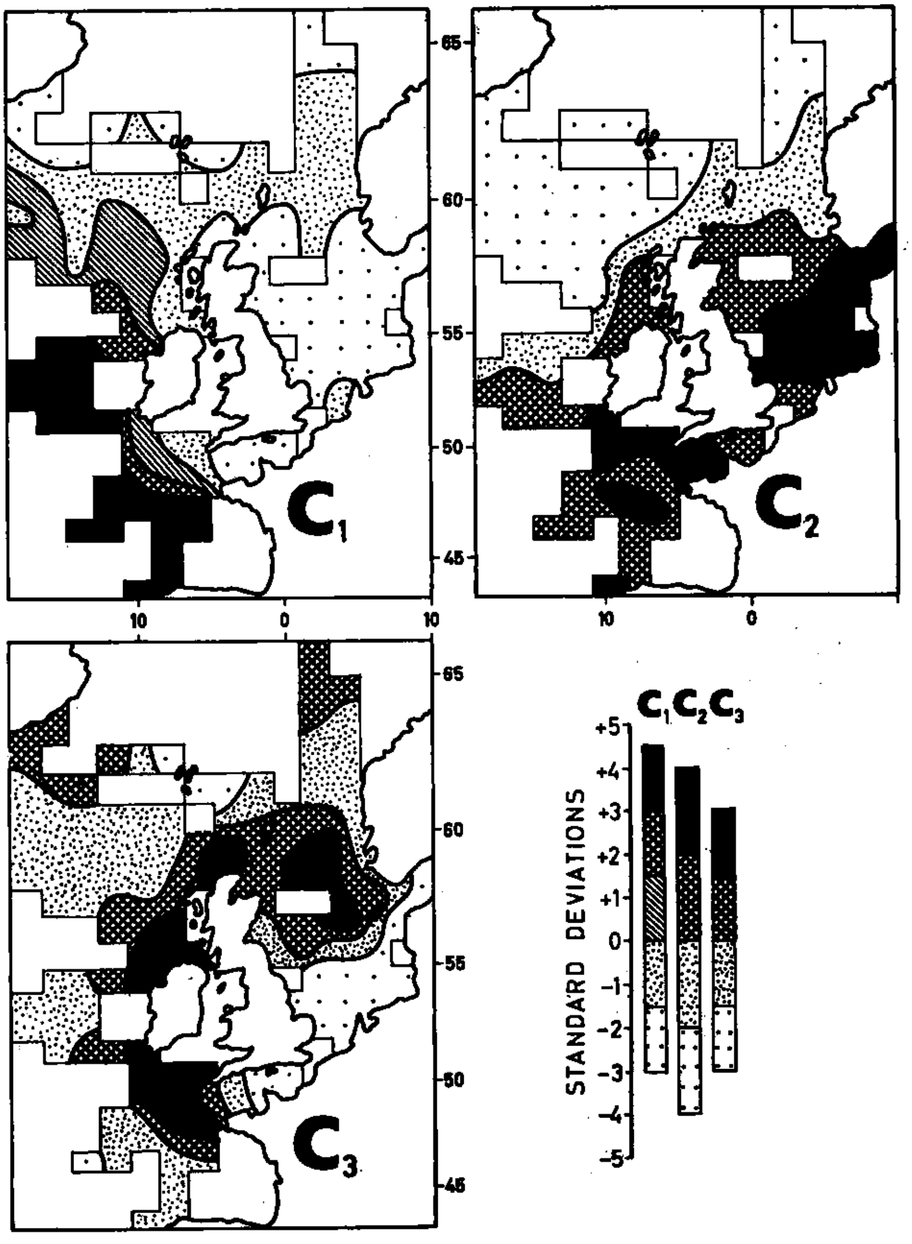


Fig. 2. Charts showing the distributions of the first three components (C_1, C_2 and C_3 of the geographical distributions of 22 zooplankton species. A key is given.

to the residual distributions after the removal of the variance associated with the first component, and so on. The details of the procedure are described by Kendall (1957). The components are row vectors with terms corresponding to the rectangles and the values may, therefore be plotted on charts and the distributions of the first three components are shown in Fig. 2. The sign of each component is arbitrary. The positive and negative forms of the first and second components and the positive form of the third component show sensible distributions which are easily related to those of individual species (Robinson, 1961; Colebrook *et al.* 1961; Vane, 1961).

The sum of the variances of these three components amounted to 65% of the total variance of the 22 species in the standardized data matrix. In the analysis of variance given in Table 2, the sources areas plus species-areas accounted for 30% of the total variability (excluding species) and had 352 degrees of freedom. The three components retain 65% of the 30% and have only 48 degrees of freedom. Clearly a considerable simplification in the representation of the variability has been achieved; the loss of information is, however, fairly high.

4. The Variability due to Months and Species-Months.

The mean seasonal variations in abundance of 18 species for the whole of the area shown in Fig. 1*b* were calculated by averaging by years and by standard large areas, thus eliminating the variability of those sources including years and areas. These seasonal variations were standardized (with zero mean and unit variance) eliminating the variability due to species. The resulting variables showed only the variability due to months and species-months, *i.e.* the pattern of variation of seasonal cycles of abundance of the different species.

The results of a correlation analysis of these variables are shown in Fig. 3*a* as a triangular matrix. The species are ranked along the principal diagonal of the matrix in such a way that as many as possible of the high positive correlations appear in the matrix as close as possible to the principal diagonal. This implies that species showing similar seasonal variations in abundance occur close together in the rank while species showing different variations occur further apart. The species in the matrix can be allocated to three overlapping groups each showing relatively high correlations within the group and lower values with the other groups. The means of the standardized seasonal variations of the species in each group were calculated and the resulting variables restandardized. They are shown in Fig. 3*b*; they account for about 86% of the total months and species-months variability. In the analysis of variance shown in Table 2 the sources months plus species-months accounted for 46.2% of the total variability and had 242 degrees of freedom. The seasonal variations shown in Fig. 3*b* retain 86% of the 46.2% and have only 33 degrees of freedom. Again a considerable simplification in the representation has been achieved and in this analysis the loss of variability is small.

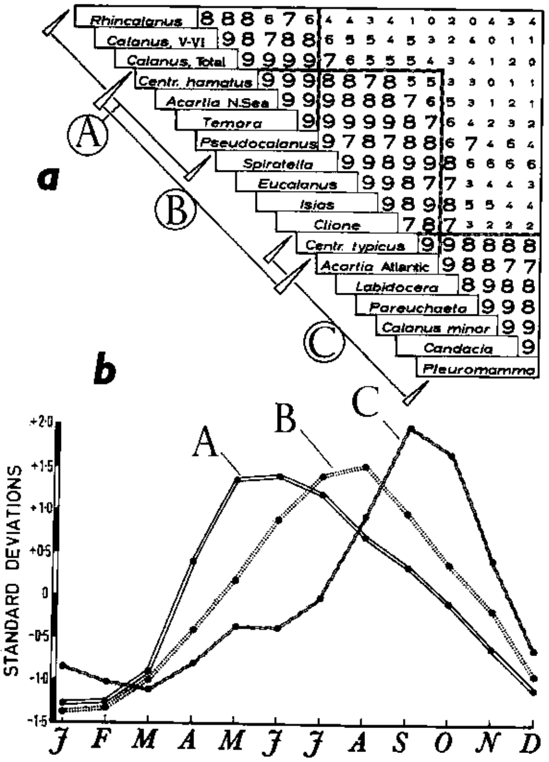


Fig. 3. (*a*) The correlation matrix of the mean seasonal cycles of 18 zooplankton species.
(*b*) Graphs of the standardised mean seasonal cycles of each of the groups of species shown in the matrix in *a*.

5. The Variability due to Months-Areas and Species-Months-Areas.

The variability included in these sources may be expressed as the geographical variation of the seasonal cycles of the different species. One of the main problems in finding methods of representing this variability is that many species do not occur throughout the area: in the analysis, the seasonal variations of 17 species in 17 standard areas (Fig. 1*b*) was included, but, because of the restricted distributions of many species, only 162 estimates of seasonal variation were available out of a possible total of 289. Because of this the more refined methods such as principal components analysis and correlation analysis could not be used, at least in the initial stages, and a relatively crude parametric representation of the variability was used and the loss of variability in the final representation cannot be estimated. Three parameters were used to represent the seasonal variations; mean abundance, timing (calculated by $T = \Sigma x_j\ j/\Sigma x_j$, where j is the number of the month, with January = 1, February = 2, etc., and x_j is the abundance in month j) and season duration (calculated by $L = \sqrt{[\Sigma x_j\ (j - T)^2\ /\Sigma x_j]}$): two examples of the relationships between the parameters and seasonal variations are given in Fig. 4. Trials

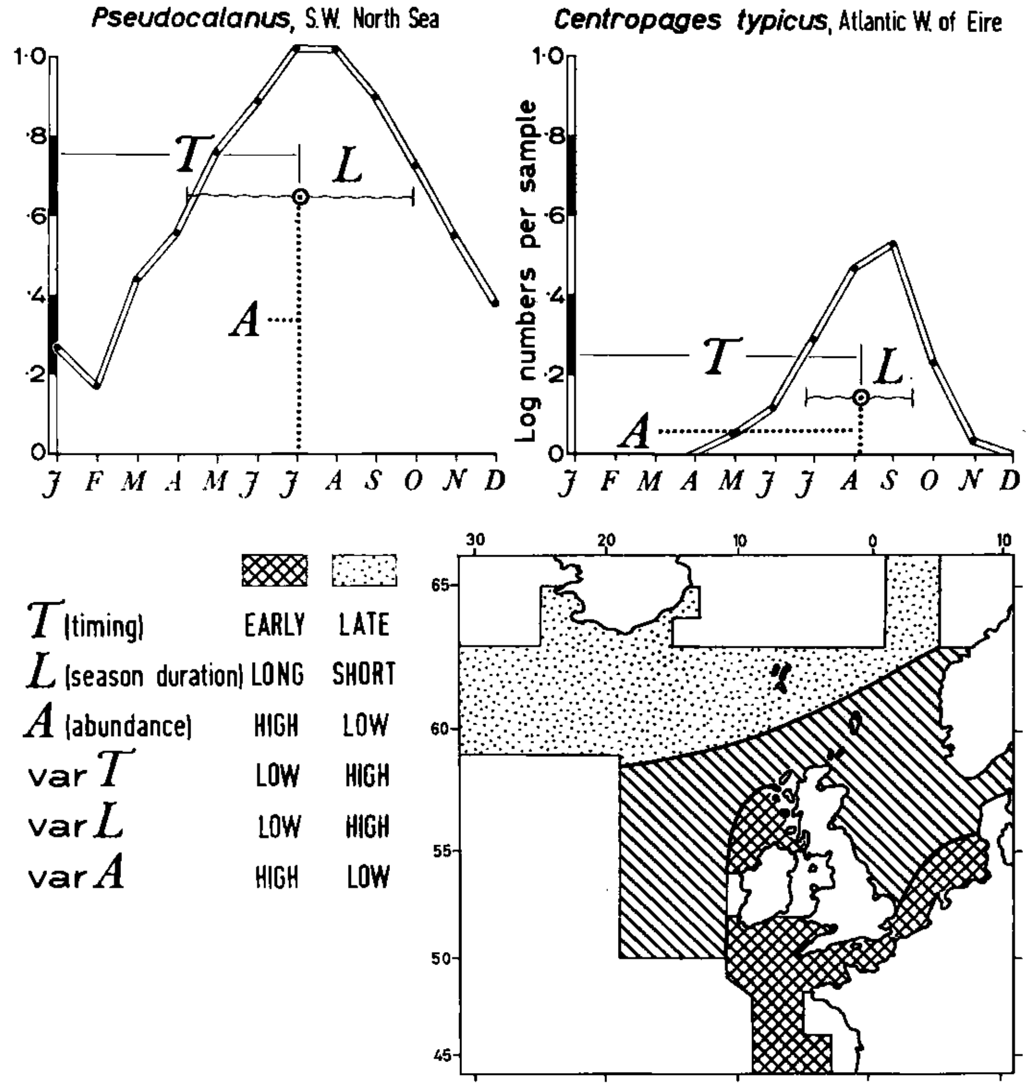


Fig. 4. The graphs show two examples of the values of the parameters *A*, *T* and *L* in relation to seasonal variations in abundance. The chart shows the distribution of the first component of the parameters and a key to the direction of variation of the parameters is given.

indicated that integration by species could be achieved by taking the mean and variance of these parameters. This was done for two groups of species. The first group contained only the common species for which nearly complete data were available; the few missing values were interpolated. The second group contained all the species included in the analysis and a system of weighting was devised to compensate to some extent for the missing values. At this stage a correlation analysis was carried out which showed that the two sets of estimates agreed quite well and that further integration of the parameters was possible. The first principal component of both sets of means and variances of the parameters was calculated and is shown in the chart in Fig. 4, together with a table indicating the direction of variation of the variables.

This chart is a representation of the variability in months-areas and species-months-areas, *i.e.* the geographical variation of the seasonal cycles of the different species; it has 16 degrees of freedom compared with a total of 1,451 in the original classification. The loss of variability is not known but is probably rather high.

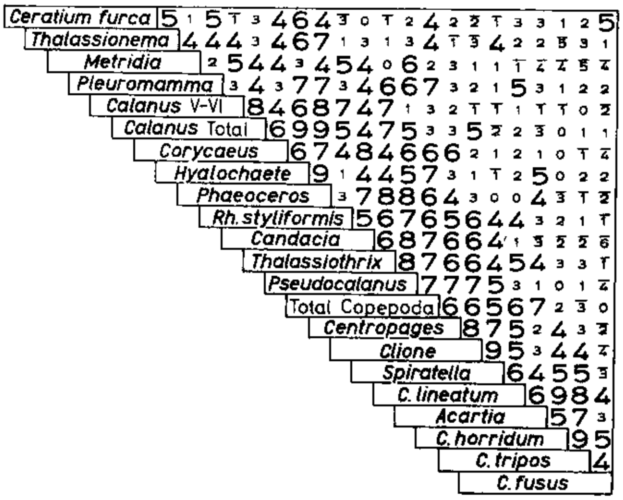


Fig. 5. The correlation matrix of the annual variations in abundance of 22 species or species groups in area *D5* (see Fig. 6).

6. The Variability due to Years and Species-Years.

In studying relationships with hydrography and fisheries, the annual variations in the plankton are, perhaps, the most interesting; they are, at the same time, the most difficult to interpret. For this reason only a preliminary study of the sources years and species-years has been carried out so far; the object being to assess the extent to which the fluctuations form coherent patterns.

Two series of correlation analyses have been carried out on data for the years 1948-1960, first on the annual fluctuations of the species in each of eight standard areas (Fig. 6) to find out whether there are any relationships between the annual fluctuation in abundance of different species, *i.e.* between-species within-area relationships; and second, on the annual fluctuations of each of 19 species in the different areas to find out whether some or all of the species showed geographical patterns of varying abundance, *i.e.* within-species between-area relationships. The correlation matrix for area *D5* is given in Fig. 5. This shows that there were clear relationships between the annual fluctuations of many of the species. In addition, there were marked similarities between the ranks of the species in the matrices for six out of the eight areas: the mean ranks of the species in the matrices were calculated and the results are given in Fig. 6*a*. This shows three clear groups of species. The order of the zooplankton species is very similar to the order in the correlation matrix of seasonal fluctuations (Fig. 3*a*) suggesting that species which occur at the same time of year tend to show similar annual fluctuations in abundance.

Fig. 6*b* shows two within-species between-area matrices which have been selected to illustrate different patterns of fluctuation. The matrix for *Calanus finmarchicus*, stages V and VI, shows two groups of areas showing similar fluctuations of abundance within the groups but with differences between the groups (a more detailed analysis of the geographical fluctuations of *Calanus* has been carried out by Colebrook, 1963). The matrix for *Ceratium horridum* shows high positive correlations between all the areas. The implication is that this species fluctuates in abundance from year to year in a similar manner over the entire area: several other species show the same result. This is clearly of great interest considering the wide range of environmental conditions found in the area, varying from oceanic conditions over water more than 2,000 m deep in the Atlantic to fairly extreme neritic conditions in the southern North Sea.

7. The Variability due to Areas-Years and Species-Areas-Years.

The variability included in these sources represents annual fluctuations in the geographical distributions of species, and the obvious first stage in the analysis would be to carry out a principal component analysis based on estimates of the distribution of species in the individual years. However, because of year to year variations in the pattern of sampling and of gaps in the information about a number of species, it would be very difficult to obtain a truly comparable series for analysis

One of the stages in the principal component analysis of areas and species areas gives a series of variables, known as vectors, with terms referring to species. One variable is associated with

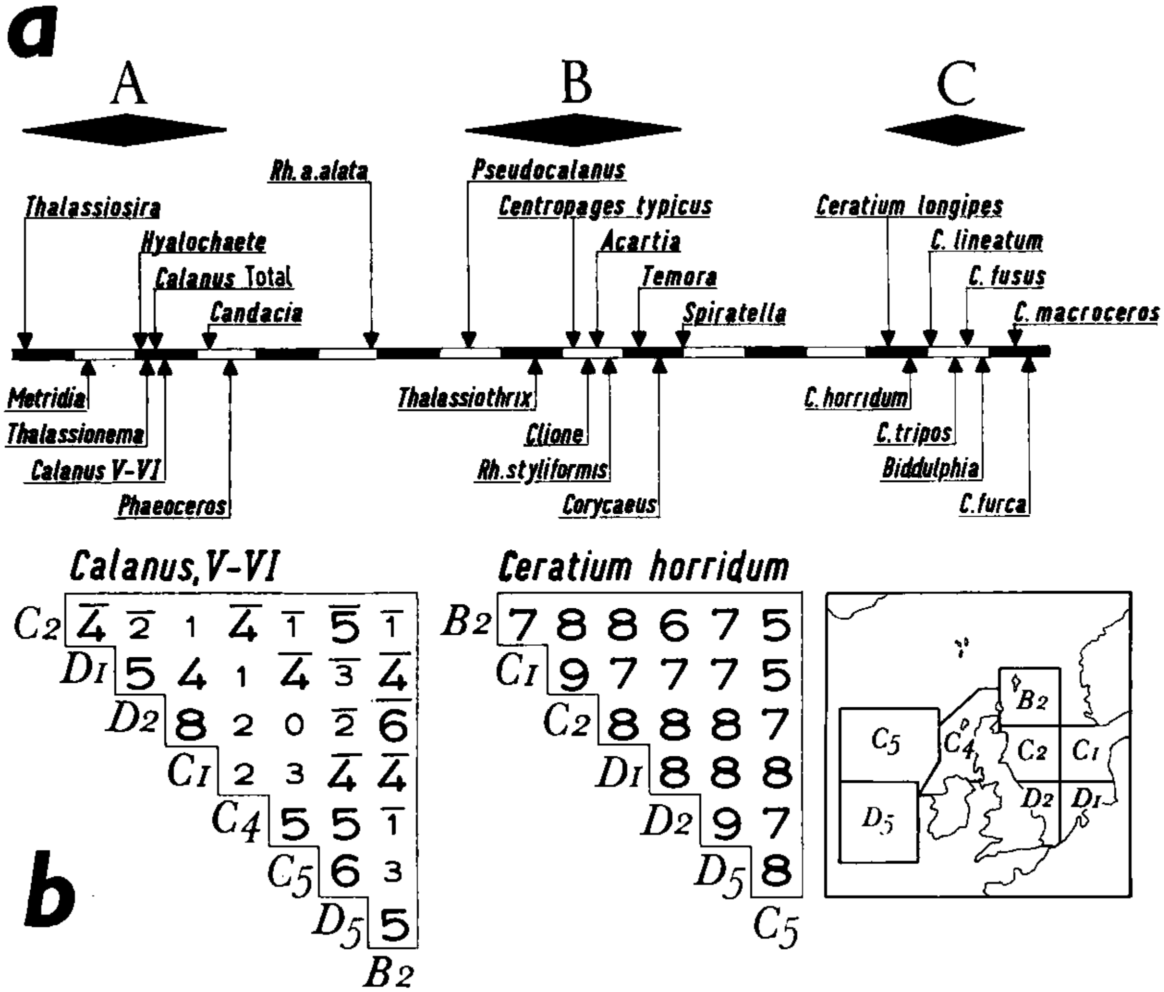


Fig. 6. (*a*) The mean ranks of the species in the correlation matrices of the annual fluctuations in abundance in each of the areas in the chart in *b*. The rank shows three clear groups of species indicated by the letters, A, B and C.

(*b*) Correlation matrices for the annual fluctuations in abundance of *Ceratium horridum* and *Calanus finmarchicus*, stages V-VI in the standard areas shown in the charts.

each component and is used in the derivation of the component. The vectors describe patterns of relationship between the species which are probably determined by variations between species in the response to environmental factors and there is no reason why these patterns should fluctuate from year to year to any great extent. And as a first approximation, these vectors, which were derived from the long-term mean distributions of the species, can be applied to the distributions of species in individual years to provide estimates of the components in individual years. This was done for the three components shown in Fig. 2 based on annual means for each species in the standard large areas (Fig. 1*b*).

The next problem is to find methods of extracting any systematic variation in the annual estimates of the components, and, as a first step the annual fluctuations of the variance of each component were calculated; they are shown in Fig. 7. Two features are immediately obvious. First, there is for each component a trend of increasing variance over the period from 1948 to 1962. A straight line was fitted to each variable using orthogonal polynomials and in each case the fit was significant, at the 1% level for C_1 and C_2 and at the 5% level for C_3.

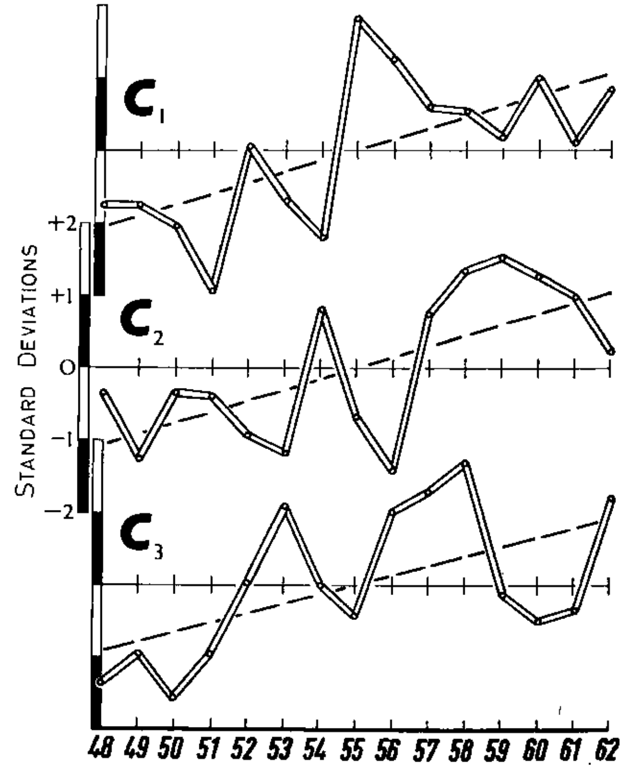


Fig. 7. Graphs showing the standardized annual fluctuations in the variance of annual estimates of the three components of geographical distribution shown in Fig. 2.

The second obvious feature was the relationship between the variance of C_3 in year n and C_2 in year $n + 1$. The correlation between the two variables in this manner was calculated and it was significant at the 1% level. To judge from these relationships the variables represent meaningful fluctuations in the geographical distribution of the plankton and they are in a form that can easily be compared with other estimates of annual variations.

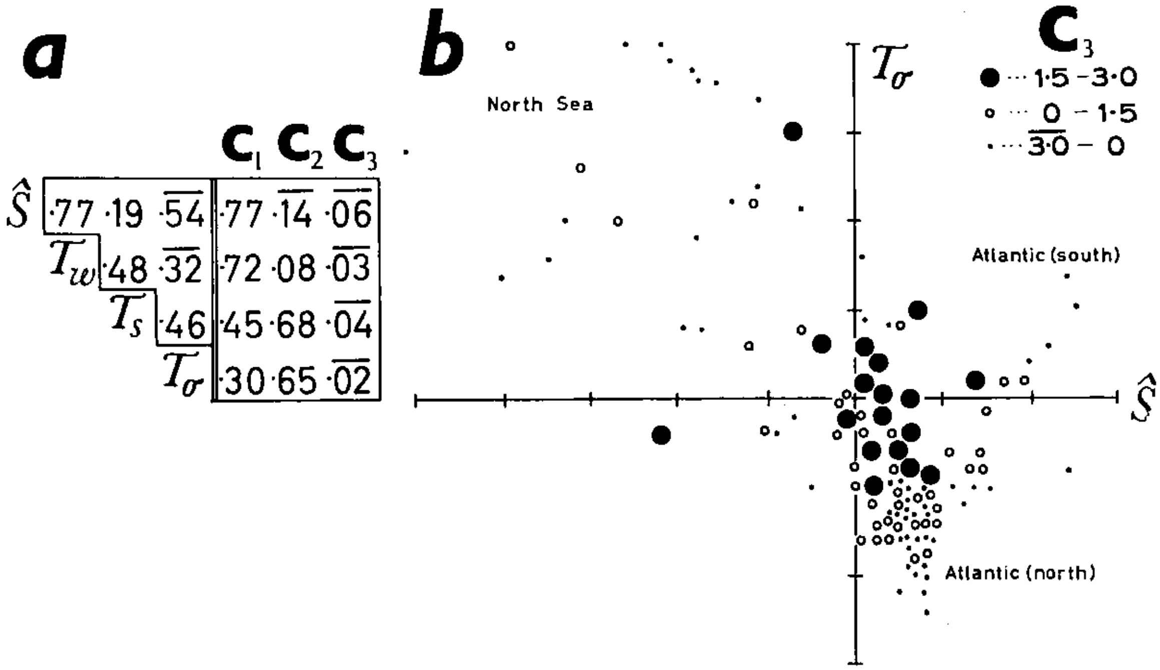
APPLICATIONS OF THE ANALYSES

The analysis of the Continuous Plankton Recorder survey is just beginning to reach the stage where it is profitable to carry out extensive studies of relationships with hydrography or with fisheries; the examination of annual variation, however, is far from complete. It is probably desirable to complete these analyses because it seems likely that internal evidence from relationships between the different variables will be of assistance in reducing the inevitable trial and error element in the search for related environmental factors. A certain amount of work has been done, however, on the distribution components shown in Fig. 2 and Williamson (1961 and in press) using techniques similar to those described here, has studied relationships between the plankton of the north-western North Sea and the hydrography and herring fishery in the same area.

Williamson derived a series of six components describing the annual fluctuations in abundance of 23 species or species groups in the plankton. The first component was correlated with an estimate of the annual fluctuations in the vertical mixing of the water in the spring. The second component was not related to any of the hydrographic or herring parameters that were tested. The third component was correlated with the mean temperature anomaly for March, April and May. The fourth component was correlated with a rank estimate of the strength of inflow of water from the Atlantic into the North Sea and also with a measure of the northerliness of southerliness of the herring stock. The fifth plankton component was correlated with the apparent mortality of the herring and the sixty component was not related to any of the hydrographic or herring parameters.

It must be stressed that these comparisons represent a very incomplete analysis of the situation; the information that was available about the hydrography, the herring fishery and the plankton did not permit a complete study of the variability. However, one feature in relation to the fishery is capable of a reasonable interpretation. In the vector associated with Williamson's fourth component of the plankton the two most abundant species, *Calanus finmarchicus* and *Spiratella retroversa*, both showed large values with the same sign. The correlation with the position of the herring stock was such that when these two species were common the stock was more southerly, when they were scarce the stock moved northwards. Further, the abundance of these zooplankton species may be related to the strength of inflow of Atlantic and coastal water into the northern North Sea.

Colebrook (in preparation) has described some possible relationships between hydrography and the components of plankton distributions shown in Fig. 2. Data for surface salinity and temperature were studied and Fig. 8*a* shows a matrix of correlations between the components and a number of temperature and salinity functions. The first component was correlated with the distribution of salinity $(\hat{S})$ and the distribution of temperature in the winter months (T_w). The second component was correlated with the distribution of temperature during the summer months (T_s) and also with the



	T_w	T_s	T_σ	C_1	C_2	C_3
$\hat{S}$	·77	·19	$\overline{{\cdot}54}$	·77	$\overline{{\cdot}14}$	$\overline{{\cdot}06}$
T_w		·48	$\overline{{\cdot}32}$	·72	·08	$\overline{{\cdot}03}$
T_s			·46	·45	·68	$\overline{{\cdot}04}$
T_σ				·30	·65	$\overline{{\cdot}02}$

Fig. 8 (*a*) The matrix of correlations between the first three components of geographical distribution, C_1 C_2 and C_3 (see Fig. 2) and the distributions of surface salinity ($\hat{S}$), winter temperature (T_w), summer temperature (T_s) and the standard deviation of the seasonal variations of temperature (T_σ).

(*b*) A scatter diagram of salinity ($\hat{S}$) against the standard deviation of temperature (T_σ). At each point the value of C_3 (Fig. 2) is shown by a symbol. A key to the symbols is given.

range of temperature (T_σ). The third component was not directly related to any of the temperature and salinity functions but Fig. 8*b* shows a form of T.S. diagram with the values of the third component superimposed; the high positive values of the component tend to fall in the centre of the plot. It seems likely that the first component was related to salinity, the second component to a complex function of temperature involving vertical stability and summer temperature and the third component might be related to the distribution of mixed oceanic and coastal water.

CONCLUDING REMARKS

It is obvious that the methods of analysis that have been described can result in considerable simplification in the representation of the variability of the standing stock of the plankton. Moreover, it seems that in some cases more has been achieved than the derivation of convenient mathematical artefacts. The three distribution components shown in Fig. 2 would appear to have identifiable separate existences and to be genuine "components" related to specific environmental factors. In other cases the final variables may be no more than convenient representations with no identifiable reality; probable examples are the three seasonal variations shown in Fig. 3*b*; there is little doubt, however, that these variables will be useful in investigating the factors which determine the variations in the timing of plankton organisms.

Plankton, hydrography and the pelagic stages of fish can be considered as subdivisions of a single ecosystem. It is obviously necessary to study this system as a whole in order to determine the interactions within the organisms and between the organisms and the abiotic environment. The methods of analysis that I have described in relation to the plankton could also be applied to hydrographical and fisheries data and they offer at least a partial solution to the problems of analysing the complex patterns of variation within the system and of studying the interactions and relationships between its various parts.

REFERENCES

COLEBROOK, J.M. 1960. Continuous Plankton Records: methods of analysis, *Bull. Mar. Ecol.*, 5: 51-64.

1963. Continuous Plankton Records: annual variations in the abundance of *Calanus finmarchicus*, 1948-1959. *Bull. Mar. Ecol.*, 6: 17-30.

COLEBROOK, J.M., D.E. JOHN, and W.W. BROWN, 1961. Continuous Plankton Records, 1948-1956: contributions towards a plankton atlas of the north-eastern Atlantic and the North Sea. Part II: Copepoda. *Bull. Mar. Ecol.*, 5: 90-97.

COLEBROOK, J.M. and G.A. ROBINSON, 1963. Ecological differentiation in the plankton of the waters around the British Isles. *Systematics Assoc. Publ.*, No. 5: 157-169.

GLOVER, R.S. 1957. An ecological survey of the drift-net herring fishery off the north-east coast of Scotland. Part II: the planktonic environment of the herring. *Bull. Mar. Ecol.*, 5: 1-43.

1961. Biogeographical boundaries: the shapes of distributions. *Int. Oceanogr. Congr.*, 1959: 201-208.

1962. The Continuous Plankton Recorder. *Rapp. Cons. Explor. Mer*, 153: 8-15.

GLOVER, R.S., G.A. COOPER, and D.C.T. FORSYTH, 1961. An ecological survey of a Scottish herring fishery. Part III: geographical and ecological groups in the plankton. *Bull. Mar. Ecol.*, 5: 195-205.

HARDY, A.C. 1939. Ecological investigations with the continuous plankton recorder: object, plan and methods. *Hull. Bull. Mar. Ecol.*, 1: 1-57.

KENDALL, M.G. 1957. A course in multivariate analysis. London. Charles Griffin & Co. Ltd. 185 p.

RAE, K.M. 1952. Continuous Plankton Records: explanation and methods, 1946-1948. *Hull. Bull. Mar. Ecol.*, 3: 135-155.

ROBINSON, G.A. 1961. Continuous Plankton Records, 1948-1956: contributions towards a plankton atlas of the north-eastern Atlantic and the North Sea. Part I: phytoplankton. *Bull. Mar. Ecol.*, 5: 81-89.

VANE, F.R. 1961. Continuous Plankton Records, 1948-1956: contributions towards a plankton atlas of the north-eastern Atlantic and the North Sea. Part III Gastropoda. *Bull. Mar. Ecol.*, 5: 98-101.

WILLIAMSON, M.H., 1961. An ecological survey of a Scottish herring fishery. Part IV: changes in the plankton during the period 1949-1959. *Bull. Mar. Ecol.*, 5: 207-229.

In press. The relation of plankton to some parameters of the herring population of the north-western North Sea. *Rapp. Cons. Explor. Mer.*

B-3

A PRELIMINARY STUDY OF *SEBASTES* LARVAE IN RELATION TO THE PLANKTONIC ENVIRONMENT OF THE IRMINGER SEA

By

V. Bainbridge[1]

ABSTRACT

The diet of young *Sebastes* from the Irminger Sea was investigated using material collected during the Continuous Plankton Recorder Survey. Individuals smaller than 10 mm were found to be feeding principally on *Calanus* eggs, *Spiratella* larvae being virtually the only other organisms eaten. *Calanus finmarchicus* is the dominant copepod in the Irminger Sea where it constitutes over 70% of the total numbers of zooplankton organisms present in Recorder samples. The extrusion of *Sebastes* larvae occurs during April and May which coincides with the main spawning period of *Calanus*. During May, when maximum numbers of both young *Sebastes* and spawning *Calanus* occur, a positive correlation exists between the spatial distribution of the numbers of fish larvae and the numbers of *Calanus* stages V and VI.

This might be accounted for if the survival of young *Sebastes* was largely dependent on the availability of food, *i.e.* the numbers of *Calanus* eggs, but direct evidence is lacking and other factors may be involved.

INTRODUCTION

The distribution of young *Sebastes* in relation to the planktonic environment was discussed by several contributors to the ICES/ICNAF Redfish Symposium of 1959[2]. Dietrich, *et al* (1961) described the results of a series of cruises in the Irminger Sea during 1955 and 1958. Highest numbers of *Sebastes* larvae were found in the area of the Reykjanes Ridge, a distribution which appeared to be associated with high turbidity, due mainly to zooplankton and detritus. A correlation with high numbers of the trachymedusan *Aglantha digitalis* during May and June was also noted. Hansen and Anderson (1961) investigated the distribution of *Sebastes* larvae from 1947 to 1958 at 21 standard plankton stations on a transect worked regularly along 62°N lat from the Faroes to East Greenland. They suggested that the considerable annual fluctuations in numbers of larvae present might be related to the food available at the time of extrusion. Einarsson (1960) considered relationships between *Sebastes* fry and zooplankton in Icelandic waters and adjacent seas. He made some preliminary observations on the food of the young fish at two stations and noted a preference for food organisms of about 150μ in diameter. *Spiratella* larvae, together with copepod and other crustacean eggs, were found to be the main items in the dietary of specimens less than 25 mm in length. Larger food organisms, such as the copepodite stages of copepods, were found in the stomachs of young *Sebastes* greater than 25 mm in length.

An attempt is now being made to extend these environmental studies using material from the Continuous Plankton Recorder Survey and a preliminary report is presented in this contribution. The work includes some observations on the food of young *Sebastes* in relation to the planktonic environment which may help towards an interpretation of their distribution and fluctuations in abundance. Charts illustrating the distributions of these larvae are given by Henderson (this symposium) who also discusses the problem of their specific identity.

Recent accounts of the Plankton Recorder and of the scope and methods of the survey operated from the Oceanographic Laboratory, Edinburgh, are given by Colebrook, *et al* (1961) and Glover (1962). The Recorder, which is towed by merchant ships and Ocean Weather Ships, takes a continuous sample of plankton at a depth of 10 m. The plankton is collected on silk with a mesh-aperature of 230–250μ.

THE DIET OF YOUNG *SEBASTES*

A detailed study has been made of the food of young *Sebastes* from the Irminger Sea during May, the month in which largest numbers were usually taken by the Recorder. Alternate "10 mile" samples collected during May of the years 1959 to 1962 within the standard sub-areas B6, B7 and C7 shown on Fig. 1 have been examined and an analysis made of the gut contents of all undamaged larvae. A total of 193 *Sebastes* ranging in length from 6 to 10 mm were dissected and the results are given in Table 1.

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[2] Spec. Publ. int. Comm. Northw. Atlant. Fish., No. 3, 1961.

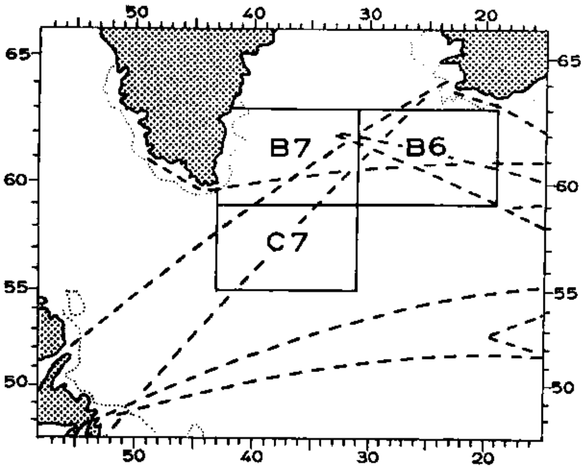


Fig. 1. Area used for the study of *Sebastes-Calanus* relationships. It comprises 3 of the standard sub-areas (B6, B7 and C7) of the Plankton Recorder survey (Glover, 1962). Recorder routes are shown as broken lines.

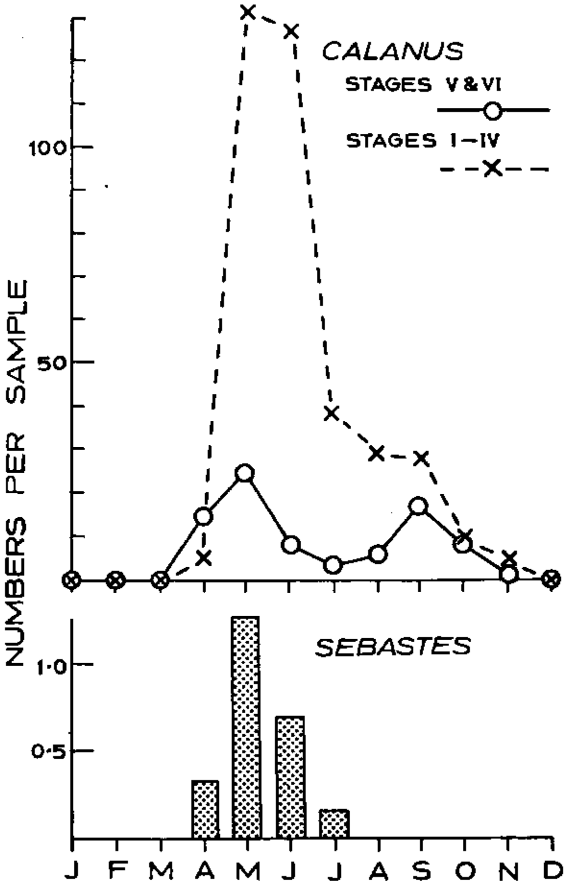
The young fish were feeding on *Calanus* eggs (140-160μ diameter) and *Spiratella* larvae (shells 100-150μ across), the only other organisms present being two specimens of the diatom *Coscinodiscus* sp. (100μ diameter). Numbers of *Calanus* eggs in the guts showed a marked diurnal variation; during the period between midday and sunset there was an average of 8.3 eggs per gut compared with an average of 1.6 between midnight and sunrise. The eggs were at various stages of digestion and numerous egg membranes were also present. This extremely restricted diet should be considered in relation to the composition of the zooplankton in the Irminger Sea. Table 2 gives the average numbers per "10 mile" sample (equivalent to 3m^3 of water filtered) of the various species and groups within the sub-areas B6, B7 and C7 during May. There was an overwhelming predominance of the various stages of *Calanus finmarchicus* while the small copepods and Cladocera, which are important members of the plankton of coastal waters as well as many oceanic areas covered by the Recorder survey, were very poorly represented. Apart from

TABLE 1. THE GUT CONTENTS OF YOUNG *SEBASTES* LESS THAN 10 MM IN LENGTH FROM RECORDER SAMPLES TAKEN DURING THE MONTH OF MAY.

	1959	1960	1961	1962	May of all four years
Percentage containing food	73%	-	68%	75%	72%
Number of larvae examined	45	2	65	83	195
Total *Calanus* eggs	136	4	384	510	1034
Total *Spiratella* larvae	2	5	130	218	355
Other organisms (*Coscinodiscus* sp.)	-	-	1	1	2

TABLE 2. THE COMPOSITION OF THE PLANKTON TO A DEPTH OF 10m DURING MAY: MEAN NUMBERS PER "10 MILE" SAMPLE (EQUIVALENT TO 3m^3 OF WATER FILTERED) WITHIN THE SUB-AREAS B6, B7 AND C7.

	1959	1960	1961	1962	May of all four years
Total *Calanus* (all stages)	101	65	127	325	154
Calanus stages V and VI	22	7	43	47	30
Copepoda other than *Calanus*	28	20	4	28	20
Spiratella (mainly *S. retroversa*)	15	10	8	21	13
Euphausiids (mainly *Thysanoessa longicaudata*)	2	1	5	10	4
Larvacea	2	10	7	1	5
Other zooplankton	1	<1	<1	<1	<1
No. of samples	68	38	90	83	279



ig. 2. Seasonal fluctuations in the numbers of *Calanus* and young *Sebastes* at a depth of 10 m in the Irminger Sea. Average numbers per sample have been calculated using all data collected from 1957 to 1962 within the three standard sub-areas shown in Fig. 1.

Calanus, the commonest copepods were *Oithona* spp. and *Euchaeta Norvegica*, two genera in which the eggs are carried in ovisacs. Of the other groups, only the gastropods *Spiratella* spp. and the euphausiid *Thysanoessa longicaudata* were present in appreciable numbers. It has not been possible to trace a reference to the egg size of *T. longicaudata* but both *T. inermis* and *T. raschii*, two species in which the early furcilias are of similar size to *T. longicaudata*, are known to have egg diameters exceeding 400μ (Einarsson, 1945), much larger than the selected particle size suggested by Einarsson (1960).

The monotonous diet of *Sebastes* larvae during the early weeks after extrusion must therefore be at least partly due to the limited choice of food organisms available, the early stages of *Calanus* and *Spiratella* being the only abundant organisms to fall within a suitable size range.

The apparent absence of nauplii in the diet is noteworthy but I have found some in the gut contents of early *Sebastes* larvae from stramin net samples taken off the east coast of Greenland during the Danish NORWESTLANT cruises. *Calanus* nauplii are present mainly in the top 50 m (Marshall and Orr, 1955), and were, in fact, frequently present in Recorder samples from the Irminger Sea during May, but like the eggs, they are too small to be samples quantitatively by silk with a mesh-aperture of 230-250μ. It is possible therefore that, in addition to size, other factors such as mobility may also play a part in determining the relative vulnerability of prey. It may be relevant that the *Spiratella* larvae present in the gut contents were veligers with cilia as the only organs of locomotion. *S. retroversa*, the common species in the Irminger Sea, does not develop swimming 'wings' until the shell measures about 300μ across (Lebour, 1932).

Although this paper is concerned primarily with *Sebastes* larvae during the first weeks after xtrusion it should be mentioned here that larvae of 15 mm or more in length which occur in the ecorder samples during June and July have a more varied diet including the calyptopsis and furcilia tages of euphausiids as well as the copepodites and adults of *Calanus*.

THE SEASONAL DISTRIBUTION OF YOUNG *SEBASTES* AND *CALANUS*.

Calanus eggs are clearly the principal food item of redfish larvae during the first weeks after xtrusion so it is interesting to consider the seasonal distribution of the young fish in relation ɔ the breeding of *Calanus*. Figure 2 shows the average monthly distributions of *Calanus* and young *ebastes* in the Irminger Sea estimated from data collected over the period 1958 to 1962. *Calanus* tages V and VI, which were virtually absent at the 10 m level during the winter months, showed a ig increase from March to April reaching a maximum in May, while highest numbers of copepodite tages I-IV were found during May and June.

These observations may be interpreted by a consideration of the findings of Østvedt (1955) who tudied the vertical distribution of *Calanus finmarchicus* at Weather Ship M in the Norwegian Sea. e found that the overwintering stock of *Calanus* consisted chiefly of stages IV and V with the maɔrity of the population below a depth of 600 m and that an ascent to the surface occurred during

April to May. Moulting from stage V to stage VI occurred both during or after the migration and was immediately followed by the spring spawning. Henderson (1961) found that newly extruded *Sebastes* were present in Recorder samples from early April to the end of May. From Fig. 2 it can be deduced that it is during these two months that highest numbers of spawning *Calanus* are present in the surface layers. During May both maximum numbers of *Calanus* V and VI and young *Sebastes* were present.

THE SPATIAL DISTRIBUTION OF YOUNG *SEBASTES* AND *CALANUS*

During the analysis of Recorder samples it was noted that during May samples with high numbers of young *Sebastes* were frequently those with high numbers of *Calanus* stages V and VI. In Table 3, the samples have been divided into two groups, those with more and those with less than 50 *Calanus* stages V and VI. The higher average numbers of redfish larvae were found in samples with more than 50 *Calanus* V and VI in every year except 1958 when, as in 1960, only a few samples contained young *Sebastes*. The young fish were too scarce to allow a similar comparison for April while, during June, distributions are likely to be confused by the effects of dispersal.

TABLE 3. AVERAGE NUMBERS OF YOUNG *SEBASTES* PER POSITIVE RECORDER SAMPLE IN MAY, GROUPED ACCORDING TO WHETHER THERE WERE MANY OR FEW *CALANUS* STAGES V AND VI IN THE SAMPLES. THE NUMBERS OF SAMPLES ARE GIVEN IN PARENTHESES.

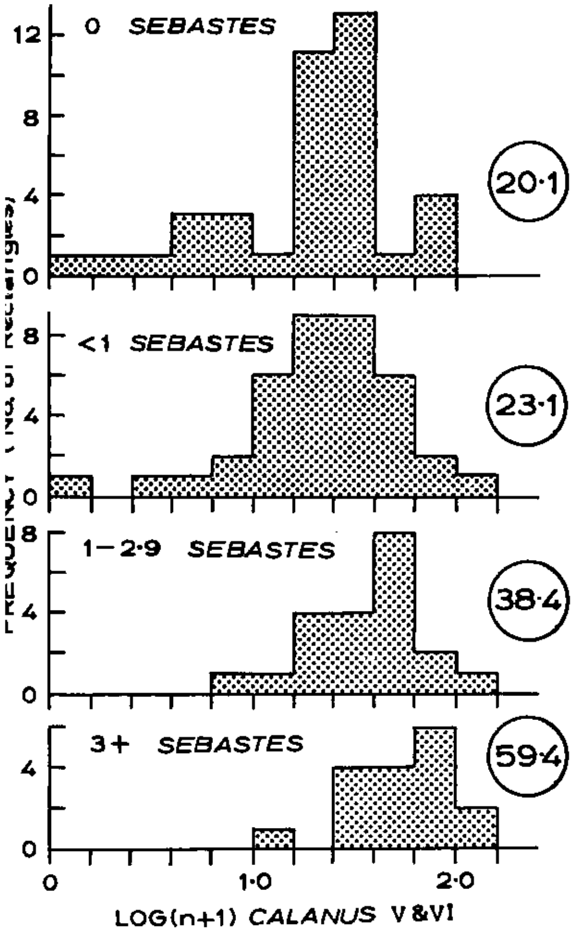
Year	Samples with 50 *Calanus* V & VI		Samples with 50 *Calanus* V & VI	
1957	2.3	(13)	1.9	(17)
1958	1.5	(2)	1.5	(2)
1959	4.7	(8)	2.3	(17)
1960	3.0	(1)	1.0	(2)
1961	5.4	(25)	3.1	(28)
1962	4.9	(17)	3.7	(27)
All years combined	4.5	(64)	2.9	(85)

The two variables can also be compared in each of the standard statistical rectangles used to present the results of the Recorder survey (*e.g.* Colebrook, *et al.*, 1961). These are the small rectangles, 1° lat 2° long, illustrated by Henderson (this symposium). Figure 3 shows the frequency of occurrence of sampled rectangles in relation to the logarithm of the mean number of *Calanus* stages V and VI per sample. The histograms are arranged in four groups according to the mean number of young *Sebastes* per sample (0,<1, 1-2.9,3+). All the rectangles sampled each May from 1957 to 1962 over the area of the Irminger Sea (*i.e.* sub-areas B6, B7 and C7) have been included. The frequency distributions show that there was a clear tendency, during the month of May over the six years, for high numbers of *Sebastes* young to be associated with high numbers of *Calanus* V and VI. An analysis of variance has shown that there is a significant difference between the groups of rectangles with 0 and <1 young *Sebastes* and the group with 3+ *Sebastes* ($P < 0.001$). The difference between the groups with 0 and <1 and the group with 1-2.9 young *Sebastes* is significant at a lower level ($P < 0.05$). The analysis of variance does not take into account the possible effects of interaction between adjacent rectangles.

The correlation raises a number of questions since the combination of data from several years conceals the effects of annual and spatial fluctuations. However, the relationship is not merely due to highest numbers of *Sebastes* larvae being extruded in exactly the same area of the Irminger Sea each year which happens also to be an area of high *Calanus* production. If, for example, the six year mean number per sample of *Sebastes* larvae and *Calanus* V and VI during May in each rectangle is calculated, no correlation between the two variables is evident.

Diurnal variations are difficult to assess but would appear to have little, if any, effect on the relationship. During May less than one-third of all samples are taken at night in this sea area and the day/night ratio of the average numbers of *Calanus* V and VI per sample was only 1:1.3.

There would seem to be two possible explanations of the apparent positive relationship between young *Sebastes* and *Calanus*. The main concentrations of adult 'spawning' redfish in the Irminger Sea



'ig. 3. Histograms showing the frequency of occurrence of sampled rectangles during May in relation to the logarithm (n+1) of the mean number of *Calanus* stages V and VI per sample. The data are grouped according to the mean number of young *Sebastes* per sample. All rectangles sampled each May from 1957 to 1962 within the three standard subareas of Fig. 1 have been included. The mean numbers of *Calanus* per sample for the four groups of histograms are shown in circles.

may be directly or indirectly related to the standing stock of *Calanus* V and VI during May. Alternatively, the survival of young might be related to the numbers of *Calanus* stages V and VI present and, since the food of *Sebastes* during the first weeks after extrusion consists mainly of *Calanus* eggs, this latter hypothesis merits further investigation.

CONCLUDING REMARKS

Sebastes constitutes about 90% of the total stock of young fish in the Irminger Sea (Einarsson, 1960, Henderson, 1961) and 'spawning' may take place in almost the entire region although the intensity of extrusion is variable (Magnusson, 1962). The monotonous nature of the surface zooplankton in this vast sea area, with the great numerical predominance of *Calanus*, and the remarkable uniformity of the diet of *Sebastes* young, mainly *Calanus* eggs, have been established. It is possible therefore, as Einarsson (1960) has suggested, that the ecological relationships between young *Sebastes* and the other plankton organisms may be more easily elucidated than the undoubtedly complex relationships between the fish larvae and plankton of coastal waters.

Further work is in progress and it is hoped to determine whether or not annual variations in the numbers of young *Sebastes* are related to the timing and intensity of the spring spawning of *Calanus*.

ACKNOWLEDGEMENTS

I wish to thank Dr G.T.D. Henderson for allowing me to use his data on the distribution of young *Sebastes*. This work was assisted by a grant from H.M. Treasury through the Development Fund and by Contract N62558-2834 between the Office of Naval Research, Department of the United States Navy, and the Scottish Marine Biological Association.

REFERENCES

COLEBROOK, J.M., R.S. GLOVER and G.A. ROBINSON. 1961. Continuous Plankton Records: Contributions towards a Plankton Atlas of the north-eastern Atlantic and the North Sea: General Introduction. *Bull. Mar. Ecol.*, 5 (42): 67-80.

DIETRICH, G., H. AURICH, and A. KOTTHAUS. 1961. On the relationships between distribution of redfish and redfish larvae and the hydrographical conditions in the Irminger Sea. *Rapp. Cons. Explor. Mer.*, 150: 124-139.

EINARSSON, H. 1945. Euphausiacea, 1. Northern Atlantic Species. *Dana Rep.*, (27): 1-191.

1960. The fry of *Sebastes* in Icelandic waters and adjacent seas. *Rit Fiskid.*, 2(7): 3-64.

GLOVER, R.S. 1962. The Continuous Plankton Recorder. *Rapp. Cons. Explor. Mer.*, 153: 8-15.

HANSEN, V.K. and K.P. ANDERSEN. 1961. Recent Danish investigations on the distribution of the larvae of *Sebastes marinus* in the North Atlantic. *Rapp. Cons. Explor. Mer.*, 150: 201-215.

HENDERSON, G.T.D. 1961. Continuous Plankton Records: The distribution of young *Sebastes marinus* (L). *Bull. Mar. Ecol.*, 5 (46): 173-193.

1964. Redfish larvae in the North Atlantic. *This symposium Contribution No. B-4.*

LEBOUR, M.V. 1932. *Limacina retroversa* in Plymouth Waters. *J. Mar. biol. Ass. U.K.*, 18: 123-130.

MAGNUSSON, J. 1962. Redfish larvae in the Irminger Sea in May 1961. ICES. C.M. 1962, (90): 1-5, illus.

MARSHALL, S.M. and A.P. ORR. 1955. Biology of a marine copepod. *Calanus finmarchicus* (Gunn.). Edinburgh. Oliver and Boyd Ltd. vii + 188p.

ØSTVEDT, O.J. 1955. Zooplankton investigations from Weather Ship M in the Norwegian Sea. *Hvalråd. Skr.*, (40): 1-93.

B-4

REDFISH LARVAE IN THE NORTH ATLANTIC

By

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ABSTRACT

The distribution of young stages of *Sebastes* in the North Atlantic between Iceland and Newfoundland in the months of April and July is described and illustrated. The results suggest the possibility that the young stages may be found in four more or less separate localities. The younger appear to be more abundant in some restricted parts of the temperature range, at the surface and at 200 m, within which they have been found. The specific identity of these young stages is discussed in relation to the catches of adult *mentella-type* at Ocean Weather Station Alfa.

INTRODUCTION

During the course of the regular survey of the North Sea and North Atlantic with Continuous Plankton on the Recorders, the young stages of the redfish (*Sebastes*) were encountered during the months of April and July in certain areas of the North Atlantic. The preliminary account of their distribution has been given by Henderson (1961, *a, b*).

Although the sampling is limited to the single depth of 10 m and the individual samples are small (representing the plankton in only 3 m^3 for each 10 nautical miles of tow) the repetition of sampling at regular intervals makes it possible to study annual and seasonal changes in distribution and abundance over a very wide area.

The first account of the distributions of these young *Sebastes* (Henderson, 1961 *a, b*) was based on the material available up to 1960. Since then the scope of the Recorder survey has been widened by the extension of existing routes and the introduction of additional ones; our knowledge of the distribution, therefore, is now much more detailed than that shown in the earlier report, and the charts in Fig. 1 are provided for convenient reference. This work was assisted by a grant from H.M. Treasury through the Development Fund and by Contract N62558-2834 between the Office of Naval Research, United States Department of Navy and the Scottish Marine Biological Association.

DISTRIBUTION OF THE YOUNG STAGES

The results of the Recorder sampling are expressed as the mean numbers of *Sebastes*, per 10 m^3 sampled, in statistical rectangles measuring 1° of lat x 2° of long.

The average distributions of the young stages of *Sebastes* are shown in Fig. 1; each of the charts for the months April to July is based on the combination of all Recorder sampling, in those months, from 1955 to April 1963. Kotthaus (this symposium) discusses the distribution of young *Sebastes* in the Atlantic from April to June 1961, and suggests that there are three main areas of abundance. He defines these and believes that they were discernible in the charts shown in the earlier account of the Recorder work (Henderson, 1961 *b*, Fig. 3) but is not certain of the separation south of Iceland which might be due to the combination of data. Because the charts in Fig. 1 represent combined results from a number of years, and because of the limitations imposed by the geographical distribution of the available sampling, the Recorder data are not yet considered adequate to demonstrate these separations with certainty. For the purposes of this paper, however, it is convenient to divide the distributions into four groups (a,b,c and d) which are similar to those of Kotthaus, although it seems possible that one of his areas may be divisible into two, (a) over the Reykjanes Ridge and south of Iceland and (b) south to southeast of Greenland.

In April the young were found in small to moderate numbers (mean length 7.3 mm). They appeared

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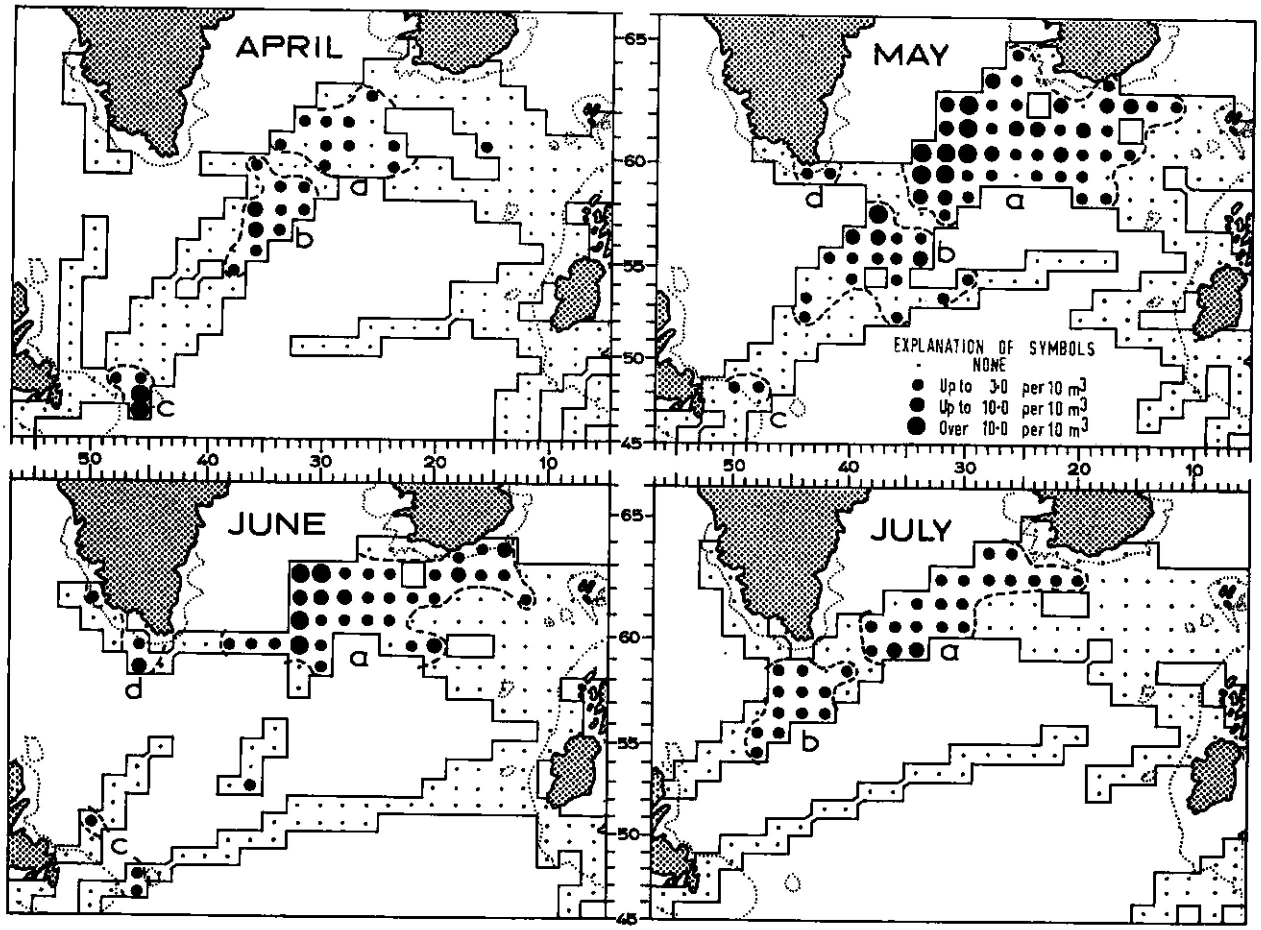


Fig. 1. Charts showing the average distribution of young stages of *Sebastes* (excluding *S. viviparus*) in the months April to July. The charts are composite ones, including all the information from 1955 to April 1963. The symbols indicate the mean numbers per 10 m^3 for all sampling in each statistical rectangle 1° of latitude by 2° of longitude. The broken lines and lower case letters a to d on the charts indicate the localities discussed in the text.

to be present in three more or less separated localities; (a) on both sides of the Reykjanes Ridge and south of Iceland, but mainly to the north of lat 59° N, with the larger numbers between 60° and 62° N lat; (b) in an area southeast of Cape Farewell (Greenland) over the mid-Atlantic Ridge between the lat of 54° and 59° N; and (c) between the northeast edge of the Newfoundland Banks and Flemish Cap. In May (mean length 8.1 mm) the pattern was generally similar but the distributions over the Reykjanes Ridge and southeast of Greenland (a and b above) have expanded in area and greatly in abundance while that near Flemish Cap (c) has diminished. There is a suggestion of a possible fourth concentration of young (d), close to the southern tip of Greenland.

In June populations of young redfish (mean length 11.4 mm) were present in three of the localities described above (a, c and d). The numbers were generally lower than those found in May, and included only a few recently extruded individuals. In July (mean size 20.0 mm) relatively small numbers of young were taken, more or less within the localities defined above as a and b. However, in June and July the limits of separate concentrations may be more difficult to define due to drift and dispersal of the now more active young stages.

The separation of these oceanic stocks of young *Sebastes* into different localities, outlined above, must be considered as tentative as it is dependent on the sampling available since 1955. Regular sampling west of 35°W. long has only been available over the last one to three years; there have been some unfortunate gaps in June; and in July one of the routes alters when the ships change to the Belle Isle track and so traverses an area south of Cape Farewell not sampled in the preceding months. It has not, therefore, been possible to establish any connection between the localities b and d which might be considered likely from an inspection of the May and July charts in Fig. 1.

HYDROGRAPHIC ASSOCIATIONS

Tåning (1949) suggested that the 'spawning' (or extrusion of young) of the large redfish (*Sebastes*) required temperatures of between 3° and 8.5°C in depths of about 300-500 m, with salinities of from 34.8 to 35.3 °/oo. Einarsson (1960 pp. 16-20) discussed the temperature requirements in relation to fluctuations observed in the numbers of young stages, and suggested the possibility of a narrower temperature range, from 4° to 6°C, at a deeper 'spawning' level of 500-800 m. He considered that this hypothesis resulted in better agreement with the distributions of young stages. Kotthaus (this symposium) expresses support for Einarsson's suggestion, pointing out that so far no 'spawning' redfish has been caught in fishing trials of any kind down to a depth of 450 m (see also below - section on adults), and that hydrographic conditions favouring this hypothesis may be found over quite large areas along the Mid-Atlantic and Reykjanes Ridges.

The Continuous Plankton Recorder survey does not provide contemporaneous observations of temperature or salinity, so that direct comparisons between the Recorder catches of young *Sebastes* and the immediate hydrographic environment cannot be made. Several attempts have been made to compare the mean numbers of young in our statistical rectangles for the individual months in various years with contemporary data for surface temperature, but so far without satisfactory results because there were too few occasions on which *Sebastes* and temperature data were available for the same rectangles, and very little temperature data for greater depths.

In the earlier account (Henderson 1961 *a*, p. 188), it was noted that the long term mean surface salinities based on observations extending over more than 50 years (Krauss 1958), were within the limits postulated by Tåning (1949) - 34.8 to 35.3 o/oo - in all areas where young were taken except for the patch off the Newfoundland Banks, where the salinity was about 34.0 o/oo. The additional material obtained since then confirms this observation, and adds only the fact that the catches close around Cape Farewell were also taken where the surface salinity was about 34.0 o/oo.

1. Associations with Surface Temperature.

Henderson (1961*a*, p. 187) noted "....some correspondence between the distribution and the surface temperatures". The additional sampling since 1960 has provided many more observations, and a detailed examination of this correspondence has been attempted. The long term mean surface temperatures for the months April to June, based on observations extending over more than 50 years (Krauss, 1958) are compared with the mean abundance of *Sebastes*, and the results are shown as histograms in Fig. 2 A.

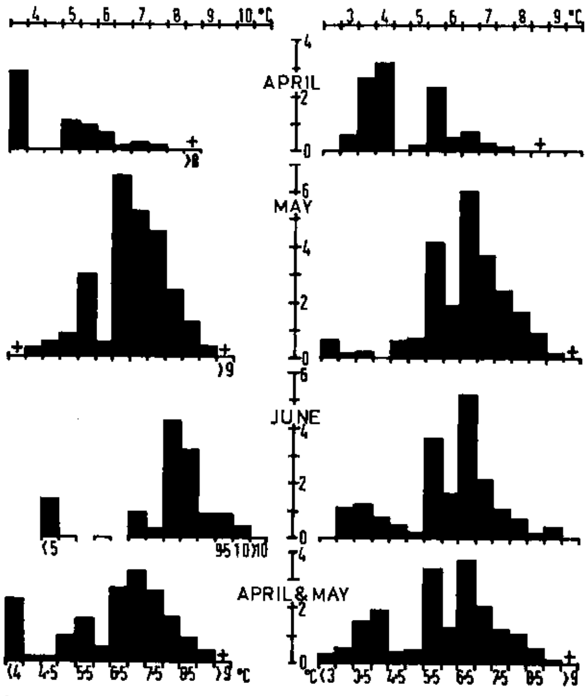
In April the mean surface temperatures over the area sampled ranged from <3°C up to >8°C, and the majority of the young *Sebastes* were found within the range of 5.0° to 7.5°C. The largest mean numbers of *Sebastes* per unit volume occurred in temperatures of from 5° to 6°C with one exception at <4°C, which is composed entirely of the catches off Flemish Cap. In May, with a mean temperature range of from <4°C to >9°C the catches occurred over the whole temperature range, but the largest numbers, exceeding 2.0 per 10 m^3, were found at 5.5°C and from 6.5° to 8°C. This is the month of greatest abundance of young stages. In June, with a mean temperature range of from <5° to >10°C the majority of the young stages occurred in temperatures between 7° and 10°C, maximum mean numbers occurring at 8° and 8.5°C. The single exception, at <5°C, represents the catches close to the southern tip of Greenland.

It is thought possible (Henderson, 1961*a*, p. 188) that the temperature requirements of the larger stages found in June and July (less than 20% are under 10 mm in length) may be less critical than are required for the earlier stages found in April and May (less than 10% are over 10 mm in length). The April and May results are shown combined in the final histogram where the largest mean numbers of young *Sebastes* are found at <4°, at 5° and 5.5° and between 6.5° and 8°C. The subscript to this histogram indicates the localities (p.309) within which the majority of the catches contributing to the individual histograms were taken.

2. Associations with Temperature at 200 Metres.

If the 'spawning' of redfish in the oceanic areas of the north Atlantic takes place only where temperatures of between 3° and 8.5°C are found in depths of 300 - 500 m (Tåning, 1949) or within the narrower range of from 4° to 6°C at 500 to 800 m (Einarsson, 1960), it would appear that a comparison of the abundance of young (at the levels at which they are sampled) with temperatures below the surface might provide clearer results than when the surface temperatures were used. It has recently been possible to make some comparisons of this kind with the mean annual temperatures at 200 m presented by Schroeder (1963). The results are shown as histograms in Fig. 2B. The three months April, May and June are plotted separately, and April and May results are combined in the final histogram to emphasise the importance of the period of extrusion. The temperatures were available as annual means only, so that any relationship with seasonal changes in temperature is obscured (although Schroeder says that "....over most of the North Atlantic temperature conditions are remarkably stable".) Catches of young *Sebastes* were taken over the whole temperature range of from <3° to >9°C. There is, however, some separation into groupings of larger mean numbers of young stages between 3° and 4°C and from 5.5° to 8°C. The subscript to the final histogram indicates the localities (p.309) within which the majority of the catches making up the individual histograms were taken.

ABUNDANCE OF THE YOUNG STAGES



A Surface Temperature B Temperature at 200 Metres

Fig. 2. Histograms showing the relationship between the mean abundance of young *Sebastes* and: A, the long term mean surface temperatures for the months April to June: B, the mean annual temperature at 200 metres depth. The scale of *Sebastes* represents the mean number per 10 m^3 found at each 0.5°C interval. The subscripts to the combined April and May histograms for both A and B indicate the localities within which the majority of the observations were contained.

In each year the average abundance of young *Sebastes* in April and May has been assessed for a standard area south and southwest of Iceland, where the sampling has generally been fairly uniform. Quite large fluctuations from year to year have been noted and possible relationships between these and other variables in the environment have been examined, so far with little success. It was noted, however, that the poorest year for young *Sebastes*, 1958, was that in which the surface temperature anomalies published by Smed (1957-1962) reached high values. The annual fluctuations in numbers of young *Sebastes*, expressed as standard deviations from the mean, are compared, in Fig. 3, with the mean surface temperature anomalies up to 1961 for March, April and May for Smed's large area F, which most nearly corresponds with the standard area from which the *Sebastes* figures are derived. The coincidence of the three highest positive temperature anomalies in this area with the three lowest points on the *Sebastes* curve seems worthy of note. However, the period of years covered is rather short, and it is as yet by no means certain how much significance there may be in associations with surface temperatures, so that this may be of coincidental significance only. Nevertheless, it is considered that these comparisons should be continued over a further period of years, and in greater detail over a wider area as results become available, to assess their possible value.

IDENTITY OF THE YOUNG STAGES

The adults of the large redfish, *Sebastes marinus* (L.) are separated into *marinus*- and *mentella*- types. Both are ovo-viviparous and the larvae have been distinguished from those of *S. viviparus* (Kr.) (Tåning 1949,1961), and from each other (Templeman and Sandeman, 1959) by the absence or presence of isolated melanophores ventrally at the root of the

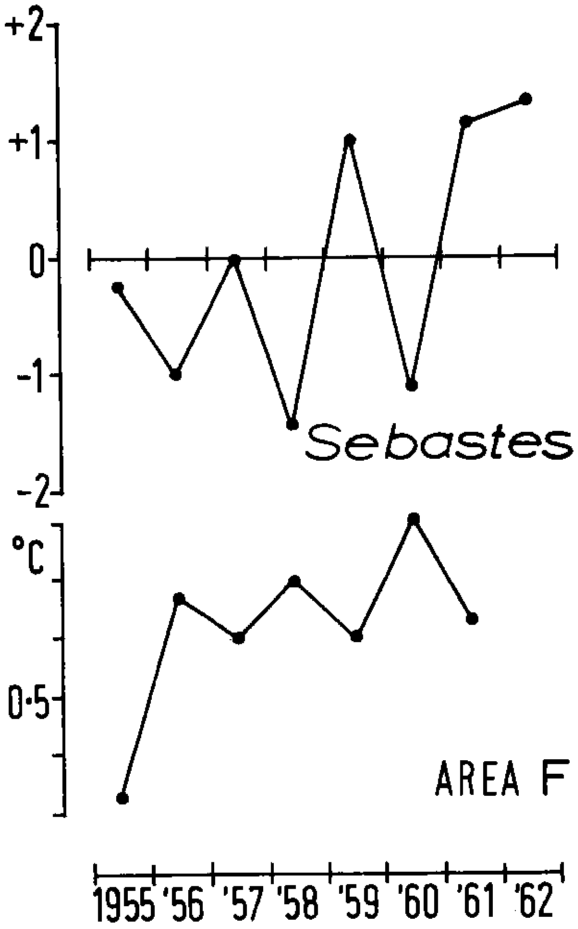


Fig. 3. Graphs showing the relation between the annual fluctuations in abundance of young *Sebastes* (based on the sampling in a standard rectangle south and southwest of Iceland in April and May and expressed as standard deviation from the mean for the years 1955 to 1962) and the surface temperature anomalies for March, April and May combined for the large Area F, for which Smed (1957-1962) has published data.

primordial caudal fin. All the young stages taken in the oceanic areas by the Recorder survey have been without sub-caudal melanophores and have been considered to be the *marinus*-type. Doubts as to the reliability of this identification are growing, however, (for example, Graham, 1962, p. 148) and it is evident that much more directly related information about parents and young is required. It is known that the only adults caught at Ocean Weather Station 'A' (see next section) are *mentella*- type, and pre-extrusion and 'left over' larvae from these have all been without the sub-caudal melanophores which should have been present in this type (Templeman & Sandeman, 1959). It will probably be some time before sufficient material is available to determine whether or not young stages from different parts of the oceanic area exhibit any characteristics which can be used to distinguish them.

IDENTITY OF THE ADULT STOCK

In late May and June 1961, the crew of the Dutch weather ship *Cumulus* caught redfish by angling at Ocean Weather Station 'A' (lat 62° N, long 33°W). This station is situated over the western slope of the Reykjanes Ridge, in an area where young *Sebastes* have usually been abundant in April and May, and a series of fishing trials was carried out from April to September 1962, with the help of British and Dutch weather ships occupying this station. These trials have been resumed, with the added help of Norwegian and French weather ships, to cover the whole of 1963. The trials were designed to sample down to 400 m, the main objectives being: (a) to catch 'spawning' redfish and, (b) to obtain as much information as possible about the adult stock from specimens preserved in formalin and returned to the laboratory. At the time of writing these fishing trials have been carried out in 1962 or 1963 (or in both years) from January to December and specimens have been obtained in each of these months except most of April and the first part of May. Although these trials are not yet completed some observed facts about the adults caught may be stated.

1. All the 172 specimens received in the laboratory so far were taken at depths of 100-250 m, the majority between 150 and 200 m.

2. All these specimens agree with the published criteria for the *mentella*-type. No *marinus*-type adults have been taken.

3. It is thought that the gap in the sequence of catches in April and early May is more likely to be due to 'spawning' activity than the absence of fish because large numbers of larvae are found at this time. The fish may be at a deeper level at this time or may be disinclined to take the hooks.

4. Some of the specimens taken in March had well developed larvae in the ovaries, and in many of the 'spent' fish caught from mid-May to mid-July some larvae had been retained. None of

these larvae so far examined exhibited the sub-caudal melanophores which might have been expected for *mentella-* type parents (Templeman and Sandeman, 1959).

5. The existence of a resident population of *mentella-* type redfish in the area around Ocean Weather Station 'A' must, it seems, now be considered a probability. These observations are, however, limited to the vicinity of Station 'A', but it may be possible to relate the findings to the larval population in the Reykjanes Ridge area. Much more information will be required before wider application becomes practicable.

SUMMARY

1. The distribution of the young stages of the redfish (*Sebastes*) in the north Atlantic, as sampled by the Continuous Plankton Recorder survey at 10 m depth, is described and illustrated for the months April to July. The possibility that this oceanic population may be found in four more or less separated localities is indicated, but precise definition of these localities is hindered by the limitations of the sampling.

2. Comparisons have been made between the mean catches of young *Sebastes* and (1) monthly mean surface temperatures, (2) annual mean temperatures at 200 m depth. The young stages are caught over most of temperature ranges encountered, but in April and May they appear to be rather more abundant in limited parts of the temperature range. There is a measure of correspondence here with the localities in which they appear to occur more or less separately.

3. The coincidence of the exceptionally poor year for young *Sebastes*, 1958, with high or maximum surface temperature anomalies in certain relevant areas in the Atlantic is noted, but some reservations exist about the significance of this.

4. The identity of the young stages is discussed and the current doubts as to the validity of the specific characteristics which have been used for some time are stated.

5. The identity of that part of the adult stock which has been sampled by fishing trials at Ocean Weather Station 'A' is found to be the *mentella-* type. The stock appears to be represented in the area for a large part of the year. Larvae taken from ripening and spent ovaries were found to be without the pigment characteristics which would have been expected for *mentella-* type.

REFERENCES

EINARSSON, HERMANN. 1960. The Fry of *Sebastes* in Icelandic waters and adjacent seas. *Rit Fiskid.* , 2 (7): 1-67.

GRAHAM, HERBERT, W. 1962. United States Research Report, 1961. *Int. Comm. Northw. Atlant. Fish. Redbook, 1962*, Part II: 143-157.

HENDERSON, G.T.D. 1961*a*. Continuous Plankton Records: The distribution of young *Sebastes marinus* (L). *Bull. Mar. Ecol.* 5: 173-193.

1961*b*. Continuous Plankton Records: The distribution of young *Sebastes marinus* (L). *Annu. Proc. int. Comm. Northw. Atlant. Fish*, 11: 103-110.

KOTTHAUS, ADOLF. 1964. The breeding and larval distribution of redfish in relation to water temperature. *This symposium, Contribution No. B-17.*

KRAUSS, WOLFGANG. 1958. Temperatur, Salzgehalt und Dichte an der Oberfläche des Atlantischen Ozeans. *Wiss. Ergebn. dtsch. atlant. Exped. "Meteor"*, Bd. V., 251-410.

SCHROEDER, ELIZABETH, H. 1963. North Atlantic Temperatures at a Depth of 200 Meters. *Serial Atlas of the Marine Environment* Folio 2. Published by the American Geographical Society.

SMED, JENS. 1957-1962. Monthly Anomalies of the Surface Temperature in Areas of the Northern North Atlantic. *Ann. biol. Copenhague*, 13: 10-11, 14: 12-14, 15: 14-15, 16: 22-23, and 17: 21-23.

In press. Monthly Anomalies of the Surface Temperature in Areas of the Northern North Atlantic in 1961. *Dansk, Nautisk Meteorol. Aarbo.*

TÅNING, Å.V. 1949. On the breeding places and abundance of the redfish (*Sebastes*) in the north Atlantic. *J. Cons. int. Explor. Mer.*, 16: 85-95.

TÅNING, Å.V. (the late) Introd. E. BERTELSEN. 1961. Larval and Postlarval Stages of *Sebastes* Species and *Helicolenus dactylopterus*. *Rapp. Cons. Explor. Mer*, 150: 234-240.

TEMPLEMAN, W. and E.J. SANDEMAN. 1959. Variations in caudal pigmentation in late state pre-extrusion larvae from *marinus*- and *mentella*-type female redfish from the Newfoundland area. *J. Fish Res. Bd. Canada* 16: 763-789.

B-5

THE DISTRIBUTION AND BEHAVIOUR OF PELAGIC AND EARLY DEMERSAL STAGES OF HADDOCK IN RELATION TO SAMPLING TECHNIQUES

By

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CONTENTS

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ABSTRACT

Data is presented on the vertical distribution and diurnal variation in the catch of haddock eggs, larvae, and pelagic juveniles, and on the diurnal variation in the catch of the early demersal stages of haddock in the Gulf of Maine.

Haddock eggs were concentrated in the surface layers and there was a decrease in their abundance with an increase in depth. Haddock larvae and pelagic juveniles were concentrated within a limited depth stratum, the depth limits of which were defined by the thermocline. There were no significant diurnal differences in the catch or in depth distribution of larval and juvenile haddock during surveys in which high-speed samplers having a high ratio of effective filtering area to sampling aperture were used.

The otter trawl catch of young-of-the-year and one-year-old haddock was greater during the night while the catch of 2+ year haddock was greater during the day. The diurnal variation in the catch of 2+ year haddock is due to a change in availability resulting from a movement off the bottom during the night, while the diurnal variation in the catch of young-of-the-year and one-year-old haddock appears to be due to an increase in avoidance or escape through the trawl meshes during the day.

Suggestions are made regarding sampling techniques which take cognizance of these distribution and behaviour patterns.

INTRODUCTION

Fishery biologists have been spared for the most part the heavy pressure for predictions that has long beset the meteorologist. A most important goal and primary obligation of fishery biologists, however, is to prepare predictions of value to the industry regarding the relative abundance of fish, the years when fish will be abundant and the areas where fish will concentrate. But what is more significant, the proof of our understanding of what is happening in the sea is the ability to specify what will happen next. In order to assess the seasonal and yearly fluctuations in distribution and abundance of fish and to make predictions regarding future availability and size of stock, it is essential that we conduct census surveys of these populations before they enter the commercial fishery. Although sampling is the heart of such studies, a more thorough examination of sampling techniques and of distribution and behaviour patterns is needed before reliable estimates and predictions of abundance and distribution can be made.

The problems involved are complex, for populations of fish are not static and are not distributed randomly in either time or space. The vertical and horizontal distribution of fishes varies with the stage of development, season of the year and time of day. In addition, many species of fish are able to avoid or escape from standard collecting gear, and this ability also varies with the stage of development and time of day. It is the purpose of this paper to present data on the vertical distribution of haddock eggs, on the vertical distribution and diurnal variation in the catch of larvae, pelagic juveniles and early demersal stages of haddock in the Gulf of Maine - Georges Bank area. Sampling techniques are suggested which take cognizance of these distribution and behaviour patterns and which are possibly applicable to other species of fish.

VERTICAL DISTRIBUTION OF HADDOCK EGGS

There have been three surveys in the Gulf of Maine - Georges Bank area in which quantitative samples were obtained in a suitable form for analysis of the vertical distribution of haddock eggs. The first series of observations was made during March, April, May and June, 1931 and April, 1932, in connection with a study of the distribution and survival of haddock eggs and larvae on Georges Bank (Walford, 1950). Sampling consisted of 30-min oblique tows with 1-m nets at a towing speed of 1.5 knots. In depths less than 100 m two nets were used, and in depths of 100 m or more three nets were used. The approximate depth ranges of the three strata sampled were 0 m to 55 m, 55 m to 110 m and 115 m to 170 m.

In Table 1 the average abundance and percentage of haddock eggs by depth strata are tabulated for stations where two nets were used in series (78 stations) and for stations where three nets were used in series (36 stations). These values were determined from Walford's Tables 4 and 5, p. 64-65. His values of eggs per minute have been converted to eggs per cubic metre.

TABLE 1.—THE AVERAGE ABUNDANCE AND PERCENTAGE OF HADDOCK EGGS BY DEPTH STRATA, MARCH - JUNE, 1931 AND APRIL 1932

	Depth strata	No. of eggs per cubic metre	Percent
2 strata	0 m - 55 m	0.258	70
stations	55 m - 110 m	0.111	30
3 strata	0 m - 55 m	0.034	87
stations	55 m - 110 m	0.002	5
	115 m - 170 m	0.003	8

Although there was considerable variation in the relative abundance of eggs in the three depth strata between individual stations, in only 5 of the 78 stations where tows were made at two levels were more eggs taken in the second stratum than in the upper stratum. In only 2 of the 36 stations where tows were made at three levels were more eggs taken in the deepest stratum than in the upper two strata. Eggs were found throughout the water column at most stations, but by far the majority of eggs were in the upper 55 m of the water column and in shallower water areas.

The second series of data was collected on Georges Bank in the springs of 1940 and 1941 in connection with studies of the distribution of *Sagitta elegans* (Clarke, *et al.*, 1943). The tabulations of fish eggs and larvae collected during these cruises have been placed at our disposal by Dr Clarke. Briefly, the zooplankton was collected by means of quantitative oblique hauls with Clarke-Bumpus Samplers (Clarke and Bumpus, 1950) arranged vertically to divide the total depth of water into two or three strata. The samplers were equipped with No. 2 silk nets and hauls were made at a speed of approximately 2 knots. The depth strata to be sampled were designated as follows:

Stratum	Water depth less than 75 m	Water depth more than 75 m
Shallow	0 m to 25 m	0 m to 25 m
Second Depth	25 m to bottom	25 m to half distance to bottom (or half distance to 200 m)
Deep	- - - - - - -	Remaining distance to bottom (or to 200 m).

The average depths actually sampled were as follows: "Shallow",- 0 m to 22 m, "Second Depth", - 22 m to 56 m, and "Deep", - 66 m to 104 m.

For each station the number of eggs per cubic metre was calculated for each stratum, and the total number of eggs under each square metre of sea surface was determined by multiplying the number per cubic metre for each stratum by its thickness and then adding the products. The average number of eggs per cubic metre for the whole water column at each station was obtained by dividing the number of eggs under each square metre by the total depth of water sampled at each station.

The abundance of haddock eggs in each depth stratum is presented in Table 2. The data are shown for individual cruises and also include the seasonal average and percentage at each depth.

TABLE 2.—THE ABUNDANCE (NUMBER PER CUBIC METRE) AND PERCENTAGE OF HADDOCK EGGS BY DEPTH STRATA AT TWO AND THREE LEVEL STATIONS, THROUGH - JUNE, 1940 AND 1941

		1940						
	Atlantis Cruise No:	95	96	97	98	100	Avg	Percent
	Date:	21 March 2 April	17-27 April	9-16 May	1-8 June	19-27 June		
2 level stations	shallow 0 m - 22 m	1.12	1.98	2.04	0.12	0.01	1.05	57
	second depth 22 m - 56 m	1.03	1.46	1.42	0.08	0	0.80	43
3 level stations	shallow 0 m - 22 m	1.92	2.47	2.46	0.11	0.01	1.39	47
	second depth 22 m - 56 m	1.42	2.16	1.19	0.07	0	0.96	33
	deep 66 m - 104 m	0.45	1.69	0.74	0.03	0	0.58	20

		1941					
	Atlantis Cruise No:	112	113	114	116	Avg	Percent
	Date:	21 March 2 April	15-23 April	7-14 May	28 May 4 June		
2 level stations	shallow 0 m - 22 m	3.00	2.90	1.91	0.26	2.02	61
	second depth 22 m - 56 m	0.96	1.66	2.41	0.16	1.30	39
3 level stations	shallow 0 m - 22 m	4.11	2.53	1.54	0.25	2.11	58
	second depth 22 m - 56 m	1.00	0.88	1.99	0.13	1.00	27
	deep 66 m - 104 m	0.77	0.64	0.75	0.06	0.56	15

In both 1940 and 1941 the average abundance of haddock eggs decreased with depth. The relative abundance in the three depth strata varied considerably between cruises, but with the exception of Cruise 114 in May 1941, when eggs were slightly more abundant in the second depth stratum in both two and three level stations, eggs were more abundant in the upper stratum during all months. The average depth range of the upper two strata (0 m to 56 m) sampled during the 1940-41 cruises coincides with the depth range of the upper stratum sampled during the 1931-32 cruises (0 m to 55 m) and confirms the finding that haddock eggs are more abundant in the upper 50 m of the water column. In addition, it is seen that haddock eggs are most abundant in the upper 20 m of the water column.

The third series of data was collected during the Continuous Plankton Recorder surveys of the Gulf of Maine - Georges Bank area during March, April and May, 1953 and February, March, April and May 1955 and 1956. These surveys were designed to locate spawning areas and to study the effects of associated environmental factors upon the survival of haddock eggs and larvae. During these cruises Recorders were towed at a speed of 10 knots, one just below the surface and one at 10 m. The average abundance (catch per cubic metre) and percentage of early stage eggs (from fertilization to the approach of the germinal ring to the equatorial position), late stage eggs (from the equatorial position of the germinal ring to hatching), and total eggs at the surface and 10 m during 1953, 1955 and 1956 are presented in Table 3.

TABLE 3.—THE ABUNDANCE AND PERCENTAGE OF HADDOCK EGGS AT THE SURFACE AND 10 m DURING 1953, 1955 AND 1956

		Early stage eggs		Late stage eggs		Total eggs	
		No. / m^3	%	No. / m^3	%	No. / m^3	%
1953	Surface	0.024	89	0.079	88	0.103	88
	10 m	0.003	11	0.011	12	0.014	12
1955	Surface	0.088	77	0.053	79	0.141	78
	10 m	0.026	23	0.014	21	0.039	22
1956	Surface	0.097	56	0.102	61	0.198	58
	10 m	0.076	44	0.065	39	0.141	42

Although the proportion of eggs at the surface and at 10 m varied between years and between cruises within a given year, the proportion of early stage and late stage eggs at the surface and at 10 m was similar within each year, during all years both early and late stage eggs were most abundant at the surface. There were only two cruises in which haddock eggs were taken in greater numbers at 10 m than at the surface. In February 1963, 68% of the late stage eggs and in March 1963, 63% of the early stage eggs were found at 10 m.

The corroborative evidence from the three series of surveys demonstrates that although haddock eggs are present throughout the whole water column, eggs in all stages of development are concentrated in the surface layers, and there is a decrease in abundance with an increase in depth. To my knowledge there have been no detailed studies made of the vertical distribution of haddock or other gadoid eggs in other areas, but the observations of Sette (1950), Silliman (1943) and Kramer (1960) which showed that the eggs of the Atlantic mackerel (*Scomber scombrus*), Pacific sardine (*Sardinops caerulea*) and Pacific mackerel (*Pneumatophorous diego*) were concentrated in the upper 20 m of the water column and above the thermocline, and of Farris (1961) who found jack mackerel (*Trachurus symmetricus*) confined to the upper 40 m of the water column, indicate that vertical segregation occurs in the eggs of many species and in many areas.

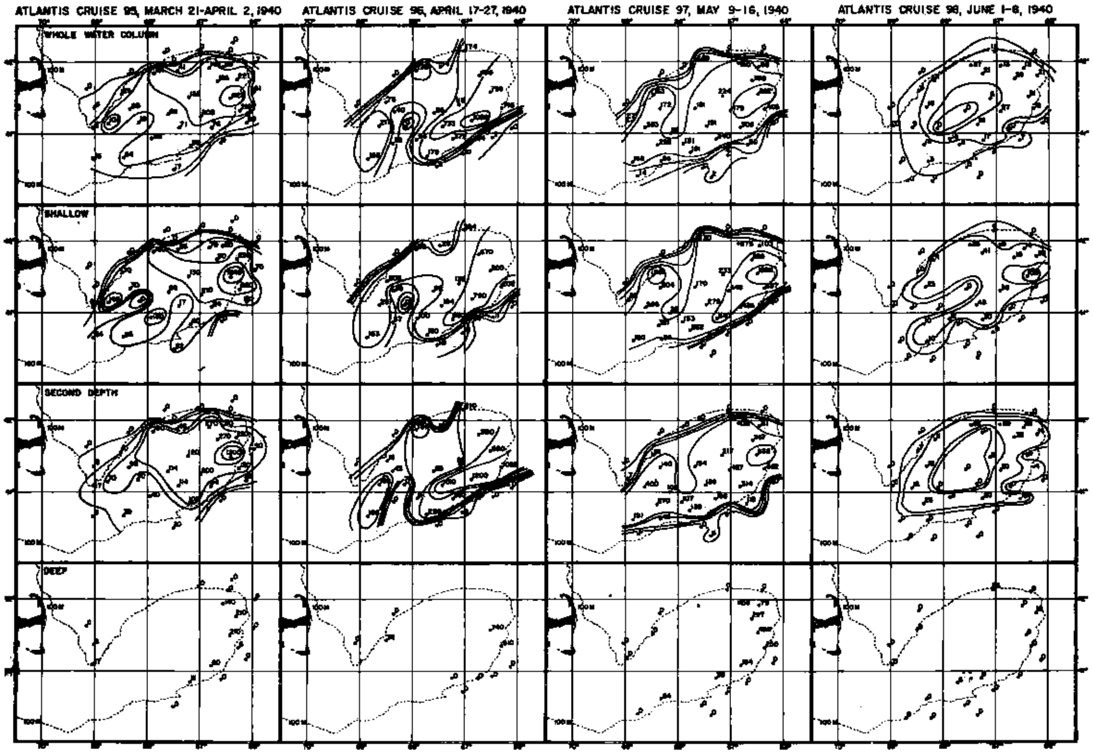

Fig. 1. Distribution of haddock eggs by depth strata, March-June 1960. Values are the number of eggs per 100 cubic metres.

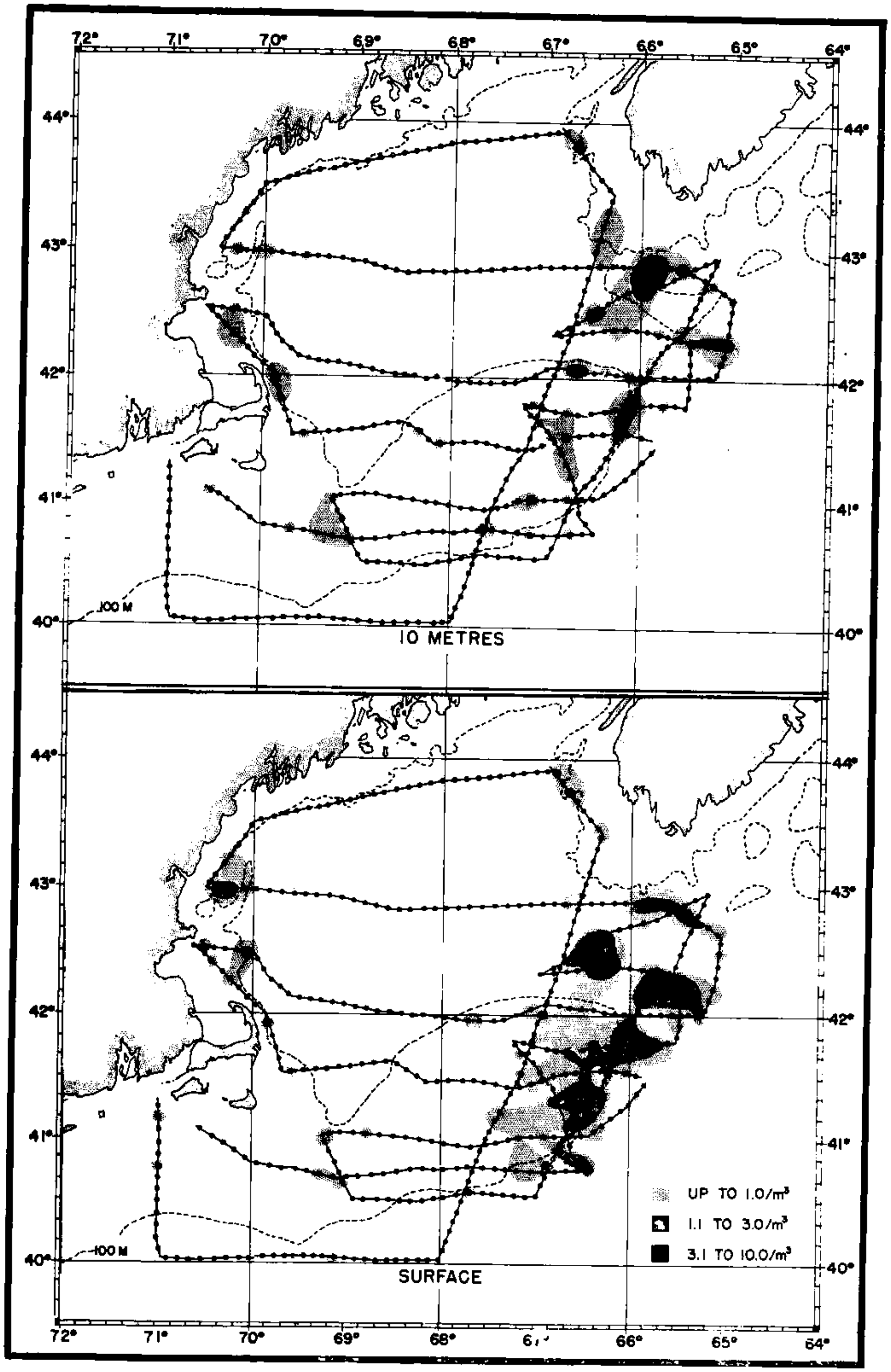

Fig. 2. Distribution of haddock eggs at the surface and 10 m, April 1956.

If, as seems likely, the vertical distribution of haddock eggs does not vary appreciably in time or space, it would be possible to obtain a reliable estimate of the relative abundance of haddock eggs between years from samples within the upper 20 m of the water column. Furthermore, if the relative abundance between stations in the depth stratum of maximum abundance was similar to that based on a sample of the whole water column, the horizontal distribution and thus the time and location of spawning could be determined from sampling a limited depth stratum. To test the feasibility of such an approach a comparison is made in Fig. 1 of the distribution of haddock eggs as determined from a sample of the whole water column and of the 0 - 22 m, 22 - 56 m, and 66 - 104 m depth strata during March, April, May and June, 1940.

In all cruises the relative abundance of eggs between stations in the shallow and second depth stratum was generally similar. The distribution of eggs in the shallow depth stratum was most representative of the distribution as determined from a sample of the whole water column.

One distinct advantage of confining sampling to a restricted depth zone is that once the depth and depth range of this stratum of maximum abundance is established for a particular species of egg a more rapid and thorough coverage of an area can be accomplished. This is not only desirable in studies of the timing of spawning, but because of the patchiness of the distribution of eggs it is also essential to obtain a maximum number of samples in order to delineate spawning locations accurately. A good illustration of the irregularity in the horizontal distribution of haddock eggs is afforded by the data collected during the Continuous Plankton Recorder surveys. The distribution of haddock eggs at the surface and 10 m during April 1956 is shown in Fig. 2.

VERTICAL DISTRIBUTION AND BEHAVIOUR OF HADDOCK LARVAE AND PELAGIC JUVENILES

1. Vertical Distribution

There have been four surveys made in the Gulf of Maine - Georges Bank area in which quantitative samples were obtained in a form suitable for an analysis of the vertical distribution of larval and juvenile haddock. The first series of data was collected during the *Atlantis* cruises to Georges Bank during the springs of 1940 and 1941. The majority of haddock collected during these cruises were prolarvae and early postlarvae (average length - 4.7 mm and size range - 3.1 mm to 10.0 mm). The average number of larvae per cubic metre in the individual depth stratum for stations where tows were made at two levels and for stations where tows were made at three levels for individual cruises and the yearly average number per cubic metre and percentage of haddock larvae in individual depth stratum for 2 and 3 level stations are presented in Table 4.

The relative abundance of larvae in the three depth strata varied considerably between cruises. In both 1940 and 1941 and on individual cruises in which appreciable numbers of larvae were caught, the average abundance of larval haddock was greatest in the shallow stratum at both two and three level stations. At three level stations, the average abundance in the second and deep stratum was similar in 1940, but greater in the second stratum than in the deep stratum in 1941.

Decidedly fewer larval haddock than haddock eggs were collected during the Continuous Plankton Recorder surveys of the Gulf of Maine - Georges Bank area in the springs of 1953, 1955 and 1956 (average number of eggs per cubic metre - 0.106, average number of larvae per cubic metre - 0.018). The average length of the larvae collected at the surface and 10 m during these surveys was 9.2 mm and the range in length 3.1 mm to 40.0 mm. The average length of larvae caught at the surface (10.0 mm) was greater than the average length of larvae caught at 10 m (8.5 mm). The average abundance and percentage of larval haddock at the surface and 10 m for individual years and for the 3 years combined are presented in Table 5.

In 1953 and in 1956 larval haddock were more abundant at 10 m than at the surface, while in 1955 they were slightly more abundant at the surface. The percentage of larvae at 10 m was greatest in 1956, the only year in which appreciable numbers of larvae were caught. Although the 1940 - 41 data indicated that both haddock eggs and larvae were most abundant in the upper 20 m of the water column, the Continuous Plankton Recorder survey data indicated that, unlike haddock eggs, which showed a steady decrease in abundance with depth, the depth at which larval haddock are most abundant is well below the surface.

During May 1958, a cruise was undertaken with the objective of getting more detailed information

TABLE 4.—THE ABUNDANCE (NUMBER PER CUBIC METRE) AND PERCENTAGE OF HADDOCK LARVAE BY DEPTH STRATA AT TWO AND THREE LEVEL STATIONS, APRIL - JUNE, 1940 AND 1941

	1940					
	Atlantis Cruise No:	96	97	98	Avg	Percent
	Date:	17-27 April	9-16 May	1-8 June		
2 level stations	shallow 0 m - 22 m	0.01	0.27	0.38	0.17	75
	second depth 22 m - 56 m	0.03	0.04	0.14	0.06	25
3 level stations	shallow 0 m - 22 m	0	0.05	0.23	0.08	46
	second depth 22 m - 56 m	0.02	0.02	0.13	0.05	27
	deep 66 m - 104 m	0	0.01	0.15	0.05	27

	1941					
	Atlantis Cruise No:	113	114	115	Avg	Percent
	Date:	15-23 April	7-14 May	28 May 4 June		
2 level stations	shallow 0 m - 22 m	0	0.13	0.48	0.21	54
	second depth 22 m - 56 m	0.01	0.17	0.34	0.18	46
3 level stations	shallow 0 m - 22 m	0	0.03	0.42	0.15	62
	second depth 22 m - 56 m	0	0.02	0.21	0.08	32
	deep 66 m - 104 m	0	0.03	0.01	0.02	6

TABLE 5.—THE ABUNDANCE AND PERCENTAGE OF LARVAL HADDOCK AT THE SURFACE AND 10 M DURING 1953, 1955 AND 1956

	1953		1955		1956		Avg	
	No./m^3	%	No./m^3	%	No./m^3	%	No./m^3	%
Surface	.005	42	.007	54	.017	31	.007	39
10 m	.007	58	.006	46	.063	69	.011	61

on the depth distribution of postlarval haddock, employing multi-depth sampling techniques. Modified Hardy Plankton Samplers (Miller, 1961) were used and sampling took place at three stations in the Georges Bank area. Each station was occupied for 2 consecutive days. Thirty-minute horizontal tows at a speed of 7 knota were taken every 2 hours at depths of 1, 10, 20, 30, 40, 50 and 75 m. The average length of haddock larvae caught during this cruise was 9.0 mm and the range in length, 4.0 to 21.0 mm. A detailed analysis of these data has been made by Miller *et al* (1963). The abundance, percentage, and mean length of larval haddock caught at each depth at the three stations are listed in Table 6.

Although there was a variation in the depth of maximum abundance of larvae between stations and between size groups of larvae, at all stations over 80% of the larvae occurred between the 10-m and 40-m levels. The average "larval-depth" (determined by multiplying the number of larvae by the

TABLE 6.—THE ABUNDANCE, PERCENTAGE, AND MEAN LENGTH OF HADDOCK LARVAE BY DEPTH, MAY 1958

	Station I			Station II			Station III		
Depth	No./m^3	%	Mean length	No./m^3	%	Mean length	No./m^3	%	Mean length
Surface	0.046	4.2	10.4mm	0.050	9.2	11.8mm	0.017	2.7	10.6mm
10 m	0.267	24.3	8.6mm	0.221	40.8	12.0mm	0.114	18.1	9.0mm
20 m	0.218	19.8	7.2mm	0.135	25.0	12.0mm	0.386	38.6	8.8mm
30 m	0.277	25.1	6.6mm	0.082	15.1	11.2mm	0.202	31.9	9.5mm
40 m	0.187	17.0	6.7mm						
50 m	0.106	9.6	6.8mm	0.040	7.4	10.9mm	0.055	8.7	9.6mm
75 m				0.013	2.5	11.7mm			

depth sampled, summing the weighted samples and dividing by the total larvae at all depths) was 25 m at Station I, 20 m at Station II, and 24 m at Station III. Larval haddock less than 8 mm in length were dispersed over a greater depth range than the larger larvae. The average larval depth for larvae smaller than 8 mm was 27 m. The data showed that over 80% of the haddock larvae in the 8 - 21 mm size range were concentrated within the depth range of the thermocline which occupied about 25% of the entire water column sampled.

Data on the vertical distribution of juvenile haddock were obtained on four cruises to the Gulf of Maine during the periods 25 July - 2 August and 5 - 11 September, 1957 and 28 July - 1 August and 9 - 16 September, 1958 (*Albatross III* Cruises 99, 102, 116 and 117) in connection with a study of the vertical distribution of redfish (Kelly and Barker, 1961). The sampling gear used was a 10-ft Isaacs-Kidd midwater trawl modified to operate as an opening and closing net. Consecutive 1-hour tows were made at a speed of 4.5 knots at depths of 10,20,30,40,60,80,100 and 110 m. A total of 366 haddock were caught in 1957 (average length - 92.6 mm, size range - 32 mm to 124 mm) and a total of 4,261 haddock were caught in 1958 (average length - 90.4 mm, size range - 27 mm to 121 mm). In Table 7 the number of tows, catch per tow and percentage of juvenile haddock by depth for the 1957, 1958 and total cruises are tabulated.

TABLE 7.—NUMBER OF TOWS AND ABUNDANCE AND PERCENTAGE OF JUVENILE HADDOCK BY DEPTH, JULY - SEPTEMBER, 1957 AND 1958

	Albatross III Cruises 99&102 July - September 1957			*Albatross III* Cruises 116&117 July - September 1958			Total Cruises		
Depth	No. of tows	Catch per tow	%	No. of tows	Catch per tow	%	No. of tows	Catch per tow	%
10 m	23	1.3	9.6	14	85.9	21.2	37	33.3	22.3
20 m	35	7.1	52.2	15	118.1	29.2	50	40.4	27.1
30 m	20	2.3	16.8	11	59.3	14.7	31	22.5	15.1
40 m	21	0.8	5.9	10	44.3	11.0	31	14.8	9.9
60 m	7	1.3	9.6	4	48.3	11.9	11	18.3	12.3
80 m	6	0.8	5.9	4	48.5	12.0	10	19.9	13.3
100 m	8	0	0				8	0	0
110 m	4	0	0				4	0	0

In both 1957 and 1958 the greatest abundance of juvenile haddock occurred at 20 m, although the proportion of fish at this depth was greater in 1957 than in 1958. No juvenile haddock were found below 80 m. During all four cruises the thermocline extended from approximately 10 to 50 m (Kelly and Barker, 1961, Fig. 2, p. 227), and it was in this zone of rapid temperature change that the greatest numbers of juvenile haddock were caught. The average depth of juvenile haddock depth was 28 m in 1957 and 33 m in 1958. The average depth of juvenile haddock from July to September was greater than that of larval haddock in May as was the average depth of the thermocline. In 1957, 85% and in 1958, 76% of the juvenile haddock were found within the depth range of the thermocline. These percentages agree closely with those obtained in May 1958 for postlarval haddock.

In Fig. 3 the percentage of 10-mm length groups of juvenile haddock at each depth are plotted for the periods July - August, 1957 and 1958 (*Albatross III* Cruises 99 and 116) and September, 1957 and 1958 (*Albatross III* Cruises 102 and 117). The average length of juvenile haddock caught during July - August was 84 mm and during September was 99 mm. The average depths during all cruises for the eight length groups in order of increasing size were 31, 28, 32, 32, 33, 39, 37 and 30 m. With the exception of haddock larger than 79 mm in July - August, all length groups were concentrated between 10 and 40 m during both periods. During the July - August period the greatest percentage of juvenile haddock 80 mm and larger was at the 80 m level. Although appreciable numbers of haddock were caught in only one of the 10 tows made at this depth, the data for both periods indicate that there is an increase in the average depth and depth range with an increase in length. Further sampling incorporating high-speed simultaneous tows is needed to validate these data.

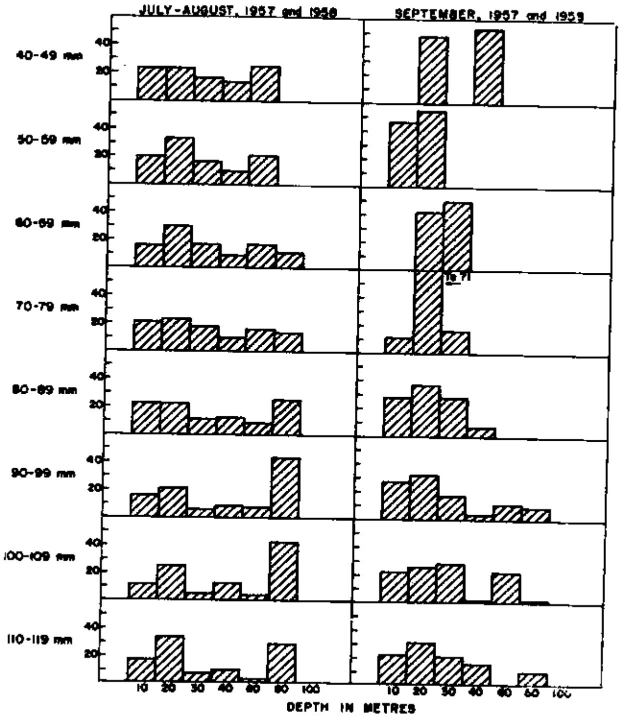

Fig. 3. The relative abundance in percent of 10 mm length groups of haddock by depth, July - August, 1957 and 1958 and September 1957 and 1958.

Vertical segregation has been observed for other species of larval and juvenile fish by many investigators (Russell, 1928; Silliman, 1943; Wiborg, 1948; and 1960; Sette, 1950; Ahlstrom, 1954, and 1959; Bridger, 1958; Kramer, 1960; Colton *et al.*, 1961; and Farris, 1961). The four series of observations in the Gulf of Maine - Georges Bank area demonstrate that prolarval, postlarval and juvenile haddock up to approximately 120 mm in length also tend to be concentrated within a narrow depth range. Over 90% of the prolarval and postlarval haddock (4.0 - 21.0 mm) occurred in the upper 40 m of the water column and over 80% of the postlarval haddock (8.0 - 21.0 mm) were concentrated within the thermocline. Although haddock larvae smaller than 8 mm were dispersed over a greater depth range than larvae larger than 8 mm, their average larval depth was only slightly greater. Wiborg (1960) found that in waters off the coast of Norway smaller cod larvae were also dispersed over a greater depth range and that there was an increase in depth stratification with an increase in length.

Over 75% of haddock up to 124 mm in length occurred between the 10- and 40-m levels, so that it appears that it would be possible to obtain a reliable estimate of the relative abundance of larval and juvenile haddock within a given area, between years, from a sample within a limited depth stratum. The depth range of maximum abundance of larval and juvenile haddock coincided with the depth range of the thermocline. The depth limits of the thermocline are readily definable and do not vary markedly with location in an area such as Georges Bank. These facts suggest that it would be possible to determine the horizontal distribution of these fish from a sample within this restricted depth zone.

2. Behaviour

There are two aspects of the behaviour of larval and juvenile fish, namely diurnal migration and escapement, that must be considered in any sampling program. Diurnal migrations, at least for many species of larval and juvenile fish, are not as extensive as once assumed (Johansen, 1925; Russell, 1928; and Sette, 1950), as it has been demonstrated that variations in the day and night catch are due in large part to the ability of many species to avoid slow-moving collecting nets (Silliman, 1943; Ahlstrom, 1954; Bridger, 1956 and 1958; and Colton and Marak, 1962). This ability to avoid capture increases with the size of the fish and the amount of light, with a resulting decrease in the catch and average size of fish caught in the surface layers during the day and an increase during the night. Bridger (1958) and Southward (1962) in experiments made with the Gulf III high-speed sampler have shown that a reduction in the shock wave that precedes the net and an increase in filtration efficiency are as important as high speed in preventing evasion by fast moving animals.

The data used in this report corroborate these findings. For example, the average size and range in size of haddock and cod larvae taken with the Continuous Plankton Recorder were considerably greater than the average size and range in size of haddock and cod larvae collected with 1-m nets on the same cruises or with Clarke-Bumpus Samplers during similar seasons (Colton and Marak, 1962). In addition, there was no consistent diurnal difference in the average number of larval haddock caught in the upper 10 m of the water column with the Continuous Plankton Recorder (54% in the day and 46% at night), while with both the metre net and Clarke-Bumpus Sampler many more larval haddock were caught during the night. More juvenile haddock were caught during the night at all depths except 80 m with the Isaacs-Kidd midwater trawl during 1957 and 1958. The average catch per tow of juvenile haddock for all depths during the day was 17.5 and during the night was 36.5. The night/day ratio in the catch tended to decrease with depth and increase with the length of fish. There was no significant difference at any depth in the abundance, average size/and size range of larval haddock, caught with the modified Hardy Plankton Samplers during the vertical distribution studies in May, 1958 (Miller *et al.*, 1963).

During both surveys in which there were no significant differences in day and night catch of haddock, high-speed samplers having a high ratio of effective filtering area to sampling aperture were used. The Continuous Plankton Recorder has a filtering ratio of 32 to 1 and the modified Hardy Plankton Sampler has a filtering ratio of 18 to 1. Both these ratios are much larger than those of the ordinary tow nets and thus assure a more rapid movement of water through the mouth of the gear.

There was no evidence of any diurnal change in the depth distribution of larval haddock in May 1958. The average larval depth at the three stations was 24 m during the day and 22 m during the night. The average depth of juvenile haddock caught with the Isaacs-Kidd trawl in 1957 and 1958, however, did show diurnal variation, being at 40 m during the day and at 30 m during the night. Considering that no juvenile haddock were found below 80 m during the day or night, that over twice as many juvenile haddock were caught during the night than during the day, and that the night/day ratio in the catch tended to decrease with depth, it would appear that this diurnal variation in depth distribution is an artifact resulting from increased daylight avoidance. In addition, simultaneous tows were not made with the Isaacs-Kidd trawl so that there was considerable variation in time and location between sampling depths. In neither series of data was there any evidence of a night-time migration of larvae or juveniles from depths below the maximum depth sampled. Such stability in the depth distribution of larval and juvenile fish has been observed in other species as well (Ahlstrom, 1959 and Farris, 1961).

VERTICAL DISTRIBUTION AND BEHAVIOUR OF EARLY DEMERSAL STAGES OF HADDOCK

Census surveys of the groundfish populations in the Gulf of Maine - Georges Bank area were made in September 1955 (*Albatross III* cruises 65 and 66), November 1956 (*Albatross III* cruises 81 and 82), and October 1958 (*Albatross III* cruises 118, 119, and 120). One of the objectives of these surveys was to estimate the abundance of young-of-the-year haddock for predictions of year class strength. The survey gear was a standard otter trawl having a 1.3 cm mesh cotton liner in the cod end and upper belly. The towing speed was 2.5 knots, and all tows were 1/2 hour long from hook-up to haul-back.

An analysis of these data showed that the abundance of young-of-the-year and 1-year-old haddock fluctuated in the same way, both being high in all areas in 1955 and 1958 and low in 1956. This tendency towards a greater abundance of haddock in certain years was also manifest to a lesser degree in the survey catches of older haddock. For example, the catch per tow of haddock of all ages was greater in 1958 than in 1956. One consequence of this fluctuation in fishing efficiency between years is that estimates of year class strength are dependent upon what age fish are chosen to represent the year class and in what year the sampling was done. From these data the 1956 year class would appear much stronger on a basis of the abundance of 2-year-old haddock in 1958 than of the abundance of young-of-the-year haddock in 1956.

The gear, method of tow and area of coverage were similar during all survey cruises, so that it does not appear that the variation in fishing efficiency between years could be due to any differences in fishing technique. However, commercial vessels tend to catch more haddock during the day than during the night and this variation in the day and night catch is greatest in deeper water. If during the survey cruises, there had been a marked variation in the proportion of day and night tows, this could, conceivably, be the cause of the variation between years in fishing efficiency. To determine if such was in fact the case, a tabulation was made in Table 8 of the number of day and night tows and of the catch per tow of young-of-the-year, 1-year-old, and 2+ year haddock during the day and night for the three survey cruises. Young-of-the-year and 1-year-old haddock are tabulated separately, for it was for these ages that the most marked yearly variation in abundance were observed. The reason for the difference in the number of tows tabulated for young-of-the-year haddock and in the number of tows tabulated for 1-year-old and 2+ year haddock in 1955 and 1956 is that at some stations only young-of-the-year haddock were counted or young-of-the-year haddock were lost due to a tear in the fine mesh liner.

TABLE 8.—THE NUMBER OF TOWS AND THE CATCH PER TOW OF HADDOCK BY DAY AND NIGHT IN THE GULF OF MAINE - GEORGES BANK AREA, SEPTEMBER 1955, NOVEMBER 1956 AND OCTOBER 1958.

		Day (0730 - 1629)			Night (1930 - 0429)		
	Year	No. of tows	No. of fish	C/T	No. of tows	No. of fish	C/T
Young-of-the year haddock	1955	46	218	4.7	53	732	13.8
	1956	34	72	2.1	37	58	1.6
	1958	46	264	5.7	50	1216	24.3
	Total	126	554	4.4	140	2006	14.3
One-year-old haddock	1955	42	45	1.1	54	349	6.8
	1956	35	74	2.1	37	48	1.3
	1958	46	286	6.2	50	548	11.0
	Total	123	405	3.2	141	945	6.7
2+ year haddock	1955	42	466	11.0	54	270	5.0
	1956	35	285	8.1	37	212	5.7
	1958	46	958	20.8	50	732	14.6
	Total	123	1709	13.9	141	1214	8.6

The day and night effort did not vary markedly, although in all years more tows were made during the night than during the day. The catch per tow of young-of-the-year haddock was slightly greater during the day in 1956 and much greater during the night in 1955 and 1958. The catch per tow of 1-year-old haddock was greater during the day in 1956 and greater during the night in 1955 and 1958. The average night/day ratio of abundance was greater for young-of-the-year haddock than for 1-year-old haddock. In all years the catch per tow of 2+ year haddock was greatest during the day as is the case in the commercial catch. The day/night ratio of abundance of 2+ year haddock was of the same order of magnitude during all years, but the abundance of young-of-the-year and 1-year-old haddock was only greater at night in the years when the survey cruises indicated that these two age groups were most abundant (1955 and 1958).

Year-class strength estimates based on the abundance of young-of-the-year haddock during both day and night would indicate that the 1955 and 1958 year classes were strong. The night time data would not only indicate that the 1955 and 1958 year classes were considerably stronger than indicated by the day time data, but that the 1958 year class was approximately twice as strong as the

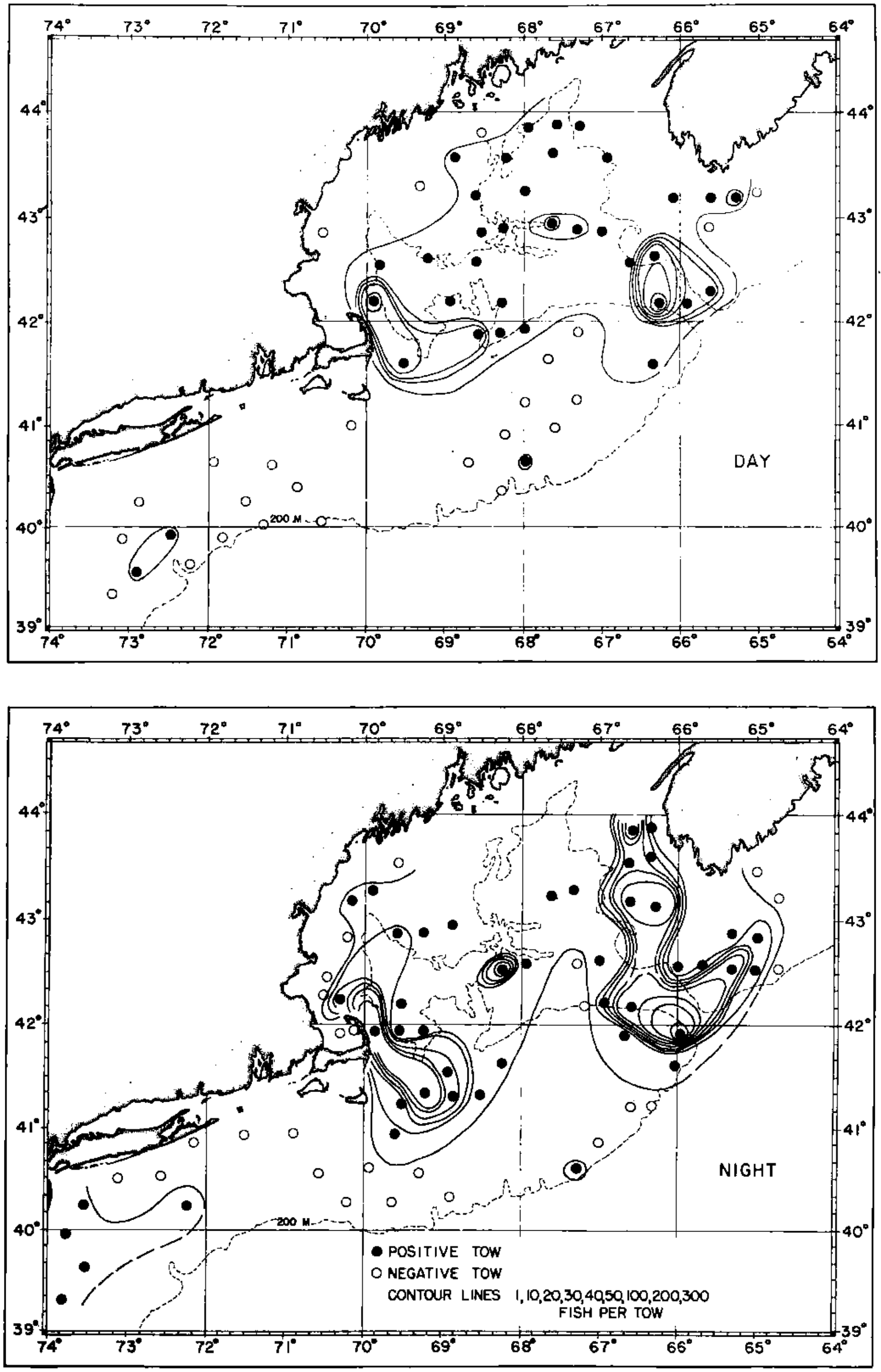

Fig. 4. Distribution of young-of-the-year haddock during the day and night, October, 1958.

1955 year class. The day time catch of 1-year-old haddock would indicate that only the 1957 year class was strong, while the night time catch would indicate that both the 1957 and 1954 year classes were strong. Although not as marked, significant yearly differences in the relative abundance of 2+ year haddock also occurred between the day and night data.

Not only do estimates of abundance of haddock based on day and night observations vary, but also the distribution pattern is different if based on night observations than if based on day observations. This is demonstrated in Fig. 4 showing the distribution of young-of-the-year haddock as determined during the day and night tows in October, 1958. Young-of-the-year haddock were found over a much wider area at night and also areas of high abundance (off southeastern Nova Scotia) were not indicated by the day time data.

When the 3-year average catch per tow of young-of-the-year, 1-year-old and 2+ year haddock was determined for hourly intervals, the plots showed marked hourly fluctuations in the abundance of all age groups. Although in general the catch per tow of young-of-the-year and one-year-old haddock tended to be higher during the night time hours and the catch per tow of 2+ year haddock tended to be higher during the daylight hours, the fluctuations in the number of fish caught, between individual tows within a given hour, were too great to attach any significance to the abundance figures. The main cause for these fluctuations appears to be the marked regional variations in the abundance of haddock. Obviously there were many tows made during the night in areas where there were few or no young-of-the-year and 1-year-old haddock, or many 2+ year haddock, and tows made during the day where the reverse situation existed. In any event, the day/night variability in the catch is real, but special sampling programs in which tows are made at set time intervals within relatively small areas for an appreciable number of days are needed before this variability can be accurately assessed.

Diurnal migration appears to be the cause of the variation in the day and night catch of 2+ year haddock. Although no sampling has been undertaken to determine if haddock move off the bottom during the night, trawling experiments and echo sounder observations have shown that haddock move off the bottom at night in other areas (Woodhead, 1961). Indications are that this is also the case in the Gulf of Maine - Georges Bank area where the commercial catch of haddock is greater during the day than at night. Diurnal migration cannot explain the variation in the day and night catch of young-of-the-year and 1-year-old haddock unless, unlike older haddock, these young fish move up in the day and down at night. It is also possible that young-of-the-year and 1-year-old haddock do not move off the bottom at night. However, observations on the diurnal migration of herring in the North Sea (Lucas, 1936) and of haddock in the Barents Sea (Woodhead, 1961) have demonstrated that smaller fish show more tendency to leave the sea bed than do larger fish. It appears that the day time decrease in the catch of young-of-the-year and 1-year-old haddock is due to a variation in the catching efficiency of the otter trawl between day and night. This variation in catching efficiency could be due either to an increase in the avoidance of the trawl during the day, as has been demonstrated in the case of larval and juvenile fish, or to an increase in escape through the unlined meshes of the trawl wings (12.7 cm stretched mesh) during the day. No doubt haddock of all ages are able to avoid the otter trawl to some extent, but it appears that the younger fish may exhibit a more rapid visual and auditory response to the trawl and that the day and night variability in the catch of young-of-the-year and 1-year-old haddock due to avoidance or escapement is greater than that due to vertical migration.

There would appear to be only two possible methods of increasing the daytime catching efficiency of the otter trawl. One would be to increase the towing speed, but this does not appear practical for it is difficult to keep the trawl on the bottom at high speed and the amount of backwash and turbulence at the mouth of the net would be increased. Another, and possibly more effective way of reducing escape, would be to decrease the mesh size of the trawl wings. It appears quite possible that all age haddock enter the net at the same rate, but the smaller fish (young-of-the-year and 1-year-olds) are able to escape through the meshes of the wings and are better able to do this during the day than during the night. In order to determine if this is in fact the case, it would be necessary to make a duplicate series of tows during the day and night with and without a fine mesh liner in the wings.

It is evident that one of the causes of the variability in fishing efficiency between years is the diurnal variation in the catch. If the various age haddock were randomly distributed and if the diurnal cycle was similar for all age haddock and for all depths, due allowance could be made for this diurnal variation. However, in addition to the variance caused by day and night differences in depth distribution there is apparently also bias caused by a variation in the fishing efficiency of the otter trawl with age of fish and time of day. Until this variance is allowed for and the bias eliminated, the relative abundance of haddock between areas and years can only be made for a specific age group and on a basis of data collected either by day or night.

SUMMARY AND CONCLUSIONS

The analysis of the data on the vertical distribution of haddock eggs collected in 1931, 1932, .940, 1941, 1953, 1955 and 1956 in the Gulf of Maine - Georges Bank area demonstrated that, although ıaddock eggs occurred throughout the water column, eggs in all stages of development were concen:rated in the surface layers and there was a decrease in abundance with an increase in depth. The :elative abundance of haddock eggs in the upper 20 m of the water column was similar to the relative ıbundance of eggs based on a sample of the whole water column.

Surveys made in 1940, 1941, 1953, 1955, 1956 and 1958, in which quantitative data on the vertical listribution of prolarval and postlarval haddock were obtained, demonstrated that haddock up to 21 mm .n length were concentrated within a limited depth stratum, the depth limits of which were defined by :he thermocline. At stations in which simultaneous samples were taken at depths down to 75 m over 0% of the larvae were found between the 10-and 40-m levels and within the thermocline.

In studies of the vertical distribution of juvenile haddock conducted in 1957 and 1958 in which amples were taken at specific depths down to 110 m, over 75% of haddock, ranging in length from 7 mm to 124 mm, occurred between depths of 10 and 40 m and within the thermocline. No juvenile addock of this size range were found at depths greater than 80 m.

In surveys in which high-speed samplers having a high ratio of effective filtering area to samling aperture were used, there were no significant differences in the day and night catch of larval nd juvenile haddock and no variation in the depth distribution between day and night.

It appears that not only would it be possible to obtain a reliable estimate of the relative bundance of the eggs, larvae, and pelagic juveniles of haddock as well as other species on a basis f samples confined to a limited depth stratum, but also that the areal distribution and thus the time nd location of spawning and the drift and migrations of larval and juvenile fish could be obtained by ampling a restricted depth stratum.

In studies of the early life history and year-class strength fluctuations of most species of marne fish it does not seem feasible or expedient to attempt to determine the absolute abundance of eggs nd larvae. Indeed, no conclusive correlation has been demonstrated between the abundance of eggs and arvae and the brood strength of these fish as measured by their contribution to the fishery in suceeding years (Thompson, 1929*a* and 1929*b*; Poulsen, 1931 and 1941; Heegard, 1947; Carruthers *et al.*, 951; Rae, 1953; and Radovich, 1962). The time and location of spawning and the subsequent disperal of larvae and juveniles are likely to have greater influence on brood strength than the absolute umber of eggs or larvae produced. The data on the vertical distribution of haddock eggs, larvae, nd juveniles indicates that such information can be obtained from samples taken within a relatively arrow depth zone. Because sampling of a limited depth stratum would be more rapid than sampling the hole water column, a greater number of samples could be obtained in a given period. Reliable estiates of abundance over broad geographical areas would be possible and more accurate data obtained n the fluctuations in abundance in time and space.

To define the vertical distribution of the eggs or larvae of any species of fish it would be dvisable to use high-speed, simultaneous, horizontal tows. Once the vertical distribution is ascerained, it would be expedient to make high-speed oblique tows with samplers of high filtering capaity to eliminate avoidance and to insure adequate samples. The studies of Bridger (1956, 1958) and f Southward (1962) show that with modifications the Gulf III high-speed sampler (Gehringer, 1952) s ideally suited for this purpose. A simple closing mechanism for this sampler has been described y Kinzer (1962).

The analysis of data on the distribution and abundance of haddock during otter trawl surveys of roundfish populations in the Gulf of Maine - Georges Bank area in 1955, 1956 and 1958 showed that ıe catch of young-of-the-year and 1-year-old haddock fluctuated in the same way, both being high in l1 areas in 1955 and 1958 and low in 1956. The variation in abundance between years appears to reılt from a decrease in fishing efficiency during daylight hours, for the average catch per tow of ›ung-of-the-year and 1-year-old haddock was markedly greater during the night than during the day ı years when the abundance figures were high. This day and night variation in the catch of young ıddock is opposite to that of 2+ year haddock, the catch of which was greater during the day in all ›ars as is the case in the commercial catch. The variation in the catch of young-of-the-year and -year-old haddock is not due to a change in availability resulting from a movement off the bottom during the night as in the case of 2+ year haddock, but appears to be due either to an increase in avoidance or escape through the trawl wings during the day. Special sampling programs are needed to determine the cause and to assess accurately the degree of this day and night variation in the catch. Regardless of the cause, the effect is real in that there are marked differences in abundance and distribution as determined from day and night observations.

This analysis of the catch of haddock eggs, larvae and juveniles shows that in studies of the early life history and brood strength fluctuations of fish we have to deal with populations of such complexity that special investigations on the nature of the distribution of the various developmental stages should be undertaken to improve sampling programs and the design of collecting gear with a view of minimizing variance and eliminating bias.

REFERENCES

AHLSTROM, E.H. 1954. Distribution and abundance of egg and larval populations of the Pacific sardine. *Fish. Bull., U.S.* 56: (93): 83-140.

1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. *Fish. Bull., U.S.* 60(161): 107-146.

BRIDGER, J.P. 1956. On day and night variation in catches of fish larvae. *J. Cons. int. Explor. Mer*, 22 (1): 42-57.

1958. On efficiency tests made with a modified Gulf III high-speed tow-net. *J. Cons. int. Explor. Mer*, 23(3): 357-365.

CARRUTHERS, J.N. *et al.* 1951. Variations in brood-strength in the North Sea haddock, in light of relevant wind conditions. *Nature*, 168 (4269): 317-319.

CLARKE, G.L. , E.L. PIERCE, and D.F. BUMPUS. 1943. The distribution and reproduction of *Sagitta elegans* on Georges Bank in relation to hydrographical conditions. *Biol. Bull.*, 85(3): 201-226.

CLARKE, G.L. and D.F. BUMPUS. 1950. The plankton sampler -- An instrument for quantitative plankton investigations. *Am. Soc. Limnol. and Oceanog., Spec. Pub.*, 5: 1-8. Revised.

COLION, J.B., K.A. HONEY, and R.F. TEMPLE. The effectiveness of sampling methods used to study the distribution of larval herring in the Gulf of Maine. *J. Cons. int. Explor. Mer*, 26 (2): 180-190.

COLTON, J.B. and R.R. MARAK. 1962. Use of the Hardy Continuous Plankton Recorder in a fishery research programme. *Bull. Mar. Ecol.*, 5 (49): 231-246.

FARRIS, D.A. 1961. Abundance and distribution of eggs and larvae and survival of larvae of jack mackerel (*Trachurus symmetricus*). *Fish. Bull. U.S.*, 61 (187): 247-279.

GEHRINGER, J.W. 1952. 2. An all metal plankton sampler (Model Gulf III). *Spec. sci. Rep. U.S. Fish Wildl. Serv. - Fish.*, No. 88, p. 7-12.

HEEGAARD, P. 1947. Investigations of the breeding season and the quantities of eggs of the food fishes of the Kattegat and the northern Belt Sea 1929-1941. *Medd. Komm. Danm. Fisk. Havundersøg.*, 11(4): 1-20.

JOHANSEN, A.C. 1925. On the diurnal movements of young of some fishes in Danish waters. *Medd. Komm. Danm. Fisk. Havundersøg.*, 8(2): 1-27.

KELLY, G.F. and A.M. BARKER. 1961. Vertical distribution of young redfish in the Gulf of Maine. *Rapp. et Proc.-Verb.*, 150: 220-233.

KINZER, J. 1962. Ein einfacher Schiessmechanismus für die Planktonröhre "Hai" (A simple closing mechanism for a modified Gulf III plankton sampler). *Kurze Mitteilungen aus dem Institut für Fiskereibiologie der Universität Hamburg*, No. 12, Dec., 1962: 13-17.

KRAMER, D. 1960. Development of eggs and larvae of Pacific mackerel and distribution and abundance of larvae 1952-56. *Fish. Bull., U.S.*, 60 (174): 393-438.

LUCAS, C.E. 1936. On the diurnal variation of size-groups of trawl-caught herring. *J. Cons. int. Explor. Mer*, 11 (1): 53-59.

MILLER, D. 1961. A modification of the small Hardy plankton sampler for simultaneous high-speed plankton hauls. *Bull. Mar. Ecol.*, 5 (45): 165-172.

MILLER, D., J.B. COLTON, and R.R. MARAK, 1963. A study of the vertical distribution of larval haddock. *J. Cons. int. Explor. Mer*, 28 (1): 37-49.

POULSEN, E.M. 1931. Biological investigations upon the cod in Danish waters. *Medd. Komm. Danm. Fisk. Havundersøg.*, 9 (1): 1-148.

1941. On fluctuations in the size of the stock of cod in the waters within the Skaw during recent years. *Rept. Danish Biol. Sta.*, 46: 1-36.

RADOVICH, J. 1962. Effects of sardine spawning stock size and environment on year class production. *Calif. Fish Game*, 48(2): 123-140.

RAE, B.B. 1953. The occurrence of lemon sole larvae in the Scottish plankton collections of 1929, 1930, and 1931. *Mar. Res. Scot.*, 1953, No. 1: 1-36.

RUSSELL, F.S. 1928. The vertical distribution of marine macroplankton. VIII. Further observations on the diurnal behaviour of the pelagic young of teleostean fishes in the Plymouth area. *J. Mar. Biol. Ass., U.K.*, 15 (3): 829-850.

SETTE, O.E. 1950. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America Part I: Early life history, including growth, drift, and mortality of the egg and larval populations. *Fish. Bull., U.S.*, 50 (38): 149-237.

SILLIMAN, R.P. 1943. Thermal and diurnal changes in the vertical distribution of eggs and larvae of the pilchard (*Sardinops caerulea*). *J. Mar. Res.*, 5 (2): 118-130.

SOUTHWARD, A.J. 1962. The distribution of some plankton animals in the English Channel and approaches. II. Surveys with the Gulf III high-speed sampler, 1958-60. *J. Mar. Biol. Ass., U.K.*, 42 (2): 275-375.

THOMPSON, H. 1929*a*. 2. Haddock biology (North Sea). A brief survey of recent data, methods and results. *Rapp. et Proc.-Verb.*, 54: 135-163.

1929*b*. General features in the biology of the haddock (*Gadus aeglefinus* L.) in Icelandic waters in the period 1903-1926. *Rapp. et Proc.-Verb.* 57: 1-73.

WALFORD, L.A. 1950. Effects of currents on distribution and survival of the eggs and larvae of haddock (*Melanogrammus aeglefinus*) on Georges Bank. *Fish. Bull., U.S.*, 49 (29): 1-73.

WIBORG, K.F. 1948. Investigations on cod larvae in the coastal waters of Northern Norway. Occurrence of cod larvae, and occurrence of food organisms in the stomach contents and in the sea. *Fiskeridir. Skr. Havundersøk.*, 9 (3): 1-27.

1960. Investigations on eggs and larvae of commercial fishes in Norwegian coastal and offshore waters in 1957-58. *Fiskeridir. Skr. Havundersøk.*, 12 (7): 5-27.

WOODHEAD, P.M.J. 1961. Diurnal variation in the trawl catches of haddock. *Cons. int. Explor. Mer, Comparative Fishing Committee*, No. 71: 1-5. (unpublished manuscript).

B-6

FACTORS CONTROLLING DISPERSAL OF THE PELAGIC STAGES OF FISH AND THEIR INFLUENCE ON SURVIVAL

By

Alan Saville [1]

ABSTRACT

The part which dispersal of the planktonic stages may play in generating differential recruitment to a fish stock is discussed in relation to the habitat of the stock. Wind is considered to be the dominant factor in bringing about differences in dispersal between years. Evidence for the effect of wind on the distribution of haddock eggs and larvae at Faroe and in the North Sea, and of herring larvae in the Clyde is reviewed. It is concluded that there is a relationship between wind direction and strength and the distribution of larvae for Faroe haddock and Clyde herring but not for North Sea haddock. The impact of this on subsequent year-class strengths of these stocks is discussed.

INTRODUCTION

Appreciation of the major role played by variation in the success of year-classes, in generating the fluctuations in productiveness to which most fisheries are subject, has made the investigation of the factors controlling this variation a major preoccupation of fisheries research. For the majority of fish stocks it has now been clearly established that the size of a year-class is fixed at least by the end of the planktonic phase (Parrish, 1950), although opinion is still divided as to the part of this phase in which the operative factors principally exert their effect.

The planktonic nature of the early spawning products, both the eggs in the majority of species of commercially important fish, and larvae for all but an insignificant proportion, must mean that dispersal could play a vital part in determining the fate of a year-class. The possible importance of dispersal was first propounded by Hjort (1914) who encountered great numbers of cod larvae over deep water in the Norwegian Sea and suggested that such drift into an unsuitable environment might be a major cause of differential mortality between years. Although differential survival of the initial production between years seems to be a feature of virtually all spawning stocks, the operative factors producing this differential survival must be expected to differ between stocks and indeed within the same stock in different years. This must be particularly true for the effects of variations in dispersal.

Stocks of fish spawning on isolated shallow banks surrounded by deep water, or on narrow shelves bordering oceanic depths would be expected to be much more vulnerable to this source of mortality than those whose chosen spawning areas are surrounded by large areas of suitable ground for the settlement and growth of the post-metamorphic stage. The presence of self-contained spawning stocks on such banks would seem to demand a current system over them, such as an eddy, which would tend to retain the planktonic stages of the life-cycle over the bank. The part played by eddy systems in maintaining benthic populations with planktonic larvae in such situations has been pointed out for bivalves by Orton (1937) and the role of convection currents in similar situations for lobsters at Bermuda by Boden (1952). Whether the planktonic stages carried beyond the habitat of the spawning stock survive to recruit to another area or perish is a moot point and must be dependent on the length of the planktonic phase, on any ability of the organism to postpone the change over to the adult mode of life until a favourable environment is reached (such as Wilson 1952 has demonstrated for the planktonic larvae of certain invertebrates) and on the proximity of alternative areas suitable for settlement. Unless, however, one postulates a reverse migration of the organism to the spawning site of the parents, whether the organism survives in a new habitat or not does not affect the generation of differential survival of the initial stock.

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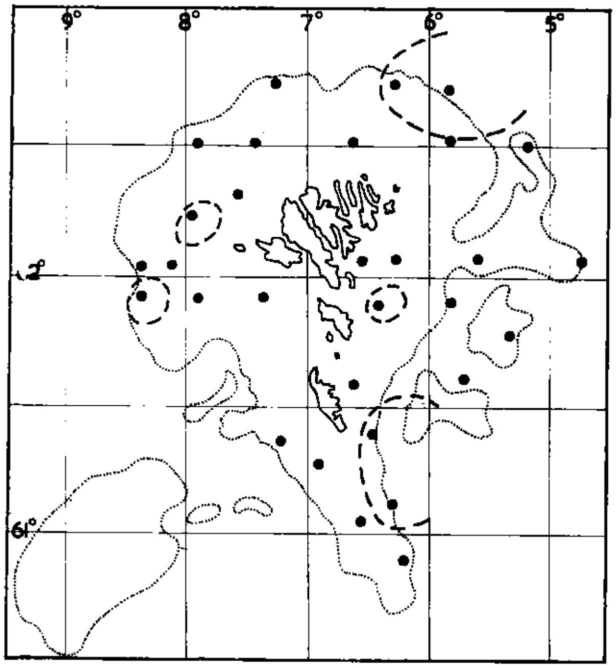

Fig.1. Distribution of haddock larvae at Faroe, June 1950. Dots show the positions of the stations; the abundance of the larvae is shown by contours at 1 to 5 per haul (broken line) and >5 (unbroken line).

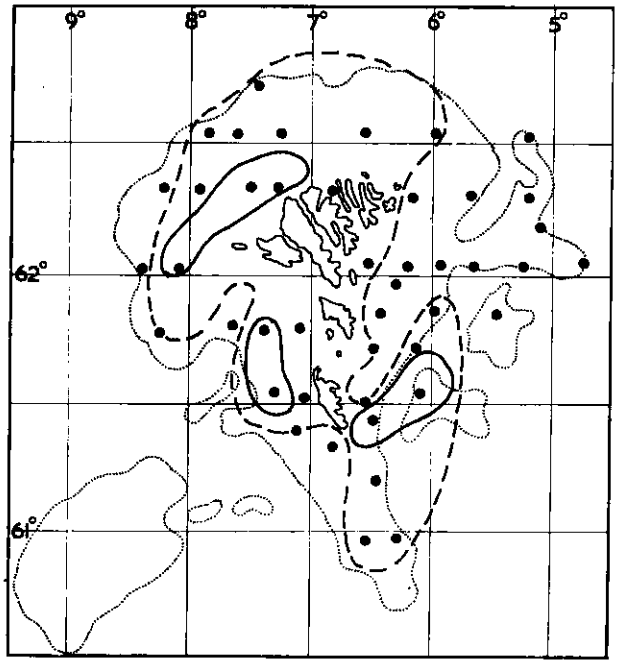

Fig. 2. Distribution of haddock larvae at Faroe, June, 1952. Contour levels as in Fig.1.

Thus the maintenance of a permanent spawning stock demands a current system over the spawning area which under normal circumstances retains the planktonic stages within that area or alternatively brings about dispersion within an environment suitable for subsequent settlement and growth, and permits of a contranatant migration back to the original spawning area. Any short-term distortion of the current system, during the spawning season, which results in a dispersion not fulfilling these conditions, could be expected to result in a poor recruitment from that year class.

Of the factors which would bring about such a distortion of the normal current pattern an abnormal persistence of wind from one direction seems the most likely. The major part of this paper deals with a consideration of wind effects on egg and larval dispersion and subsequent year-class size in different types of spawning situations.

DISTRIBUTION OF HADDOCK EGGS AND LARVAE AT FAROE

The Faroe plateau, which forms part of the submarine ridge connecting Scotland and Iceland, comprises an area of about 23,000 sq km within the 200 m contour. This area is intensively fished, largely for cod and haddock, - the haddock landing in a typical year amounting to something of the order of 400,000 cwt. Tait (1934), largely on the basis of drift-bottle returns, postulated an anti-cyclonic eddy system around the islands and this is supported by the fact that the plateau appears to maintain its own plankton population, which is quite different from the typical oceanic fauna of the surrounding waters (Fraser 1939; Hansen, 1955). The haddock stock of the area is considered to be a self-contained one (Raitt, 1936) and, considering the extensive area of deep water separating Faroe from the contiguous haddock stocks of Iceland and off the north and west Scottish coasts, it is difficult to believe that haddock larvae carried off the Faroe plateau and possibly reaching these areas to settle subsequently are able to return. On this basis the Faroe stock would appear to be an almost classic case, in which any influence which disrupts the normal eddy system operating over the Faroe shelf will have very serious repurcussions on the size of the recruitment to the year class born in that year.

In the years 1950-53 inclusive an intensive investigation of this area was carried out by Scottish research vessels to sample the planktonic stages of the haddock. This material has been reported by Saville (1956) with particular reference to the demarcation of the spawning season and locations, and the assessment of egg

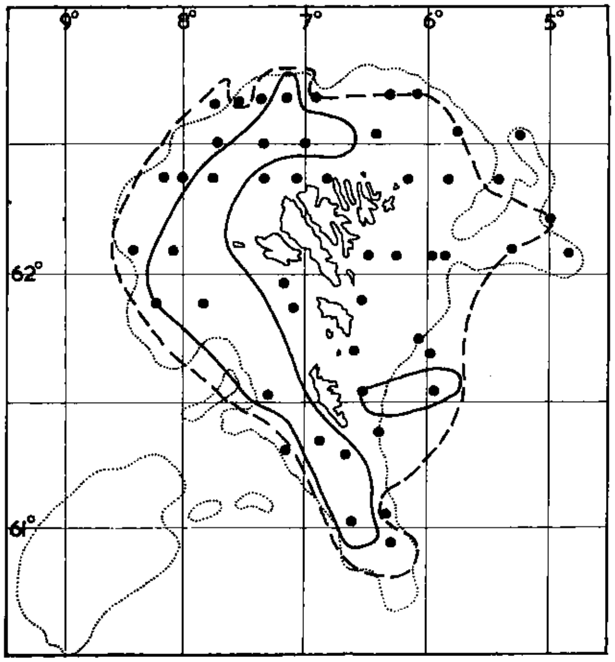

Fig. 3. Distribution of haddock larvae at Faroe, June 1953. Contour levels as in Figure 1.

production and of the subsequent larval mortalities in the different years. The favoured centres of spawning were markedly constant from year to year and it is noteworthy that they are situated near the edge of the shelf where the spawning products would seem particularly liable to displacement over the adjoining deep water. Unfortunately in all years the cruises were too widely spaced in time to allow the drift of the eggs and larvae to be traced in any great detail. Figures 1-3 however show the distribution of haddock larvae in June for the years 1950, 1952 and 1953. It is clear from these that in June, when the larvae are near the end of the planktonic phase in 1952 and 1953 a considerable body of haddock larvae was still present in the area, with a generalised distribution over the Faroe shelf such as one would expect from the operation of an eddy system around the islands. The 1950 picture is very different; larvae in that year were very scarce in the area, with the greater number on the eastern edge of the shelf in June. This situation in June was to some extent forecast by the May cruise of that year when, although a considerable body of larvae was still present within the area, they were very markedly concentrated to the east of the islands compared with the distribution in the same month in 1951. The distribution of the planktonic haddock stages over this period would seem to suggest that in the years 1951-53 the bulk of them were retained within the Faroe plateau but that in 1950 there was a major loss of these spawning products over the deep water to the east. The same may also have been true of cod larvae which were also markedly scarce in June 1950 compared with 1952 and 1953.

From these data the best index of recruitment to the adult stock was considered to be the abundance of larvae in June when they were nearing the end of the planktonic phase. As these covered a variable size range between years, from the calculated mortality and growth rates their abundance were first converted to the equivalent numbers at a standard size and then to the mean number at this size below 10 sq m of surface. The figures so derived, for the years 1950, 1952 and 1953, showed a satisfactory degree of agreement with the strength of these broods in their first year of life assessed from trawl surveys, and published by Jones (1951) and Jones and Main (1953, 1954). This suggests that in these years at least there is no appreciable differential loss of haddock larvae from the area after June and, as the assessment of juvenile haddock is a satisfactory index of their subsequent strength throughout their fishable life, that any loss from the area through larval drift is not subsequently made good by a compensatory return migration during the adolescent or adult phase.

Thus from these data it appears that the planktonic haddock spawning products at Faroe are normally retained within the eddy system overlying the Faroe plateau and that their abundance there late in the planktonic stage gives a valid index of the resultant year-class strength. In 1950 however there was a marked scarcity of haddock larvae within the area in June and the resulting year-class was a poor one. Events during the planktonic stage make it probable that this scarcity of larvae was due to many having drifted out of the area and over the deep water to the east. The most likely force to bring about such a distortion of the normal circulation pattern seemed to be persistent winds from the west. Wind directions and strengths for Faroe are available in the daily reports of the British Meteorological Service. These were plotted during the course of the planktonic phase of the haddock (March-June) and resultants calculated for each month. Normally one quarter of the annual production of haddock eggs are present in the area in March and the total has been produced by the end of April. As March winds must therefore exert a lesser effect than those of the ensuing months the strength of the March resultant was reduced to one quarter of its real value. The resultant for the season as a whole was then calculated and the water transport assessed on the assumption that it would be 45° to the right of the wind direction. The easterly component of transport was then calculated for each of the years on a comparative basis taking 1953 as a standard with an arbitrary value of 1.

These data are given in Table 1 along with the assessment of haddock larval abundance in June for those years in which the area was sampled in that month, and the abundance of haddock in their first year of life from trawl surveys given by Jones (1951) and Jones and Main (1952, 1953, 1954).

TABLE 1.—EASTERLY WIND COMPONENT AND ABUNDANCE OF FAROE HADDOCK AS LARVAE AND AS 1-GROUP.

Year	Easterly wind component	Larvae abundance in June	Abundance of haddock as 1-group
1950	14.8	1.2	228
1951	-25.0	?	538
1952	6.0	2.4	488
1953	1.0	2.7	495

The data are admittedly based on a very short series of years but they do suggest that a persistence of strong winds from the west is inimical to the retention of haddock larvae in the Faroe area and to the subsequent recruitment to the demersal stocks.

This situation at Faroe seems to parallel closely that of haddock on Georges Bank. There too there is a considerable population of spawning haddock more or less surrounded by natural hazards; by high temperatures to the southwest; by oceanic depths along the southern edge; and by deep water and muddy bottom along the northern edge. On the eastern edge is a deep channel which probably forms at least a partial trap on that side (Walford, 1938). Chase (1955), by using the winter temperatures to estimate the time of the spawning season and calculating the off-shore wind component for the period of planktonic life so assessed, got a very satisfactory correlation with the brood-strengths of haddock for the 24 years for which brood-strength data were available.

NORTH SEA HADDOCK

Considerable interest was aroused in the part played by wind induced transport of fish larvae in the North Sea following on the work of Carruthers and his collaborators. These authors presented a series of correlations between fluctuations in wind direction and strength and the strength of the corresponding year-class of various species of commercial fish (Carruthers, 1950; Carruthers *et al.*, 1951; Carruthers *et al.*, 1951; Veley, 1951). The mechanism underlying these correlations was in no case categorically stated but in general terms it was inferred that the surface currents induced by the winds controlled whether the larvae were dispersed into environments favourable or unfavourable for survival.

In particular for North Sea haddock the close correlation found between the wind function used and resulting year-class strength led to the suggestion that the poor brood survival found with south-westerly winds was due to the planktonic spawning products being carried by the surface currents induced by such winds, north-eastwards into the north-going stream along the Norwegian coasts. Winds from other quarters were in general found to be favourable and this was explained as being the result of dispersion over the main body of the North Sea, which is the customary haddock nursery area.

In the period 1952-57 research vessels of the Department of Agriculture and Fisheries for Scotland carried out a series of cruises to investigate the planktonic stages of haddock in the northern North Sea and in particular to trace their drift and its variations from year to year. The material collected on these cruises has already been reported by Saville (1959). The most striking conclusion arrived at from this investigation was that any drift of the planktonic haddock stages in the northern North Sea, at least during the years covered by the investigation, was extremely small. In Figures 4 and 5 are shown the distributions on successive cruises of eggs and the resulting larval stages in 1955 and 1956. The other years investigated gave very similar distributions. It will be seen that any transport which took place must have been exceedingly small and certainly inadequate

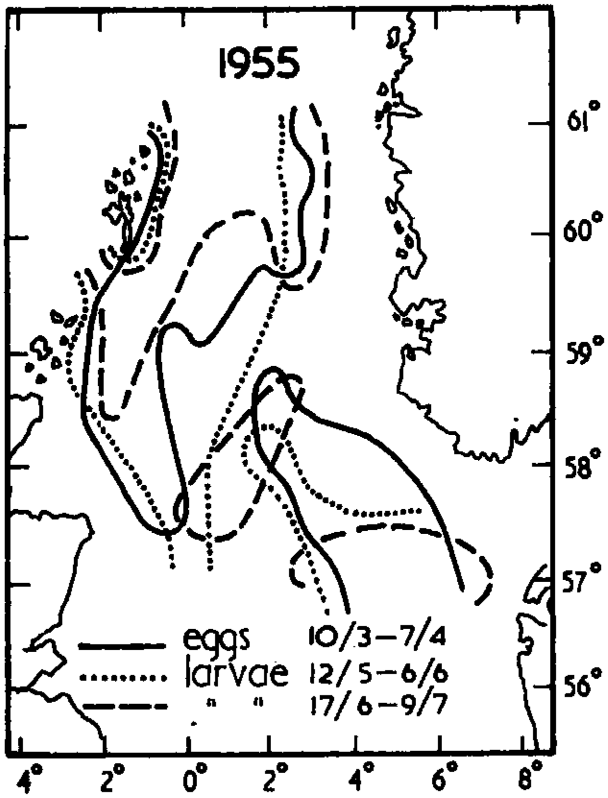

Fig. 4. Distribution of haddock eggs and larvae in the North Sea on successive cruises, in 1955.

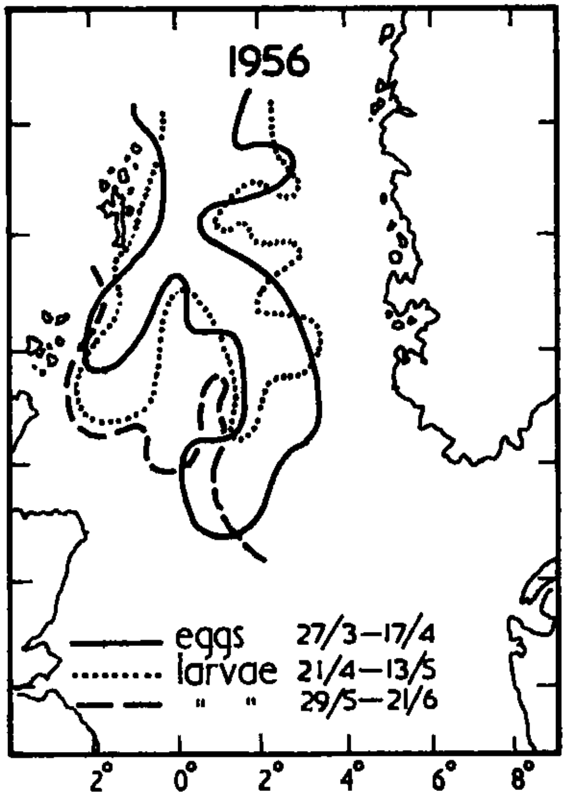

Fig. 5. Distribution of haddock eggs and larvae in the North Sea on successive cruises, in 1956.

to account for major variations in year-class strength. In Table 2 are given the average northerly and easterly components of the wind for the months April-June inclusive for each of the years investigated and the strength of the south-west component over these three months all in terms of sea miles per day.

TABLE 2.—ANNUAL VARIATIONS IN WIND IN APRIL-JUNE OVER NORTHERN NORTH SEA 1952-57.

1952			1953			1954			1955			1956			1957		
N	E	SW	N	E	SW	N	E	SW	N	E	SW	N	E	SW	N	E	SW
-73	-120	140	-23	-36	42	- 8	-75	61	+ 39	-93	40	+ 28	-95	46	+ 57	-82	18

With the exception of 1952, with a very large component of wind from the S.W., and 1957 with a rather small one, there was not much variation in this respect between the various years. The year class of 1952 was a fairly good one - up to the mean of the series of good broods produced between 1951 and 1955. On the other hand 1956 and 1957 were both particularly poor broods. On this limited evidence it would seem that winds from the south-west bear little relation to brood prospects and, in view of the rather static distributions of haddock spawning products found over these ranges of wind strength and direction, it would seem doubtful whether wind plays any major part in inducing transport in the North Sea. Steele (1957), discussing the hydrography of the northern North Sea in spring and summer, states that in this area at this time the water below the thermocline is relatively stationary. Above the thermocline the dominating influence is the westwards spread of low salinity water coming from the Baltic out-flow. The fact that this spread is in the opposite direction from that of the prevailing wind implies that the wind effect is not predominant. It is probable that the balance produced between this westwards spread and the westerly wind component accounts for the relatively static distributions of haddock eggs and larvae found in this area.

Rae (1957) was able to relate the distribution of *Metridia* in the northern North Sea in the winter months to the direction and strength of the prevailing winds and showed a relationship between the wind function at this time and the strength of the haddock brood born in the following spring. In autumn and winter the hydrographic picture in the northern North Sea is completely different from that of the spring and summer with the dominating influence being inflow of Atlantic water. The extent of the easterly spread of this water might well be affected by wind stress. Rae tentatively suggested that the principal effect of the wind function he used on haddock year-class strength was in orientating mixed oceanic-coastal water, of which *Metridia* is an indicator, over the haddock spawning grounds, and that such water provided a favourable environment for the development of the planktonic haddock stages. Saville (1959), using data on the distributions of plankton indicator species, was able to show a high degree of correlation between the proportion of the haddock spawning area occupied by such mixed water conditions and the size of the haddock broods over the period 1936-57.

CLYDE HERRING

Although not strictly applicable to a consideration of ground-fish stocks, the situation of the Clyde herring is of considerable interest in illustrating another situation where dispersion could play a major role in determining recruitment. The Clyde herring stock is a spring-spawning one with spawning taking place on Ballantrae Bank — a small bank of around 12 sq miles in extent situated near the entrance to the Clyde estuary. In addition to the fishery on the adult spawning shoals there is throughout the rest of the year a fishery within the estuary on adolescent fish and fish approaching first maturity. After spawning these fish leave the Clyde for feeding grounds off the Scottish west coast. The indications are that the Clyde adolescent fish recruit to the Clyde spawning stock and that the strength of a brood in its first and second years of life in the adolescent fishery is closely related to its subsequent strength as three year old first time spawners in the spawning fishery (Wood, 1960). This situation led to the hypothesis that the Clyde estuary formed a nursery ground for the recruits to the Clyde spawning shoals and that little if any recruitment to these shoals of first time spawners took place from any other nursery areas. In view of the situation of Ballantrae Bank — the major if not only spawning ground — it appeared highly probable that variations in direction and speed of drift could play a major role in determining year class strength. The situation of the spawning ground is such that minor variations in drift pattern could result in larvae going northwards into the Clyde estuary, southwards into the Irish Sea or westwards into the Atlantic and the Scottish west coast. If the interpretation of the stock characteristics is correct, then drift northwards into the Clyde would result in recruitment to the Clyde adolescent and subsequently to the Clyde spawning fishery whilst drift in other directions would mean poor recruitment to both branches of the Clyde fishery.

In 1957 a programme was commenced to investigate this situation and has been continued each year since. This programme took the form of a close grid of plankton stations over the spawning ground, repeated at short time intervals, to measure the production of larvae throughout the hatching season; and a grid of more widely spread stations, at less frequent intervals, to trace their subsequent dispersal. Each year, in the first fortnight of May, a survey of the upper reaches of the Clyde estuary was carried out to give a measure of the abundance of larvae, near the end of the planktonic phase in this region, as an index of recruitment to the Clyde stock.

In the 1958 season sampling over the spawning ground showed that over 90% of the season's hatching took place in the period 9th to the 15th March. Unfortunately sampling on the wider grids at this time was rather inadequate both in timing and in the extent of the area covered. The grids sampled on the 11th and 12th of March however both showed high concentrations of larvae over and to the south-west of the spawning area (Fig. 6). There was then a gap in the sampling until the 19th March. By then herring larvae were very scarce but the contoured distribution was suggestive of higher concentrations of larvae to the south and west of the area sampled (Fig. 7). In the remaining cruises of the 1958 season very few herring larvae were taken and the May cruise in the upper reaches of the estuary yielded the smallest numbers of herring larvae of any year in which the area was investigated.

The 1960 season showed a rather similar picture. The overwhelming preponderance of a fairly large hatching took place in the period 10th-18th March. A cruise covering a major part of the outer Clyde estuary on the 16th March yielded an abundance of early herring larvae with the contours open to the west and south of the area sampled (Fig. 8). On the next cruise to this area between the

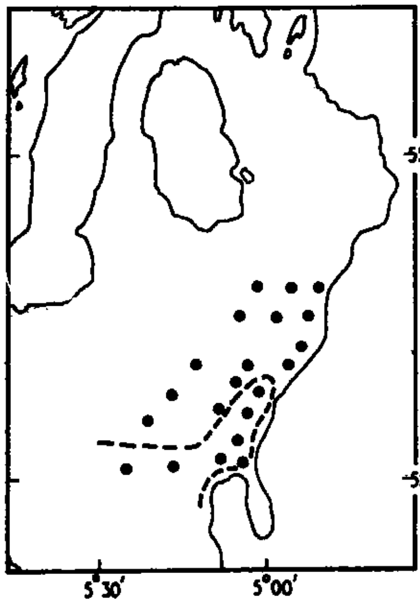

Fig. 6. Distribution of herring larvae in the Clyde on the 11th March 1958. Broken line 50 larvae per 15 min tow, 1 m net.

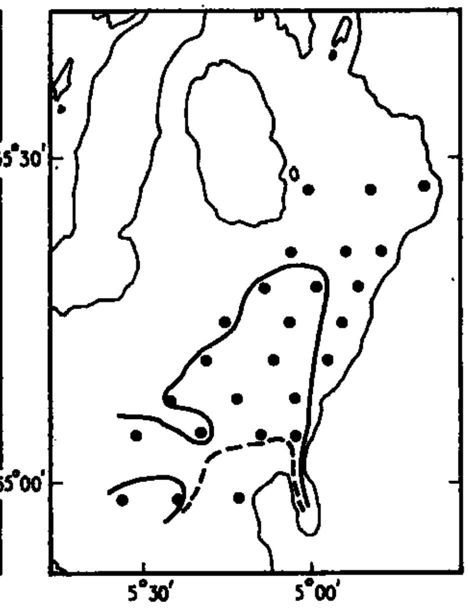

Fig. 7. Distribution of herring larvae in the Clyde on the 19th March 1958. Broken line 50 larvae, solid line 1 larva per 15 min tow, 1 m net.

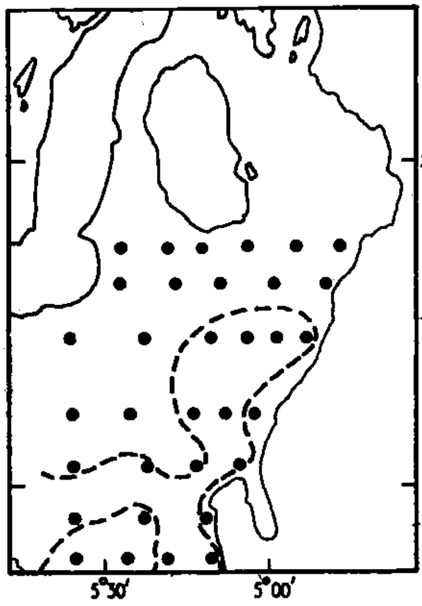

Fig. 8. Distribution of herring larvae in the Clyde on the 16th March 1960. Broken line 50 larvae per 15 min tow, 1 m net.

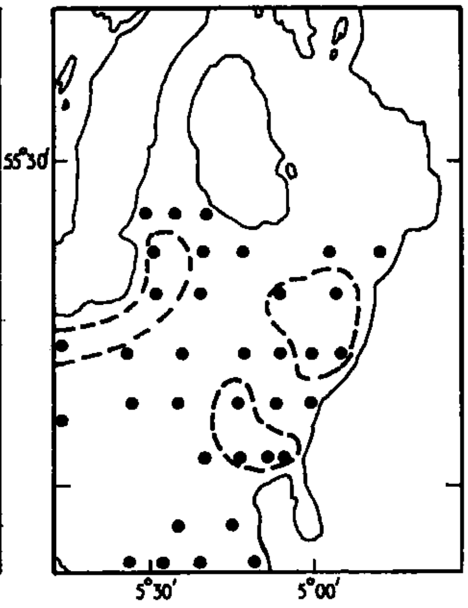

Fig. 9. Distribution of herring larvae in the Clyde on the 30th March 1960. Broken line 50 larvae per 15 min tow, 1 m net.

29th - 31st March the numbers of larvae had been very markedly reduced - giving an apparent mortality rate of almost 18% per day - and again there was evidence of a leakage of larvae westwards beyond the area sampled (Fig. 9). In 1959 and 1961 - the only other years for which the data have so far been completely analysed - the picture is rather different. In both years the centres of larval abundance on all cruises showed a marked restriction to the eastern part of the outer Clyde estuary and a steady progression northwards into the inner estuary between successive cruises (Figs. 10-12). In the years (1959, 1961) when the dispersal took place into the inner estuary the pattern is clear from the distribution on successive cruises. In the case of apparent dispersal outwith the area the evidence from this source is less conclusive - probably because of the short time it took the main body of larvae to drift from the spawning area to the limit of the surveyed area. As a result the distribution shown on succeeding cruises probably largely represents the proportion of larvae which were retained rather than the main body of larvae. This is supported by Fig. 13 which illustrates the reduction in larval numbers on succeeding cruises in each of the years considered. In 1958 and in 1960 larval abundance within the surveyed area suffered a very marked reduction within a short time of the main hatching peak with apparent mortality rates of 35% and 18% a day; in the years when dispersal was into the Firth the initial reduction in abundance was lower at under 10% per day.

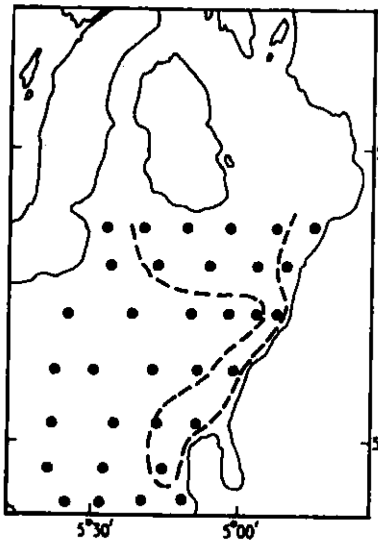

Fig. 10. Distribution of herring larvae in the Clyde on the 21st March 1961. Broken line 50 larvae per 15 min tow, 1 m net.

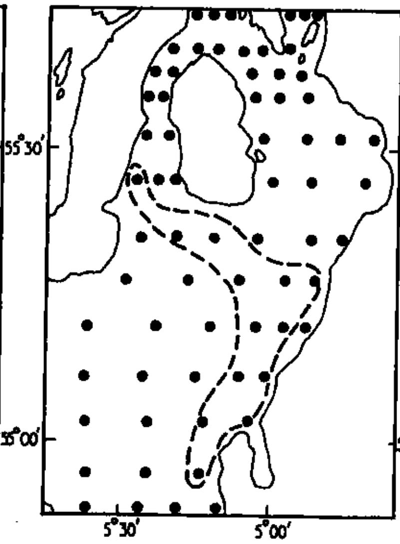

Fig. 11. Distribution of herring larvae in the Clyde on the 25th March 1961. Broken line 50 larvae per 15 min tow, 1 m net.

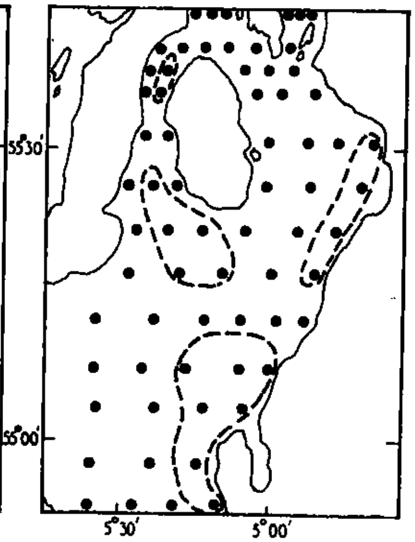

Fig. 12. Distribution of herring larvae in the Clyde on the 5th April 1961. Broken line 50 larvae per 15 min tow, 1 m net.

As previously mentioned, in the first fortnight of May in each year the upper reaches of the Clyde estuary were sampled to gauge the numbers of larvae which had reached this area. This number must be a function of three factors - initial number of herring larvae hatched in that year, larval mortality between the time of hatching and the time of the survey, and the proportion of larvae which were transported northwards into the area. In the years considered there were very marked variations in the amount of hatching which took place. In order to estimate the proportion of larvae reaching the upper Clyde these have been allowed for by dividing the abundance of larvae in the inner estuary (expressed as the mean catch per haul) by the ratios of the hatching in the year in question to that of 1959 taken as a standard. The material on the amount of hatching in 1963 has not yet been fully analysed but a preliminary value has been assigned to that year from a cursory inspection of the samples. This will be at least of the right order of size. No correction can be made for mortality because of the absence of any criterion to distinguish between transport out of the area and mortality *sensu stricto*. If however transport is a major factor in determining recruitment to the upper estuary any relationship between factors inducing transport and the proportion of larvae reaching the upper estuary should emerge in spite of the effects of other causes of loss in disturbing the relationship.

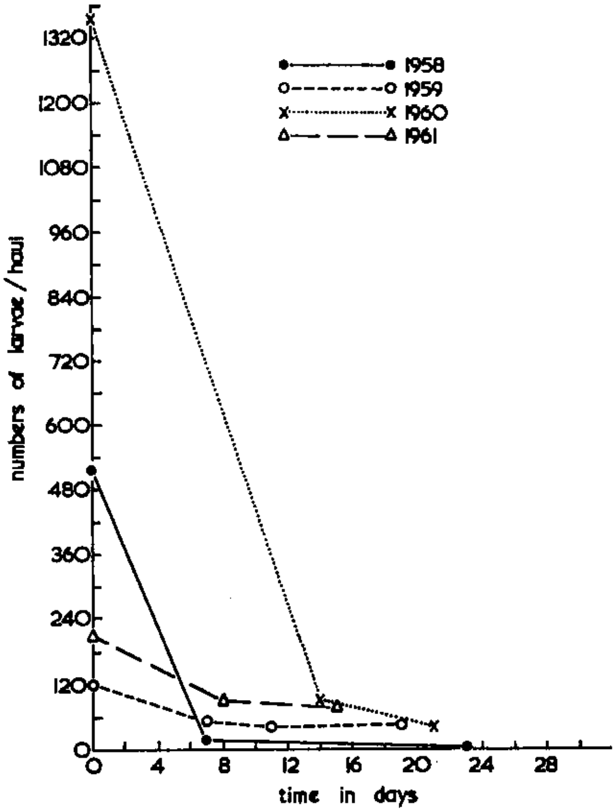

Fig. 13. Reduction in the abundance of herring larvae on succeeding cruises, 1958-1961.

These values for proportionate recruitment to the Clyde estuary are given in Table 3.

TABLE 3.—ABUNDANCE OF HERRING LARVAE IN CLYDE ESTUARY IN MAY 1957-63.

Year	Larval Abundance in May	Larval Abundance in May corrected for variations in hatching
1957	5.0	5.0
1958	0.05	0.01
1959	3.2	3.2
1960	7.1	0.8
1961	78.0	2.7
1962	1.0	0.3
1963	10.6	3.5(?)

It will be seen that in the corrected data the values for these years fall into two well-defined groups —1958, 1960 and 1962 with very low values and the remaining years with high values.

Additional information which supports the view that much of the variation in recruitment of larvae to the inner Clyde estuary is the result of water movements is supplied by drift bottle releases. In the years 1958-63 inclusive, whilst sampling of the spawning ground was in progress 10 drift bottles were released on each day the research vessel was over the spawning grounds. I am indebted to my colleague Mr R. E. Craig for information on the returns derived from these drift bottle releases. For the present purpose only returns from these releases made whilst hatching of herring larvae was in progress have been utilised. In Table 4 are given the number of drift bottles released during the period in each year, the number of returns from within the Clyde estuary and the numbers returned outwith the Clyde. These latter were principally from N. Ireland, the west coast of Scotland, and from the shores of the Irish Sea.

TABLE 4.—RETURNS OF DRIFT-BOTTLES RELEASED OVER CLYDE SPAWNING GROUNDS 1958-63.

Year	No. of D.B.'s released	No. returned from Clyde	Returns outside Clyde	% of returns from Clyde
1958	70	2	10	17
1959	80	26	0	100
1960	60	4	11	27
1961	35	15	0	100
1962	75	11	11	50
1963	90	33	0	100

These data show that the years also fall into the same two well-defined groups - 1959, 1961 and 1963 when all the returns came from the Clyde and 1958, 1960 and 1962 when half or more of the returns came from outwith the Clyde estuary. In 1957 when this work in the Clyde was begun the programme was more of an exploratory nature. In that year drift bottle releases were widely spread over the south-eastern part of the outer estuary and took place in two periods only, namely 4-5th March and the 25th-26th March. The returns from the releases of that year have already been reported by Craig (1959) who states: "The earlier releases suggested that most of these larvae would be carried into the Firth while the deduction from the second series is that most of the larvae produced near the later date would be carried out of the Firth". In view of the fact that the preponderance of hatching of herring larvae took place almost half way between these two release periods this information is not in itself of much value in deciding the role played in larval dispersion by water transport in that year (see however p.345).

In view of the major role played by wind in determining water movement wind data were extracted from the Daily Weather Reports of the British Meteorological Office. These give observations, at six hourly intervals, of wind direction and speed in knots at certain specified stations. For this purpose the observations selected were those taken at Renfrew, as being the closest to the Clyde area, and an arbitrary choice was made of the observations taken at 1200 hours on each day as being reasonably representative of the twenty-four hour period. For this purpose the daily wind values were considered over a three-week period, chosen to cover the three weeks occurring immediately after the inception of considerable hatching in that year. This period was chosen because experience of the course of hatching during the spawning seasons sampled, and the speed of drift experienced, suggested that this would be the maximum time necessary to determine whether the bulk of the season's production of larvae would reach the inner Clyde estuary or be lost to it. The winds for the days so selected were plotted in direction and strength and the northerly and easterly components for each week were calculated. These are given in Table 5.

TABLE 5.—NORTHERLY AND EASTERLY WIND COMPONENTS IN CLYDE DURING HATCHING PERIOD 1957-63.

Year	Week 1		Week 2		Week 3		Mean	
	N	E	N	E	N	E	N	E
1957	6.7	- 6.3	3.6	+ 0.8	3.8	+ 1.7	4.7	- 1.3
1958	1.8	+ 7.3	0.8	+ 6.7	- 1.0	+ 6.0	0.5	+ 6.7
1959	1.0	- 6.0	5.7	- 0.5	2.7	- 1.0	3.1	- 2.5
1960	0.5	+ 6.3	- 2.0	+ 6.7	- 1.0	+ 7.7	- 0.8	+ 6.9
1961	2.3	- 7.3	1.7	- 9.0	0.8	- 4.3	1.6	- 6.9
1962	- 0.3	+ 3.5	- 1.0	+ 0.8	0.3	- 1.1	- 0.3	+ 1.1
1963	2.7	- 0.5	- 2.0	- 4.7	0.3	+ 0.5	0.3	- 1.6

It will be noted that, as in the larval data of Table 3, and the drift bottle release data of Table 4, the years 1958, 1960 and 1962 are distinguished as being years with a prevalence of winds from the east, and with a weak northerly component, in contrast to the other years when the prevailing winds were from the west. This relationship would however seem to be of a qualitative rather than a quantitative nature; the particularly strong component of wind from the west in 1961, with a particularly low northerly value, did not result in an improved recruitment to the inner Clyde in that year when compared with the years of less strong westerly components; similarly the rather weak easterly component of 1962 appears to have been as deleterious as the much stronger one of 1960. This is only to be expected in view of the other factors which must play a part in controlling larval survival.

In view of the apparent relationship between wind and drift bottle returns shown in Tables 4 and 5 it seemed worth re-examining the wind data for 1957 in the light of Craig's (1959) drift bottle results. This showed winds consistently from the west in March up to the 22nd of that month with a reversal thereafter for the remainder of the month into winds from the east. It would appear likely therefore that the change in the current system in the Clyde, which Craig found between the 5th and the 25th March, took place probably as late as around the 22nd March. By that time the main hatching of herring larvae was over and the current system depicted by Craig for the first series of releases probably played the major role in determining larval drift. From this evidence, 1957 would fall into the same group as the years 1959, 1961 and 1963 (Table 4). Barnes and Goodley (1961), also concluded that the pattern of surface drift in the Clyde is markedly wind dependent.

There thus seems to be reasonably strong evidence that the direction of dispersal of spring-spawned larvae from Ballantrae Bank is largely determined by the east-west and north-south wind component over a short period after hatching and that this influences the abundance of later stage herring larvae in the inner reaches of the Clyde. It would seem however that the abundance of such larvae in this area is by no means a criterion of future year-class strength in the commercial fishery. In Table 6 are given the catch per unit effort of each of the year classes investigated in their planktonic phase which have so far recruited to the fishery as adolescents between 1 and 2 years old and as recruit spawners spawning as 3 year olds. These were computed from routine landing statistics and from the age composition of the landings assessed from one or two random samples taken each week.

TABLE 6.—CATCH PER UNIT EFFORT OF YEAR CLASSES OF CLYDE HERRING.

Year Class	Catch/effort as 1+ fish	Catch/effort 3 year old spawners
1957	10.28	17.22
1958	14.38	5.84
1959	2.13	0.32
1960	5.87	0.41
1961	7.80	?

The two indices of year class strength are not in as close agreement as one might wish - particularly with respect to the low index of the 1958 brood as spawners compared with their abundance in the adolescent fishery. This has also been a feature of this year class in subsequent years and deserves further investigation. Both of these indices however are in agreement in marking 1958 as a successful year class in the scale of this series of years and 1959 as a very poor one, in contrast to their rating in Table 3. The evidence from these data with regard to the 1958 year class would suggest therefore that drift out of the Clyde is not necessarily inimical to the prospects of a year class and presumably a return movement may take place during the post-planktonic stage. A comparison of the data of Tables 3 and 6 would also suggest the possibility of considerable differential mortality between year classes in a late planktonic or post planktonic stage in herring.

DISCUSSION

The early work of Carruthers (1937) and Carruthers and Hodgson (1937) suggested a relationship between both year-class strength of North Sea haddock and Southern Bight herring and the wind regime prevailing during the planktonic stages in the life-cycle. This suggestion of a relationship between brood-strength and wind was further formalised and extended to cover a wider range of species in the post-war papers of Carruthers and his collaborators. A similar relationship between wind and year-class strength was demonstrated for Georges Bank haddock by Chase (1955). In spite of these apparent associations between wind and brood strength, there appear in the literature to be few authenticated cases of a direct effect of wind on the transport of eggs and larvae. In particular successful predictions have been few, although Graham (1925) was able, in a very generalised way, to predict the distribution of cod larvae in the central North Sea in one year from a consideration of wind direction and strength.

In the present paper some evidence is produced that under an unusual wind regime the normal distribution of haddock larvae at Faroe is disrupted, and for herring larvae in the Clyde the effect of wind variations on larval transport seems well authenticated. In the North Sea haddock, on the other hand, wind variation, within the range found in the years investigated, seems to have no appreciable effect on larval transport. It would appear, on this evidence, that only in certain situations, where comparatively minor variations in wind from the normal pattern can produce wide ranging effects is wind variation likely to produce marked differences in dispersal pattern. One such situation is where isolated stocks occupy banks of small extent when short periods of persistent winds from one quarter can push the planktonic fauna overlying the bank over oceanic depths or into well-defined stream currents. This situation is well illustrated at Faroe and on Georges Bank. In the north Atlantic there are several such banks which maintain what are apparently self-contained stocks of ground fish. Fraser (1958) has discussed the problem of the retention of the planktonic stages within the habitat of the stock in such situations. It is of interest in this connection that what little is known about the population structure in such habitats suggests that year-class fluctuations are more violent than in populations with less restricted distributions. This would seem to be so for the haddock stocks on Porcupine Bank in the north-east Atlantic (Hickling, 1946) and on St. Pierre Bank in the north-west Atlantic (Beverton and Hodder 1962).

The Clyde situation is probably a peculiar case where comparatively slight northwards transport brings the larvae within the sheltering arms of the Firth while initial southerly or westerly transport of limited extent results in larvae being carried into a current system which militates against subsequent return in the planktonic phase. Even here however there seem to be no demonstrable relationship with the subsequent number of recruits to the commercial shoals.

REFERENCES

BARNES, H. and E.F.W. GOODLEY, 1961. The general hydrography of the Clyde Sea Area, Scotland. Part 1: Description of the area; drift bottle and surface salinity data. *Bull. Mar. Ecol.*, 5: 112-150.

BEVERTON, R.J.H. and V.M. HODDER, 1962. Report of working group of scientists on fishery assessment in relation to regulation problems. *I.C.N.A.F. supplement to Annual Proc.* Vol. 11.

BODEN, B.P.,1952. Natural conservation of insular plankton. *Nature, Lond.*, 169 : 697-699.

CARRUTHERS, J.N. 1937. A note on plaice fluctuations in the southern North Sea. *Rapp. Cons. Explor. Mer*, 105: 14-15.

1950. An attitude on fisheries hydrography. *J. Mar. Res.*, 10: 101-118.

CARRUTHERS, J.N. and W.C. HODGSON, 1937. Similar fluctuations in the herrings of the East Anglian fishery and certain physical conditions. *Rapp. Cons. Explor. Mer*, 105: 10-13.

CARRUTHERS, J.N., A.L. LAWFORD, and V.F.C. VELEY, 1951. Fishery hydrography: brood strength fluctuations in various North Sea fish with suggested methods of prediction. *Kieler Meeresforsch.*, 8: 5-15.

CARRUTHERS, J.N. *et al.* 1951. Variations in brood strength in the North Sea haddock, in the light of relevant wind conditions. *Nature, Lond.*, 168 : 317-319.

CHASE, J. 1955. Winds and temperatures in relation to brood strength of Georges Bank haddock. *J. Cons. int. Explor. Mer*, 21: 17-24.

CRAIG, R.E. 1959. *Ann. biol. Copenhague*, 14 (1957) : 63.

FRASER, J.H. 1939. The distribution of chaetognatha in Scottish waters in 1937. *J. Cons. int. Explcr. Mer*, 14: 25-34.

1958. The drift of the planktonic stages of fish in the northeast Atlantic and its possible significance to the stocks of commercial fish. *Spec. Publ. int. Comm. Northw. Atlant. Fish.*, No. 1, 289-310.

GRAHAM, M. and J.N. CARRUTHERS, 1925. The distribution of the pelagic stages of the cod in the North Sea in 1924 in relation to the system of currents. *Fish. Invest., Lond.*, *Ser 2*, 8 (6): 1-31.

HANSEN, V. 1955. Zooplankton and hydrography in the southern part of the Norwegian Sea. *Cons. int. Explor. Mer, C.M. 1955, Plankton Committee* No. 29.

HICKLING, C.F. 1946. Haddock on Porcupine Bank, September 1944. *J. mar. biol. Ass. U.K.*, 26: 398-407.

HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. Cons. Explor. Mer*, 20: 1-228.

JONES, R. 1951. *Ann. biol., Copenhague*, 7:(1950): 28-31.

JONES, R. and W. MAIN. 1952. *Ann. biol., Copenhague*, 8(1951): 36-39.

1953. *Ann. biol., Copenhague*, 9(1952): 35-38.

1954. *Ann. biol., Copenhague*, 10(1953): 32-35.

ORTON, J.H. 1937. Some interrelations between bivalve spatfalls, hydrography and fisheries. *Nature, Lond.*, 140: 505.

PARRISH, B.B. 1950. Brood fluctuations in the North Sea haddock population. *Challenger Soc. Abstracts*, 3 (2): 18.

RAE, K.M. 1957. A relationship between wind, plankton distribution and haddock brood strength. *Bull. Mar. Ecol.*, 4: 247-69.

RAITT, D.S. 1936. The haddock stocks of the north-east Atlantic, 1916-35. *Sci. Invest. Fish. Scot., 1936*, No. 1: 1-32.

SAVILLE, A. 1956. Eggs and larvae of haddock at Faroe. *Mar. Res. Scot., 1956*, No.4: 1-27.

1959. The planktonic stages of the haddock in Scottish waters, *Mar. Res. Scot., 1959*, No. 3: 1-23.

STEELE, J.H. 1957. The role of lateral eddy diffusion in the northern North Sea. *J. Cons. int. Explor. Mer*, 22 : 152-62.

TAIT, J.B. 1934. Surface drift-bottle results in relation to temperature, salinity and density distributions in the northern North Sea. *Rapp. Cons. Explor. Mer*, 89: 68-79.

VELEY, V.F.C. 1951. Fishery hydrography; brood strength fluctuations in the hake with a suggested method of prediction. *Ann. Biol. Copenhague*, 7(1950): 44-46.

WALFORD, L.A. 1938. Effects of currents on distribution and survival of the eggs and larvae of haddock (*Melanogrammus aeglefinus*) on Georges Bank. *Fish. Bull. U.S.*, 49 (29): 1-73.

WILSON, D.P. 1948. The relation of the substratum to the metamorphosis of Ophelia larvae. *J. mar. biol. Ass. U.K.*, 27: 723-60.

WOOD, H. 1960. The herring of the Clyde estuary. *Mar. Res. Scot., 1960:* No. 1, 1-24.

B-7

COMPARATIVE CHARACTERISTIC OF SOME BIOLOGICAL INDICES OF THE BOTTOM STAGES OF O-GROUP COD BELONGING TO THE 1956, 1958, 1959, 1960 AND 1961 YEAR-CLASSES.

By

I.Ja. Ponomarenko[1]

ABSTRACT

Annual fluctuations in the fatness and nutritional condition of cod fry in the southern part of the Barents Sea are governed by the availability of Euphausiacea in their food, the main item of the diet of the O-group of cod. The more Euphausiacea there are in their food, the higher is the level of fatness and nutritional condition of the fry.

The length of cod fry at the end of the first year of life is closely related to the temperature conditions in a given year. In warmer years the fry grow faster than in colder ones. Due to the annual fluctuations in length and condition of fry, their accessibility to small predators (for instance the young cod of age groups I, II and III) changes from year to year. The smaller and less nourished are the fry, the more can predators feed on them.

Feeding conditions and the thermal regime of the sea, affecting growth indirectly (through predators), influence the mortality of the fry; that is, the formation of the year-class strength. Due to the faster growth rate of the O-group, the conditions for maintaining the strength of a year-class of cod at a high level are better in warmer years than in colder ones, all other conditions being equal, particularly the feeding conditions.

To determine the factors influencing variations in the amount of fish recruited to the commercial stock of the Barents Sea cod, the Polar Institute (PINRO) annually carries out investigations on feeding, fatness, nutritional condition and sizes of the bottom stages of O-group cod.

In this report the following indices for cod fry belonging to the five generations are compared:

1) food composition (weight in %);

2) stomach fullness index in ^{o}/ooo (the relation of food weight to fish weight multiplied by 10000, *i.e.*, per decimille);

3) fatness (the relation of liver weight to fish weight in %);

4) nutritional condition (the relation of the weight of a fish to the long-term mean weight of fish of the same length in %);

5) mean length (in cm);

6) the importance of the bottom stages of O-group cod to the feeding of cod fry of the I-II-III age groups in November-December.

These indices are compared with the abundance of the bottom stages of O-group cod belonging to the given year-classes and with the temperature anomalies occurring along the Kola hydrological section. The materials were collected by PINRO research vessels in November-December of 1956 and 1958 to 1961 to determine the abundance of the young of the commercial fishes. The 25-meter bottom trawl with a fine-mesh net (10 mm), inserted into the codend was used. The quantitative analysis of young cod is carried out annually in the autumn-winter period in the Barents Sea. From the catch of the bottom stages of O-group cod per hour, one can determine the abundance of a year-class at the first year of life. The data on catches of fry per hour's trawling are taken from the work of A.S. Baranenkova.

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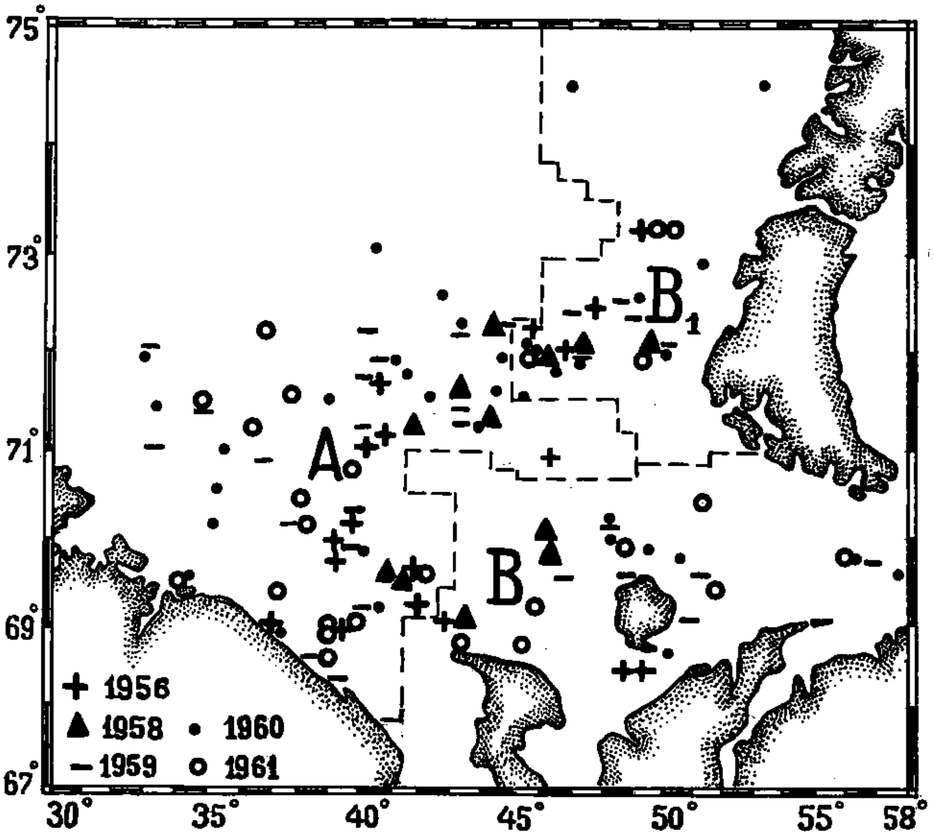

Fig. 1. Areas where samples of 0-group cod were taken for the analysis of food, fatness and nutritional condition. The dotted line separates the Central Zone (A) from the South-eastern (B) and North-eastern (B_1) zones.

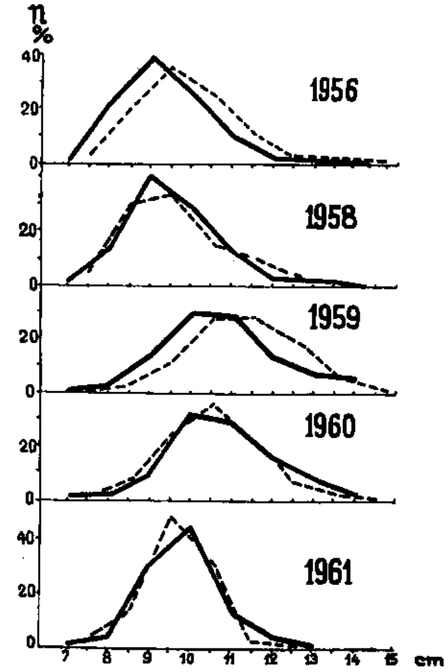

Fig.2. The size composition of the fry of 0-group cod which were examined (dotted line) and of all the 0-group fry caught by trawl during the period of the study.

Samples were collected from the Murman Coast to Novaya Zemlya Bank (Fig. 1). The length composition of the fry examined and of all fry of the 0-group taken with a trawl is given in Figure 2.

Euphausiacea (32.5% by weight), Gammaridea (15.6%), Polychaeta (10.6%) and Pisces (17.4%) were the main food items of cod fry over the average period of five years in the near-bottom layers of the Barents Sea (Figs. 3 and 4). Appendicularia (4.9%), Hyperiidea (4.5%), Decapoda (4.3%), Chaetognatha (4.1%), Mysidacea (2.0%), Cumacea (0.6%), Caprellidea (0.5%), Isopoda (0.4%), and others are of secondary importance in the food of cod fry. A total of 101 species were found in the stomachs of 0-group cod.

Local differences are traced in the feeding of the bottom stages of cod fry. On these grounds we can divide the southern part of the Barents Sea into the three conventional zones (Figs. 1, 3, 4 and 5): Central (A), where the main fry food is Euphausiacea; South-eastern (B), where Gammaridae and Polychaeta prevail; and North-eastern (B_1), where the fry of *Boreogadus saida* and the young of *Lumpenus* are the dominant food objects. All the quantitative data on feeding, represented in Figures 3, 4 and 5, were calculated separately for each of the three zones and for the whole sea.

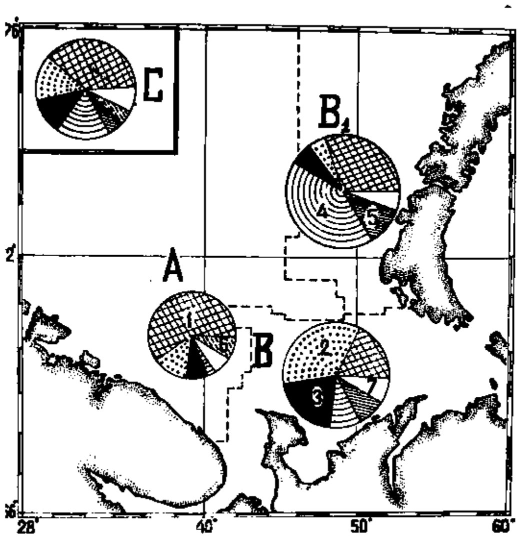

Fig. 3. Food composition (as % by weight) of the bottom stages of 0-group cod according to the five year observations:

A-in the Central zone;
B-in the South-eastern zone;
B_1-in the North-eastern zone;
C-all zones combined;

1. Euphausiacea (together with Hyperiidea and Mysidacea):
2. Gammaridea (together with Caprellidea, Cumacea and Isopoda);
3. Polychaeta;
4. Pisces;
5. Appendicularia;
6. Chaetognatha;
7. Others.

The radius of each circle is in proportion to the average index of stomach fullness.

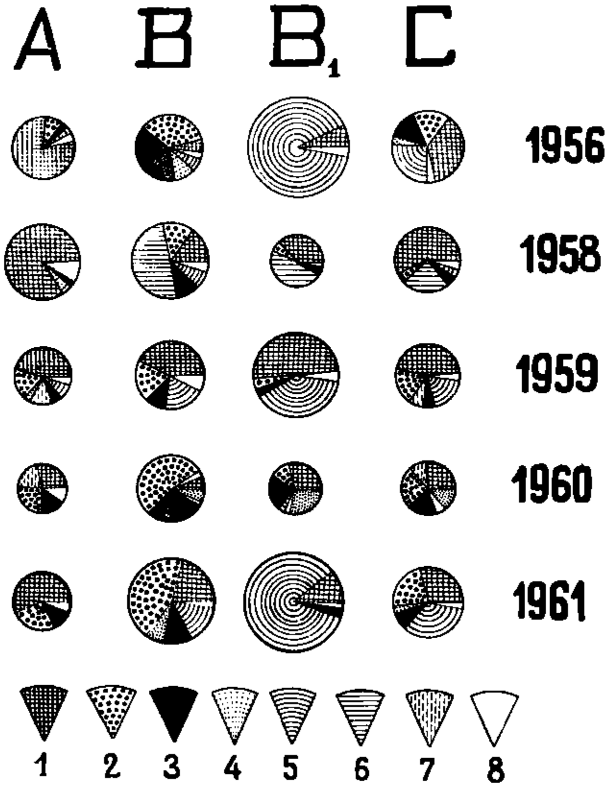

Fig. 4. Food composition (as % by weight) of the bottom stages of 0-group cod of the 1956, 1958-61 year-classes. The zones (A - C) and organisms (1-7) are the same as those shown in Figure 3.

Food composition of cod fry in 1956 and 1958 to 1961 is shown in Figure 4; fatness (I), nutritional condition (II), stomach fullness index (III) and the single index of Euphausiacea (the relation of the weight of the Euphausiacea eaten to fish weight in %) are presented in Figure 5. The percentage of feeding specimens did not differ greatly from one year to another (from 76% to 86.3%) and over the course of five years it averaged 82.8% in the Central zone, 83.8% in the South-eastern zone and 82% in the North-eastern zone.

Most of the material was collected in the Central zone, where the greatest abundance of the bottom stage of 0-group cod occurred in the years investigated (Fig. 5). Annual variations in fatness, nutritional condition and stomach fullness index of 0-group cod in the Central zone are closely connected with the annual changes in importance of Euphausiacea in the diet of fry. Thus, the highest (in 1958) and the lowest (in 1960) fatness, nutritional condition and stomach fullness index correspond to the greatest (98°/ooo in 1958) and the least (7.8°/ooo in 1960) importance of Euphausiacea in the food of fry (Fig. 5, A.I,II,III). The importance of Euphausiacea in the diet of fry determines the annual variations in fatness and nutritional condition of the bottom stages of 0-group cod in the southern part of the Barents Sea. The stomach fullness index, fatness and nutritional condition of cod fry belonging to the moderately abundant 1956, 1958, 1959 year-classes were similar. The relative importance of Euphausiacea in the food of fry was approximately the same during these years (special index 39.2, 51.7 and 48.8 respectively). The fry of the 1960 and 1961 year-classes occurred in low numbers in the southern part of the Barents Sea and were characterized by lower

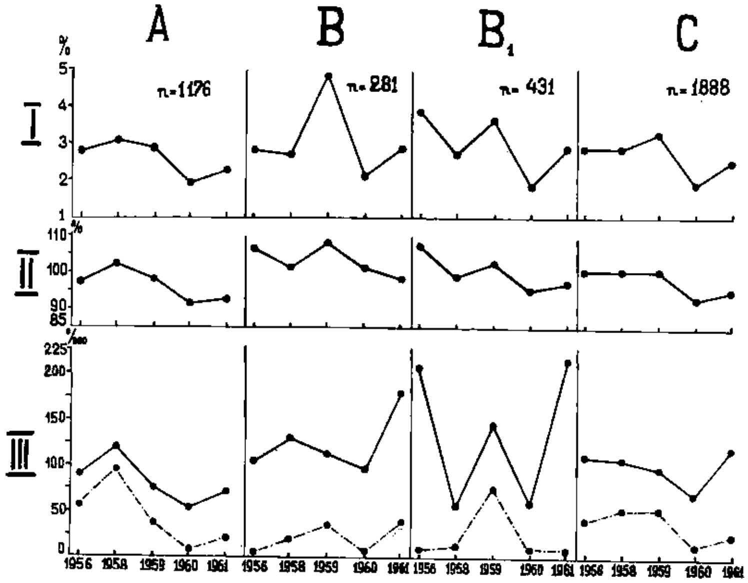

Fig. 5. Quantitative index of feeding of the bottom stages of 0-group cod in November/December. The zones (A - C) are the same as those shown in Figure 3.
I - Fatness.
II - Nutritional condition.
III - Total index of stomach fullness (solid line).
Index for Euphausiacea (broken line).

fatness, and nutritional condition, which corresponded to the lesser importance of Euphausiacea in the food of cod (Fig. 5, C, I, II, III Table 1). Probably, Euphausiacea play a great part in the diet not only of the bottom but also the pelagic stages of 0-group cod. This assumption is confirmed by the PINRO data on feeding of the pelagic fry of cod (Sysoeva and Degtereva, 1964, and Wiborg's data, 1960). The transition of cod fry to the near-bottom life is evidently closely associated with the descent of Euphausiacea to the bottom layers.

For the five years investigated, the three values change almost in parallel from one year to another: 1) importance of Euphausiacea in the diet of 0-group cod at the bottom stages; 2) nutritional condition of 0-group cod; 3) abundance of 0-group cod. Such interdependence can probably be explained by the drift of cod fry and the young of Euphausiacea from the west to the east and by the greater survival-rate of cod fry during the years when the young of Euphausiacea are abundant. However, further investigations are necessary.

No link was traced between the temperature conditions during the year and the quantitative data on the feeding of the bottom stages of 0-group cod. Thus, in the cold years (1956 and 1958), when the annual temperature anomalies in the 0-200 m layer in the Kola section were -0.65° and -0.58°, and in the relatively warm year (1959), the fry of cod had similar stomach fullness index, fatness and nutritional condition. In 1959 and 1960, when similar temperature conditions occurred (anomalies +0.18° and +0.17°C), the fatness and nutritional condition indices of fry strongly differed (Fig. 5). However, a close relationship between the sizes of cod fry in November-December, and the temperature in February-October was found (Fig. 6). The growth rate of 0-group cod was somewhat lower in the cold years than in the warm years. In November-December, the average length of fry of the 1956 and 1958 year-classes was 9.29 and 9.57 cm and of fry of the 1959 and 1960 year-classes was 10.79 and 10.81 cm. Temperature and the length of fry are average for the other years, 1957, 1961 and 1962.

One of the most numerous small predators of cod fry in the bottom layers of the Barents Sea is small cod of the I, II and III age groups (length 15-35 cm). The importance of fry in the diet of cod of these age groups depends upon the abundance of the 0-group, and also upon the length and nutritional condition of fry. Our data show that in November-December the small cod feed mainly

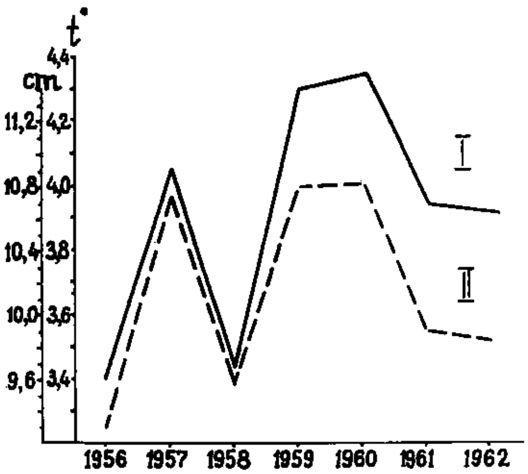

Fig. 6. Relation between the mean water temperature (I) in the 0-200 m layer in February/October (along the Kola section) and the mean length of the bottom stages of 0-group cod in the Southern part of the Barents Sea in November/December (II).

on cod fry not over 10 cm in length (Ponomarenko, 1961). The larger fry, however, are fed on only if they have a low nutritional condition value. The fry of the 1956 and 1958 year-classes, having the lowest length, and the fry of the 1960 year-class, having the lowest nutritional condition, were eaten in the greatest quantity. The large fry of the 1959 year-class, with high value for nutritional condition, were eaten in the smallest quantity. (Table 1). If one now considers the small size and low nutritional condition of fry of the 1961 year-class, one would expect these fry to be found in numbers in the stomachs of cod of the I, II and III age groups. The fry of this generation were, in fact, fed upon in small numbers. This is another demonstration of the low abundance of the 1961 year-class in the southern part of the Barents Sea. Thus, in the years when the bottom stages of 0-group cod are small or in low nutritional condition or both, they become more available to the predators and the number of predators which are able to live on the fry in the bottom layer increases.

TABLE 1.—THE IMPORTANCE OF THE BOTTOM STAGES OF 0-GROUP COD IN THE DIET OF COD FRY OF AGE GROUPS I, II AND III* IN COMPARISON WITH THE ABUNDANCE OF 0-GROUP FRY, THEIR SIZES AND NUTRITIONAL CONDITION.

Year-classes:	1956	1958	1959	1960	1961
Importance in the diet					
% by weight	42.8	55.0	4.4	20.7	5.2
occurrence	31.7	25.5	2.9	13.2	5.4
Average catch per hour of 0-group cod in the southern part of the Barents Sea	12	11	11	7	3
Average length of 0-group cod	9.29	9.57	10.79	10.81	9.9
Nutritional condition of 0-group in % of the long-term mean	100	100	100	93.1	94.0

The thermal regime of the sea and the feeding conditions of 0-group cod influence the sizes and nutritional condition of fry. The latter two indices determine the degree of fry mortality caused by the small predators. Owing to the more intensive growth of 0-group cod, their survival-rate in the warm years will be better than in the cold years.

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* Samples for study of the feeding of cod fry of the I, II and III age groups, 15-35 cm in length, were taken in the same areas and in the same way as the samples for study of the 0-group feeding. Age-composition was approximately the same during all the years. A total of 2289 stomachs were examined. The analysis of stomachs was made by the quantitative-weight method.

REFERENCES

PONOMARENKO, I.Ja. 1961. On Possible Influence of Feeding of Cod Fry upon their Abundance. *Trud. Soveshch. ikhtiol. Kom.*, XIII.

SYSOEVA, T.K. and A.A. DEGTEREVA. 1964. The Relation Between the Feeding of Cod Larvae and Pelagic Fry and the Distribution and Abundance of their Principal Food Organisms. *This symposium, Contribution No. B-16.*

WIBORG, K.F. 1960. Investigations on Pelagic Fry of Cod and Haddock in Coastal and Offshore Areas of Northern Norway in July-August 1957. *Fiskeridir. Skr. Havundersøk.* (Report on Norwegian Fishery and Marine Investigations), XII (8).

B-8

DRIFT MIGRATIONS AND THEIR SIGNIFICANCE TO THE BIOLOGY OF FOOD FISHES OF THE NORTH ATLANTIC

By

Ju.Ju. Marty[1]

ABSTRACT

The passive transport of fish by water currents is discussed in relation to the evolution, feeding and development of the fish stocks. It is shown that knowledge of such drift migrations is needed for assessing the productivity of a sea area and for predictions of recruitment to the commercial stocks. In calculating growth rates it is necessary to remember that different contingents of a species may have differing histories of drift migration and hence of feeding and development. Detailed investigations of the dynamics of fish stocks are needed and international collaboration will be necessary.

Drift migrations, *i.e.*, the passive transport of living organisms by water masses, are common amongst representatives of the animal world living in the hydrosphere. These migrations occur not only among planktonic organisms, whose possibilities for horizontal movement are very limited, but among nekton as well and particularly among various species of fish. Drift migrations are especially characteristic of fishes inhabiting the boreal waters of the North Atlantic (Meek, 1916; Schering, 1929; Schmidt, 1947; Zenkevitch, 1963). The drift of eggs, larvae and fry has been well studied for cod, haddock, herring and redfish of the Norwegian, Greenland and Barents Seas (Hjort, 1914; Lea, 1929; Baranenkova, 1957, 1960; Baranenkova and Khokhlina, 1959, 1961; Maslov, 1944, 1957 and 1960; Marty, 1941, 1956 and 1961). Eel larvae brought by the Gulf Stream to the European shores serve as a classic example of a prolonged drift migration (Schmidt, 1929). Passive dispersal starts either at the stage of developing egg (gadoids; flatfishes), or at that of hatching for demersal eggs (herring) (Marty, 1961).

Drift migrations result in the extension of the species habitat and wider utilization, as feeding areas, of enormous sea spaces which for various reasons cannot be used by a given species for reproduction. Through the resulting extension of the habitat, drift migrations reduce the possibility both for interspecific and intraspecific competition.

Drift of eggs, larvae and fry represents the first stage in the migration cycle of immature fish. The second stage of this cycle is a return migration of fish to the spawning grounds. For the majority of species the drift migration lasts for about 6-8 months. During this period the young are carried from the spawning grounds to the feeding areas over a distance of 500 to 800 or more miles. The return migration is accomplished within 3 to 8 years depending on the rate of growth and maturation of particular species.

Passive dispersal of living organisms takes place not only in the hydrosphere but also in the atmosphere where the air currents carry, first of all, plant seeds. However, there are some radical differences in the passive dispersal of living organisms in the atmosphere and in the hydrosphere (Marty, 1961). Plant seeds can be carried and deposited by air currents into various, even lethal conditions. Eggs and larvae of fish and of other marine animals are transported with water masses within which their development began and which are characterized by a very slow and gradual change of their physical and chemical qualities. Yet, even in the hydrosphere, it is possible that the young may find themselves in unusual environmental conditions. For example, the young of the coastal fish can be carried out to the open sea; pelagic eggs and larvae can drift into areas occupied by floating ice etc. Such conditions are known to exist in a number of areas of the Pacific Ocean.

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The main condition for drift migration of the young is the proximity of the spawning grounds to the permanent currents. The next condition for favourable drift of the young of the bottom and demersal fishes is the direction of the currents along the shelf or towards the shallow waters. Pelagic fishes and herring, in particular, can be carried even to the remote areas of the open sea. There are a variety of ways in which the young may "withdraw" from the drift. The young may cease to drift when the movement of the water masses stops, or if they get into the eddy zones, sink to the bottom, or swim out of the areas of the permanent currents.

Habitats of the main commercial species in the Barents Sea (Figs. 1,2,3,4,5) are quite different. These differences are based, first, on the different starting points of the drift, *i.e.*, on the location of the spawning grounds and, second, on the biological peculiarities of the young.

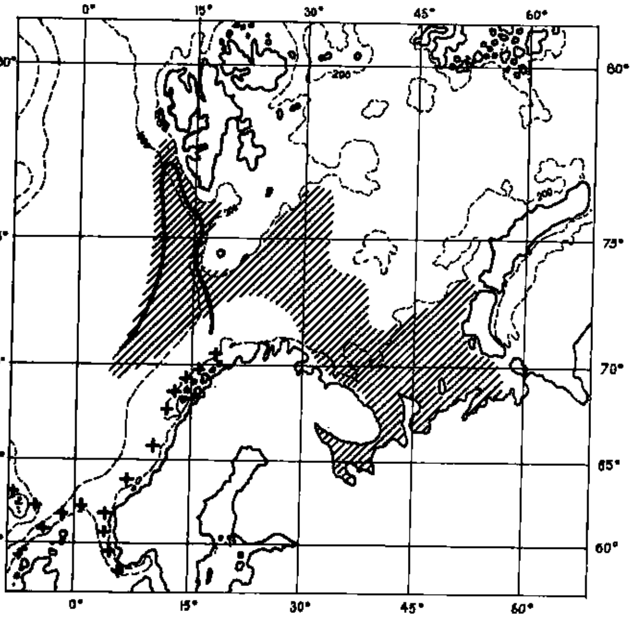


Fig. 1. Atlanto-Scandian Herring. Showing distribution of fingerlings (shading), spawning areas (crosses), limits of distribution of adults (heavy line). (from Marty and Shutova-Korzh).

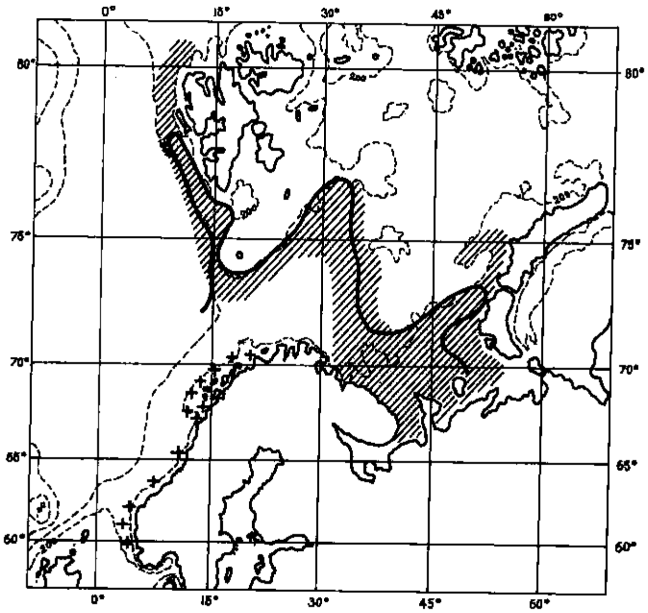


Fig. 2. Cod. Showing distribution of fingerlings (shading), spawning areas (crosses), limits of distribution of adults (heavy line). (from Maslov and Baranenkova).

It is not yet clear to what extent the habitat of the young of certain commercial species reflect the natural mortality of the young in different areas as being influenced by the abiotic factors or predation.

The greatest habitats of the young herring as a pelagic fish are mostly found in the Norwegian, Greenland and Barents Seas. They are encountered in the eastern part of the Norwegian Sea and in the Spitsbergen Current up to 76 - 77°N and further north. The young herring inhabit both the southern part of the Barents Sea and the White Sea.

The distribution of young cod in the Barents Sea is similar to that of herring. In the Norwegian Sea young cod are observed in the eastern branch of the Norwegian Current and in the Spitsbergen Current — along the whole western coast of Spitsbergen. Some of the young cod, according to observations made by the Polar Institute, are carried into the Arctic Ocean. The young cod are undoubtedly carried to the White Sea as well, though to a much less extent than herring. Haddock are characterized by a more westerly distribution. The young of the "golden redfish" are found predominantly in the northwest areas of the Sea, as well as along the main branch of the Norwegian Current. The young of *Sebastes mentella* inhabit the northwest areas of the Barents Sea and do not occur in its central part.

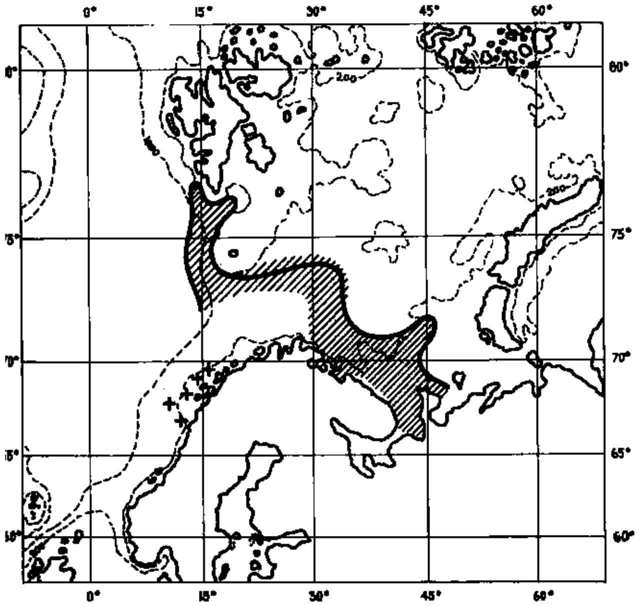


Fig. 3. Haddock. Showing distribution of fingerlings (shading), spawning areas (crosses), limits of distribution of adults (heavy line). (from Baranenkova and Sanina).

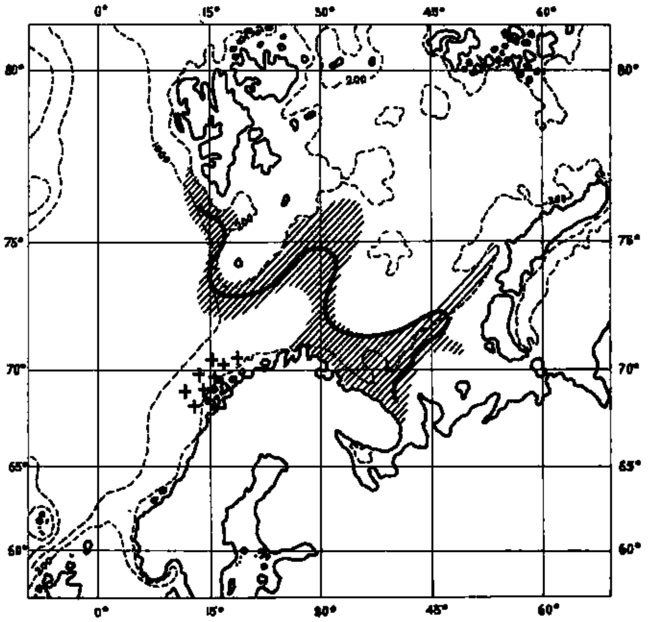


Fig.4. *Sebastes marinus*. Showing distribution of fingerlings (shading), spawning areas (crosses), limits of distribution of adults (heavy line). (from Baranenkova and Khokhlina).

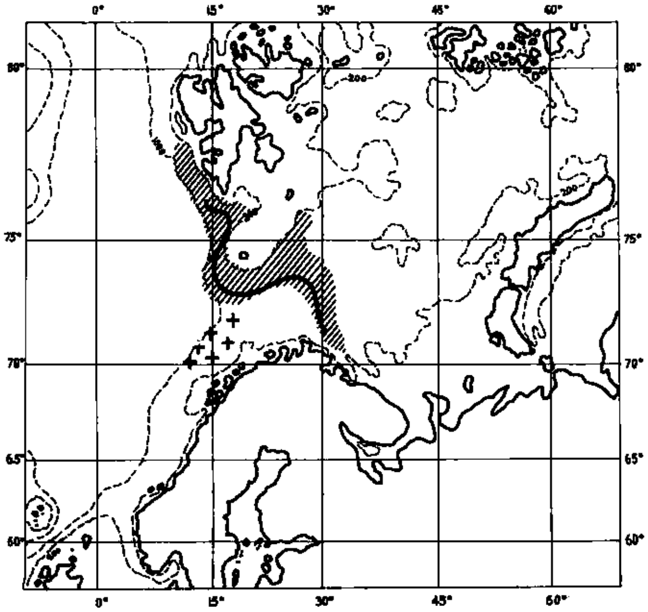


Fig. 5. *Sebastes mentella*. Showing distribution of fingerlings (shading), spawning areas (crosses), limits of distribution of adults (heavy line). (from Baranenkova and Khokhlina).

Observations on the distribution of the individual year-classes of herring in the Barents Sea were begun as far back as in the thirties and have been continued to the present day by Dr Shutova-Korzh (Marty, 1941, 1956; Shutova-Korzh, 1960). The widest distribution was observed for the 1937 and 1950 year-classes. Inshore distribution characterised the abundant 1930 year-class, the bulk of which penetrated into the White Sea, returned along the Murman coasts and entered the inlets of the Motovsky Gulf. The abundant 1934 year-class had an open sea distribution. A similar pattern of distribution was registered for the 1943 and 1944 year-classes. The rich 1959 year-class was distributed widely. However, it did not penetrate into the east and northeast areas.

The drift migrations of the ichthyofauna of the boreal area probably originated during the glacial epoch; first, the reproduction of all relatively warm-water species could then occur only in the areas affected by the warm currents; secondly, the drift of the young perhaps had already been taking place in the more northward latitudes (Marty and Wilson, 1960). Alternate cold and warm periods have made the migrations a habit (Marty and Wilson, 1960). It seemed to be equally advantageous for the boreal species in the period of stabilization of the temperature regime of the sea as in the periods of temperature ups and downs.

Experience gained in the cod and herring fisheries in the North Atlantic shows convincingly that, during the periods of temperature rise of the Subarctic areas and the extension of the boreal area, the abundance of boreal species tends to go up, resulting in extended feeding areas and longer feeding migrations. In hydrologically warmer years drift migration of the young of boreal species is also extended. Research conducted by Wiborg (1957) showed that the abundant year-classes of cod relating to warm years are carried from the northwest coast of Norway much faster than poor ones. This is undoubtedly due to acceleration of the current in warmer years. The young of cod, haddock and herring are brought to the Barents Sea earlier and distributed wider and more to the east during warm years than in colder years.

Thus, there seems to be a definite relation between the spawning conditions, the abundance of the young and the factors favouring the dispersal of the latter. The great speed with which the young adapt to favourable life conditions resulting from the drift migration, is specially interesting. The extension of the boreal area due to an increased intensity of the warm currents causes a rapid "stocking" of the areas affected by the warm water masses by the young of commercial fish (Kisljakov, 1960).

Drift migrations of the young represent a most interesting example of the unity of the organism and the environment; besides, what we observe in this case is not a simple adaptation of the organism to the life conditions, but a deep assimilation of these conditions by the species. A true understanding of various aspects of the biology of commercial fish is impossible without thorough knowledge of drift migrations. Their study allows us to understand the scheme of the migration cycles of the species and to determine the conditions necessary to retain the intraspecific integrity or to form races and local stocks.

Wherever there are long drift migrations of the young and return migrations of the maturing fish, the possibility of race formation is out of the question (Marty, 1958). At the same time, a stable extension of the habitat by the species at the expense of any branch of the warm current may lead to the formation of a local tribe. An obvious case is provided by the conditions which exist in the Barents Sea. As long as the northwest Norwegian coast remains the area of reproduction owing to its favourable temperature conditions, it has one tribe of the Arctic cod, although some contingents of the maturing fish in the Southern Barents Sea and in the Bear Island-Spitsbergen area live separately.

Drift migrations result in the fact that for many species the area of distribution of the young can be just as wide as that of the adult fish performing spawning migrations. In a number of cases the habitat of the young is much wider than that of the adult fish and the limits of the habitat are determined by the pattern of distribution of the young at the age of one or two years.

Passive distribution of the young is possible only because of their exclusive eurybiotic and, particularly, eurythermal qualities which are formed in the process of phylogenesis. During the first years of life, young cod, herring and haddock are limited in their movement and the above mentioned eurythermality allows them to survive rather severe winter conditions, with temperatures of about -1°C and even lower (Marty, 1941).

Study of the age distribution of herring in the Barents Sea showed that the younger year-classes always keep more to the east and north than the older ones. Migration contours of the maturing year-classes are being constantly shifted against the current. Because maturation of fish depends not only on the age but also on the size of fish in the areas of distribution of young individuals, one can observe a stable withdrawal of specimens having the higher growth rate which move to the west with older year-classes (Marty, 1941). Our observations on the individual year-classes of herring have shown that their reaction to the temperature conditions remains unchanged for a number of years. Thus, those populations of the young that had grown up under the severe conditions of the White Sea prefer cooler waters in the subsequent years as well, and the young that had grown up in the Finmarken waters remain in the areas of higher temperature range.

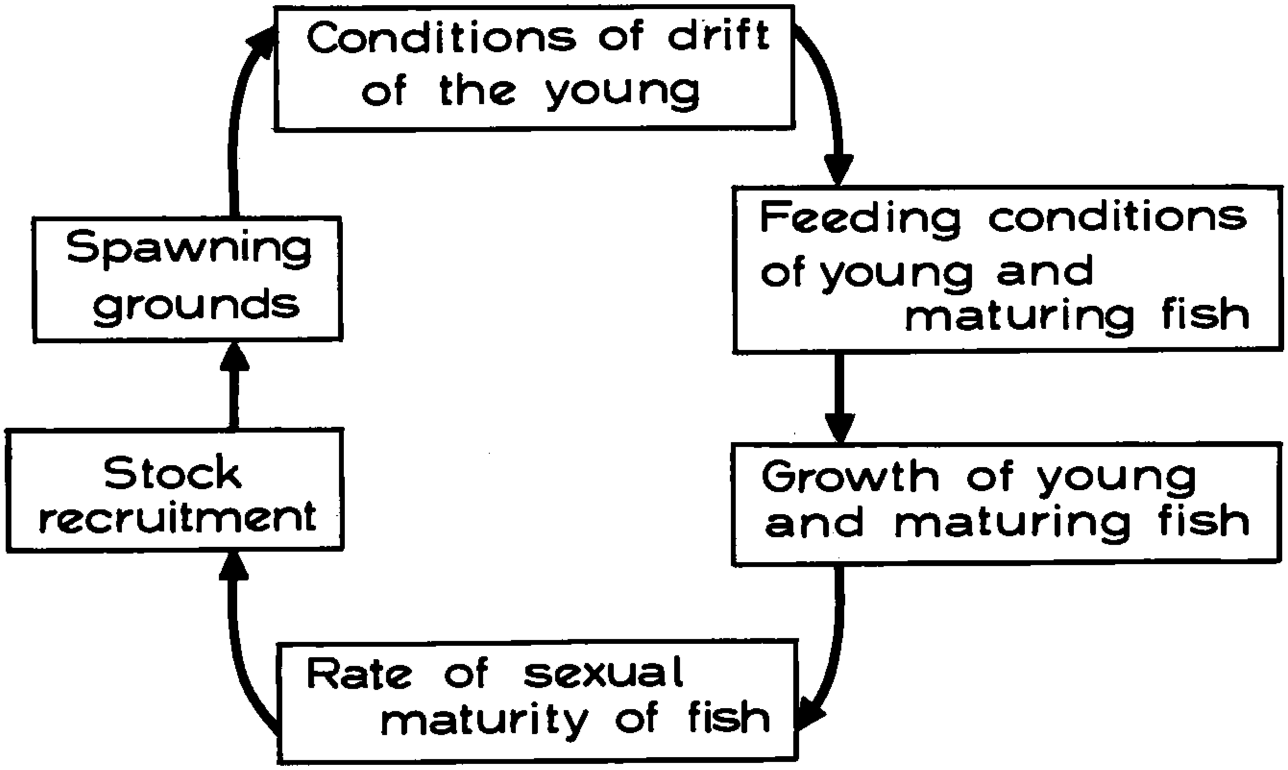
The study of the distribution of the maturing year-classes of commercial fish is of great importance for forecasting the strength of the year-classes; also for planning selective fisheries by excluding from the fishing operations the areas known to be occupied by non-commercial size fish.

Studies of the distribution of the young of commercial fish are important in assessing the productivity of the basins. Wherever drift migrations exist, the fishing productivity of the basin can be differentiated into the productivity of young fish resulting from their passive distribution, and the productivity of the adult fish performing feeding migrations. The relationship between the first and the second types of productivity depends first of all on the age composition of the populations characteristic of a given species. Changes in the age composition of the population, as shown by Maslov (1961) may reduce the feeding migrations and utilization of the feeding resources of the basin.

Knowledge of the drift migrations of the young is most important in forecasting the rate of recruitment to the commercial stocks. The extent of the drift of the young determines the extent of its feeding grounds and the growth and maturity rates of year-classes: the farther the young are carried by the drift, the slower they grow and mature. Without knowledge of the feeding grounds, it is impossible to estimate the growth of separate contingents of the young that had grown up in separate areas, and to predict the rate of recruitment to the stock. Therefore, the attempts of many investigators to describe an average growth rate of individual year-classes cannot be successful. Our experience shows that in a number of cases we have quite definite contingents of maturing fishes with noticeably different growth rates and attempts to calculate growth rate averages only complicate the problem instead of aiding its solution.

In our opinion, in order to get a true idea of the growth rate, it is necessary to study the growth of individual contingents of fish with due regard to their distribution and significance in the composition of the year-class. Such well-organized investigations can greatly help us to understand the dynamics of the formation of the commercial stock and its exploitation.

To summarize, the growth and maturity rates of the recruits are closely related to the feeding grounds and, consequently, to the conditions of the drift migrations of the young. Schematically, this interdependence seems to assume the following shape:



Drift migrations are particularly important in the northeast part of the Atlantic. In the northwest areas they should be less important, first of all because of the more limited boreal area (Marty, 1962). However, the drift migrations do exist in the northwest Atlantic and it is important that they shall be studied. International investigations into the distribution of eggs, larvae and young of fish in Davis Strait, commenced in 1963 and the recent studies of the distribution of young of food fishes by the Soviet investigators will undoubtedly help to get more accurate information on many problems pertinent to the biology of the food fishes in the ICNAF area.

REFERENCES

BARANENKOVA, A.S. 1957. Assessment of the numerical strength of cod and haddock year-classes in the Barents Sea based on the estimation of the young and on the commercial fisheries data. *Trudy PINRO*, X: 54-77.

1960. The results of estimation of young cod and haddock in the Barents Sea in 1946-1959, p. 267-275. *In* Soviet Fisheries Investigations in North European Seas. Moscow.

BARANENKOVA, A.S. and N.S. KHOKHLINA. 1959. Drift of larvae and fry of the Barents Sea cod from the spawning to the feeding grounds. *Nauch.-tekh. Biull. PINRO*, No.1 (9).

1961. The distribution and size composition of larvae and young redfish in the Norwegian and Barents Seas. *Spec. Publ. int. Comm. Northw. Atlant. Fish.*, No.3, p.177-187.

1961. The distribution of larvae of commercial fishes of the Barents Sea in 1959 and 1960. *Nauch.-tekh. Biull. PINRO*, No.2-3 (16-17).

HJORT, J. 1914. Fluctuations in the great fisheries of Northern Europe. *Rapp. Cons. Explor. Mer*, XX: 228 p.

KISLYAKOV, A.G. 1960. Fluctuations in the regime of the Spitsbergen Current, p.39-49. *In* Soviet Fisheries Investigations in North European Seas. Moscow.

LEE, E. 1929. The oceanic stage in the life history of the Norwegian herring. *J. Cons.* IV (1): 1-42.

MARTY, Ju. Ju. 1941. Investigations of life cycle of the Murmansk herring. *Trudy PINRO*, VII: 38-124.

1956. Main stages of the life cycle of Atlanto-Scandian herring. *Pishchepromizdat*, Moscow: 69 p.

1958. Race formation and Marine Herring Races. *Rapp. Cons. Explor. Mer.* 143, 11, 1958.

1961. Migrations and the problem of provision of sea fish with food. Transactions of the meeting on fish population dynamics, 1960. *Akad. Nauk. SSR.* vol. 19: 78-81.

1962. Some similarities and differences in conditions of existence of boreal fish species in the Northeast and Northwest Atlantic, p.57-68. *In* Soviet Fisheries Investigations in North-Western Atlantic. Moscow.

MARTY, Ju.Ju. and A.P.WILSON. 1960. Migrations of the Atlanto-Scandian herring, p.329-339. *In* Soviet Fisheries Investigations in North European Seas. Moscow.

MARTY, Ju.Ju. and I.G.JUDANOV. 1962. Population dynamics, stock condition and perspectives of fisheries of Atlanto-Scandian herring. *Trudy PINRO*, XIV: 151-181.

MASLOV, N.A. 1944. Bottom fish and bottom fish fisheries of the Barents Sea. *Trudy PINRO*, VIII: 3-186.

1957. On the improvement of methods of long-term forecasting the stock conditions of cod and haddock. *Trudy PINRO*, X.

1960. Soviet investigations on the biology of cod and other demersal fishes of the Barents Sea, p.185-231. *In* Soviet Fisheries Investigations in North European Seas. Moscow.

1961. A change of geographical distribution of fishery and an expected effect of the regulation. *Nauch.-tekh. Biull, PINRO*, No.1 (15).

MEEK, A. 1916. The migrations of fish. London.

SCHEURING, Z. 1929. Die Wanderungen der Fische Ergebnisse der Biologie Bd.

SCHMIDT, J. 1923. Die Laichplatze des Flussales. *Inter. Rev. ges. Hydrobiol. and Hydrogr.* Bd. XI.

SCHMIDT, P.Ju. 1947. Fish migrations.

SHUTOVA-KORZH, I.V. 1960. Peculiarities in the distribution, growth and maturation of some herring year-classes in the Barents Sea. p.361-370. *In* Soviet Fisheries Investigations in North European Seas. Moscow.

WIBORG, K.F. 1957. Factors influencing the size of the year-classes in the Arcto-Norwegian tribe of cod. *Fiskeridir. Skr. Havundersøk,* XI (8).

ZENKEVITCH, L.A. 1963. Biology of the USSR seas.

B-9

SURVIVAL OF THE YOUNGEST STAGES OF FISH, AND ITS RELATION TO YEAR-CLASS STRENGTH

By

J. A. Gulland[1]

ABSTRACT

Most fish have enormous fecundities, and there must be a correspondingly enormous mortality etween the egg and adult stages. Most of this mortality is believed to occur in the first few onths of life, and this stage is believed to be important for two other reasons; because the diffrences between good and bad year-classes are determined at this stage, and because the regulatory density-dependent) effects which prevent the population expanding without limit in favourable conitions, or dwindling to extinction under poor conditions (*e.g.* with heavy fishing), may occur in his stage.

Year-class fluctuations are presumably due to some environmental factor. Attempts to show the nvironmental effect by correlation techniques have generally not been successful; the wide range f possible environmental factors makes the usual statistical tests of significance invalid if the actor studied has been chosen on the basis of goodness of fit. Also the correlation coefficient or even an environmental factor directly responsible for year-class changes is not likely to be igh because of difficulties of estimating both the year-class strength and the environmental actor.

The relation between year-class strength in the Arcto-Norwegian stock was studied. Relations reviously suggested between year-class and wind, or plankton were shown not to be firmly supported, ut there seemed to be a relation, though not a close one, between year-class and temperature in the arents Sea.

In this, and other stocks, the mortality between eggs and recruitment (for the cod, recruitment ccurs at 4 years old) was shown to decline with increasing adult stock, and a pattern of the deline in numbers during the first years of life is proposed. It is suggested that further undertanding of the happenings in these early stages will be reached by using the techniques of populaion dynamics, *i.e.* direct measurement of growth, mortality etc. Low mortality, as deduced from the elative abundance of larger (and presumably older) larvae is shown to be related to good year-class trength in several stocks.

Most marine teleosts have enormous fecundities. A female cod in her lifetime may produce millions of eggs, but in a stable population an average of only two will survive to maturity. While he fish are of commercial size the mortality is (by these standards) low, of the order of 30-75% er year. Mortality between the end of the first few months of life and the time of reaching comercial size is not known so precisely, but is probably also fairly moderate, and the bulk of the 9.9999% mortality occurs in the first few months of life.

The mortality in these early stages is believed to be important to the study of fish populations n two ways. First, it is at this time that the difference between good and bad year-classes is esablished - certainly this difference is usually established and observable by the time the fish are ig enough to be sampled with normal fishing gear (cf. Baranenkova, 1960, for Barents Sea cod). econd, any population must have some basic density-dependent factors controlling it, preventing it rom expanding without limit when conditions improve, and from declining when conditions worsen *e.g.* when adult mortality increases due to fishing). This effect, for at least some fish stocks, robably occurs in the early larval stages (Beverton, 1962).

Variations in year-class strength are presumably due to variations in the environment at some ime in the early life. Failing the information needed to make a direct study of the effect of arious environmental factors on the survival of young fish, correlations between year-class strength nd various environmental data have been made for several fisheries. Thus Carruthers and his olleagues (Carruthers *et al.* 1951) used wind data, mainly because these were regularly and easily

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available without the need of any special investigation, and wind could reasonably be expected to influence other more direct factors such as the distribution of larvae in unfavourable areas, rather than because of its direct effect on young fish.

The use of correlations to establish a connection between environment and year-class strength is made more difficult by the small number of pairs of observations available (one per year). On one hand there is the statistical danger, pointed out by Gulland (1953), that with the wide range of possible environmental factors available, including the choice of precise season, a high degree of correlation between some factor and year-class strength is likely to arise merely by chance. On the other hand the estimates of year-class strength, and probably also of the environmental factors, are likely to contain considerable observational variance. Thus Beverton and Holt (1957, p. 270), comparing for the North Sea haddock the variances of year-class strength and of the total annual catch, concluded that, for the period 1922-37, the variance of the estimated year-class strength was considerably greater than the variance of the real year-class strength. Also, as shown below, there appear to be discrepancies in later data between changes in year-class indices and in catch per unit effort of the fishery. Thus, however close the real relation may be, the correlation between the estimates of year-class and environmental factor cannot be very large, perhaps not large enough to be significant except when determined over a considerable number of years. For example, estimates of year-class strength have been made for the Bear Island cod - a stock for which the data are probably rather better than average - based on the abundance of 7- and 8-year old fish. The correlation between these two estimates is 0.896, and this is about the best degree of correlation that could be expected between either of these (fairly good) estimates and an environmental factor which could be measured precisely, and which determined the true year-class strength absolutely precisely. Even this fairly high correlation needs seven pairs of observations (*i.e.* seven years) to be significant at 1%. Thus tests of statistical significance give only a poor guide to the reality of a derived correlation and, as Saville (1959) points out in his survey of such correlations for the North Sea haddock, the best test is given by the passage of time, and by the relation between variables in the years after the correlation was first suggested.

Despite these difficulties, it is worth examining the relation between the estimated year-class strength of the Arcto-Norwegian cod and some environmental factors, particularly where such a relation has already been suggested (*e.g.* Hill and Lee, 1958; Corlett, 1958*a*). Hill and Lee, working with very limited data, both in number of years and precision of year-class strength in the Bear Island-Spitsbergen area, suggested that there was a correlation between good year-classes and strong southerly wind during the period when the larvae were drifting from the Lofoten spawning grounds to the Bear Island area, the latter causing increased northerly water transport. Mr Lee has kindly put the complete series of wind data at my disposal. A series of pairs of observations of wind (mean southerly component at Bear Island during April and May) and year-classes (using the data of Gulland, 1964) can be obtained for twenty-eight years between 1921-56. These data have been plotted in Fig. 1; distinct symbols have been used for the periods 1921-32, 1937-41 and 1946-55. No clear relation emerges, nor, examining the early and late years separately, does there appear to be any relation in these shorter periods. The correlation between the two variables is 0.1, which is not significant.

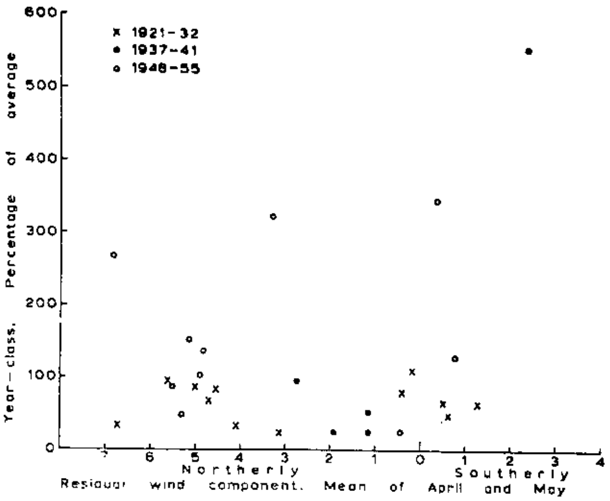

Fig. 1. The relation between year-class strength (expressed as the percentage of average) in the Bear Island region, and the mean wind component at Bear Island.

Another correlation has been suggested by Corlett (1958*a*) between dry weight of summer plankton and year-class strength. Only one year (1956) can be added to his series, but with the year-class strengths expressed in quantitative terms it is possible to calculate a correlation coefficient. For the eight years 1949-56, this is 0.56 (P>0.1, not significant). Corlett (this symposium) also correlates year-class strength with plankton and wind. Using different periods of years, and another estimate of year-class strength (one based on only one year's data, and likely to be affected by the amount of fishing in the previous year or two), he obtains correlation coefficients of 0.758 between plankton and year-class, and 0.594 between wind and year-class. This again illustrates the degree to which the value of the correlation coefficient obtained depends on precisely which sets of data, of both year-class strength and environmental factors, are used, often from a considerable choice. Under these conditions the levels of significance as given in statistical tables can be very poor measures of the probability of the observed relation between the selected pairs of year-class indices and environmental factors occurring by chance, and the level of significance may be grossly overestimated.

This of course in no way disproves the hypothesis that plankton or wind in fact affects year-class strength, but merely that the correlation approach is unlikely to provide useful evidence one way or another. In fact other evidence on growth, as discussed later in this paper, suggests that plankton - or rather the indices of plankton used by Corlett - is not related to year-class survival. Also, even ignoring the fact that the depth from which samples were taken was different in 1949-53 and in 1953-59, it is extremely doubtful if the single figure used by Corlett, based on a few irregularly timed samples, can adequately represent the changing plankton standing crop throughout the period of nearly six months from mid-April to the end of September. Even with perfect sampling the mean standing crop of total plankton over this period is likely to be a poor measure of the food available to the cod at the critical period, when in any case it is possibly only certain preferred species that are of vital importance. This critical period, as defined later in this paper, is likely to occur fairly early in the year, but the correlation coefficient between year-class strength (using Corlett's indices) and dry weight of plankton in April and May for the seven years available - 1950 to 55 and 1957 (Corlett, 1953, 1958*c*) is +0.01. This last calculation probably attempts to make more use of the data than is profitable. Further research into the factors determining year-class strength in the Arcto-Norwegian cod stock, or any other stock, requires detailed quantitative study of the dynamics of the eggs and larvae, such as the surveys of eggs, larvae and 0-group cod made by Russian scientists, and reported to this Symposium by Baranenkova.

For the other main feeding/nursery area of the stock in the Barents Sea, data collected by PINRO are available for the mean temperature in the 0-200 m zone along the Kola meridian (33 1/2°E), together with corresponding brood indices for twenty-five years between 1924-56. These are plotted in Fig. 2. Again separate symbols are used for the periods 1924-32, 1937-40 and 1945-55. There is some slight relation, as indicated by the fitted regression, though the correlation coefficient is only 0.23, which is not significant. The lack of statistical significance, of course, does not prove that there is no relation, but only that the data are not inconsistent with the hypothesis that the year-class strengths are independent of the environmental factor considered. Probably, in fact, at least in the Barents Sea, the temperature may have an influence, but if the true correlation is only 0.23, then, purely by the statistical method of correlation, it would take seventy years of observation to establish it, even at the 5% level of significance. Another relation with temperature has been derived by Kislyakov (1961). He related the temperature off the west Norwegian coast (*i.e.* close to the spawning grounds) to year-class strength, as measured by the total yield, in arbitrary units, and obtained a correlation coefficient of 0.91. When comparing his results and the present ones in detail, the most striking discrepancy is not so much in the greater value of the correlation coefficient observed by Kislyakov (if the critical phase is very early in life it is presumably more closely related to temperature nearer the spawning ground) as in the apparent differences in year-class strength. It is not precisely clear how his estimates were obtained, nor to what group of fish they refer - to the whole stock spawning at Lofoten, or to some part of it - but taking the same data of year-class strength for regions I and IIb as used earlier in this paper, and also a single weighted mean (factors of 2:1) to give a best estimate for the whole Arcto-Norwegian stock, and relating this to the temperature data in his Table 1, the following correlation coefficients were obtained.

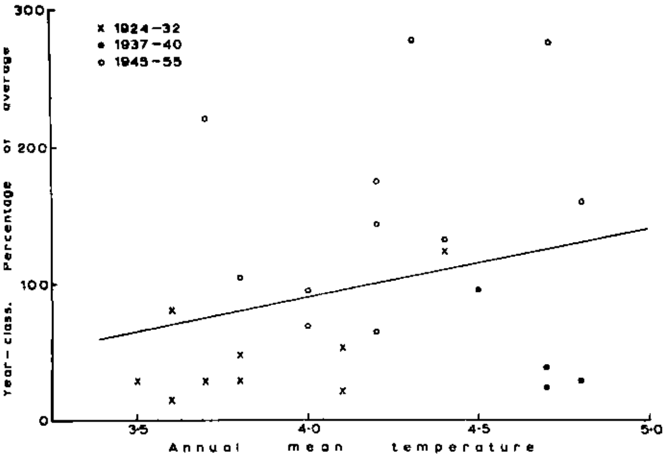

Fig. 2. The relation between year-class strength in the eastern Barents Sea, and the spring temperature on the Kola meridian.

Region I : 0.48
Region IIb : 0.55
Weighted mean of both areas : 0.66.

These are considerably smaller than the correlation coefficient of 0.91 mentioned above, which is in fact larger than the correlation between the two most reliable single estimates of year-class strength based on English data. This suggests that the closeness of Kislyakov's observed relation between temperature and year-class strength, based on a rather short series of data, is fortuitous. The basic weakness of the correlation approach is illustrated by the different conclusions reached by Kislyakov and in the present paper, and particularly by the fact that, without using different techniques, the discrepancy will only be settled by the passage of time, possibly of quite a large number of years.

In fact, though many such correlations between year-class strength and environmental factors have been suggested, few if any have stood the test of time. Thus one of the most promising, relating wind force and direction to year-classes of North Sea haddock (Carruthers, 1938), which at the time when it was proposed fitted data for some fifteen years extremely closely, has given an extremely bad fit for the post-1945 data (Saville, 1959). Attempts could be made to improve matters by considering additional environmental factors either in the initial analyses, so as to produce a very high correlation coefficient, or later, when the simple relation fails to hold. Such attempts have to be made with caution because the danger of introducing spurious correlations is very great.

Density-dependent mortality

It is easy to show that if a population of animals is to remain reasonably stable under different conditions, for example if a fish population is to be able to stand the large additonal mortality caused by fishing without declining to extinction, then one or more of the vital parameters (mortality, growth, reproduction) must change with the abundance of fish. While growth can decrease with increased stock abundance, the more important factor seems to be the recruitment. This has often been assumed to be independent of the abundance of the parent stock, and this is equivalent to assuming that the average survival from eggs to recruits decreases with increasing adult stock. This decreased survival has been clearly shown for such different stocks as the Karluk River sockeye salmon (Rounsefell, 1958), the North Sea plaice (Beverton, 1962) - a marine stock where the recruitment does not vary much, - and the Californian sardine (Radovich, 1962), where there is much greater variation independent of stock abundance. It is probable that this relation would be found for most fish stocks but at present sufficient data on adult stock and subsequent recruitment are available for only a few stocks.

The following data have been obtained for the Arcto-Norwegian cod. Recruitment has been taken as the sum of the numbers of fish at four years old in regions I and IIb. Stock estimates are based on the catch (in weight) per man at Lofoten (which gives the longest series of data) converted to actual numbers of eggs. From the Arctic Working Group (ICES, 1959), it is known that the effort in region IIa from 1951-58 was equivalent to 40,000 men at Lofoten. During this period the total mortality coefficient was 0.99, so that allowing for natural mortality (*ca.* 0.2), and for fishing mortality due to fishing in other regions, we may take 40,000 men as causing a fishing mortality coefficient of 0.4, so that the estimate of stock is obtained by multiplying the catch per man by

$$\frac{40{,}000}{0.4} = 10^5.$$

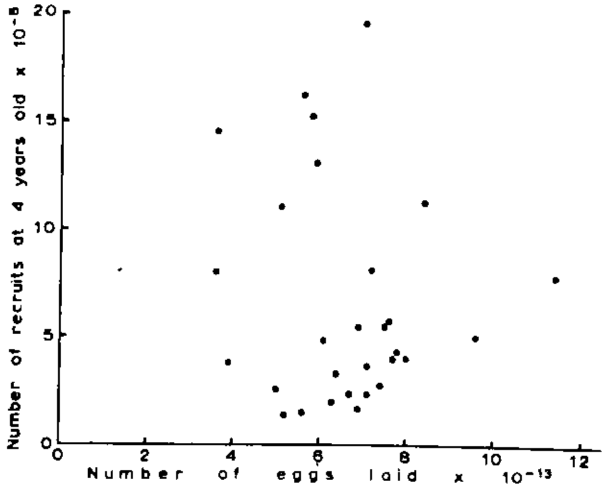

Fig. 3. The relation between the number of eggs laid at Lofoten and the resulting number of recruits.

The fecundity has been estimated by Mrs Woodhead (personal communication) to be closely, though not exactly, proportional to weight, and as equal to about 1.5×10^6 eggs per female of 85 cm, *i.e.*, *ca.* 8 kg, so that a catch per man of 1 kg is equal to an egg production of, say, $1/2 \times 10^5 \times \frac{1.5 \times 10^6}{8} = 10^{10}$ (taking a sex ratio of unity). In Fig. 3 the estimated number of recruits has been plotted against estimated egg production. There is clearly no significant relation ($r = 0.13$). In Fig. 4 the survival from eggs to recruits, *i.e.* the number of fish surviving to four years old per million eggs laid, has been plotted against the number of eggs laid. There does seem to be a relation, as indicated by the curve drawn by eye. The correlation coefficient is significant (≃ = 0.434, P 0.02). This test is not the most sensitive, because of the probable true curvilinear relation, but a relation of this type could be developed by chance due to errors in estimating the egg-production. These are probably not very large, and we may conclude that there is a real difference of about two-fold in average survival over the observed range of stock density.

While the survivals above were calculated from egg to four years old, the surveys by Baranenkova (1960) show that year-class strength is already determined by two-three years old. In the table below, the data from her Tables 1 and 3 are grouped to give a single average value of catch per hour for each age-group.

Area	Catch per hour's fishing of each age			
	0+	1+	2+	3+
Southern Barents Sea	13.1	19.7	20.1	16.6
Near Bear Island	5.3	40.9	32.8	10.6

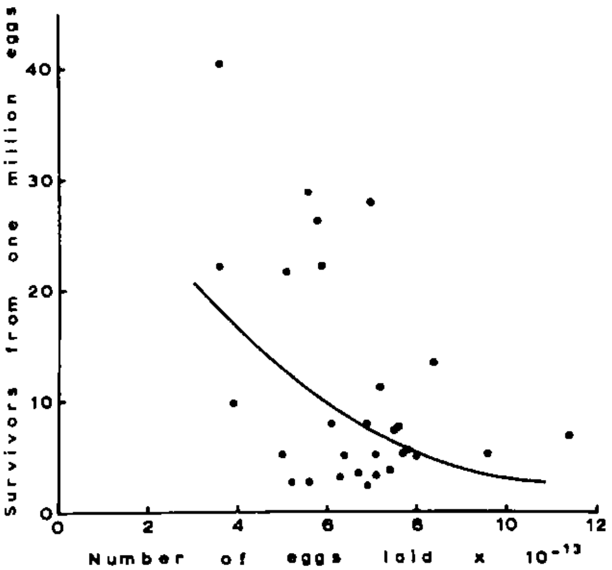

Fig. 4. The relation between the number of eggs laid and their survival.

The results suggest that mortality among these ages is not very high (even allowing for probable lower vulnerability of the younger ages); probably it is of the same order as the natural mortality in the older fish, 20-30% per year. Thus, of the total mortality between eggs and four-year-olds, which reduces the numbers by a factor of 2 x 10^5, *i.e.*, *ca.* 5.3 logarithmic units, the last three years account for 3 x 0.1-0.15 log units. Taking an upper limit of this mortality leaves nearly 5 log units for the mortality in the first year, *i.e.* half a unit (nearly 70%) per month, or *ca.* 3% per day. This decline in numbers is shown diagrammatically in Fig. 5, for average conditions of stock and year-class. Even if an extreme upper limit of mortality after the first year (0.2 log units or 35% per year) is taken, the survival curve in the first year must be very much steeper than in the next three years.

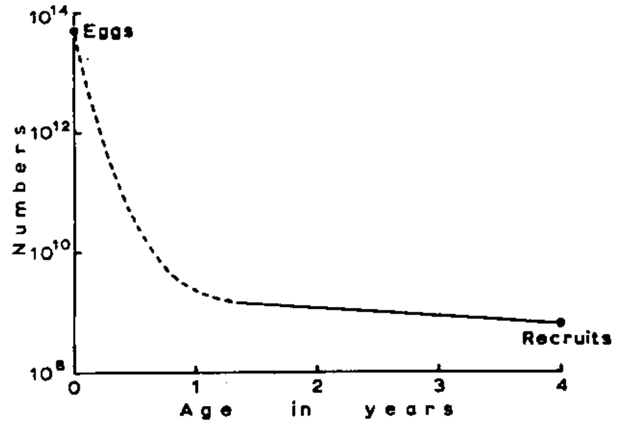

Fig.5. The mortality of Arctic cod during its first years of life.

A curve, or set of curves may now be drawn to represent the presumed decline in numbers of a given year-class from eggs through the first few months of life. This curve must firstly show a very high mortality of around five orders of magnitude, common to all year-classes. At some point during these months there is what may be defined as the density-dependent phase, in which mortality is higher for year-classes with an initially high number of eggs than for one with an initially low number of eggs. There is also the critical phase, which in the sense used here is the phase during which the strength of a year-class is determined, *i.e.* the phase during which the mortality of an ultimately poor year-class is higher than that of an ultimately rich year-class. These definitions do not imply anything about the duration or timing of, or total mortality during, either phase. If, however, the density-dependent mortality is caused by competition between larvae of the same age (*e.g.* for some scarce food at a critical stage of development) rather than say competition with, or predation by, the adults, then the density-dependent phase must at least in part precede the critical phase. Otherwise the differences caused by the latter would be removed by the density-dependent effect.

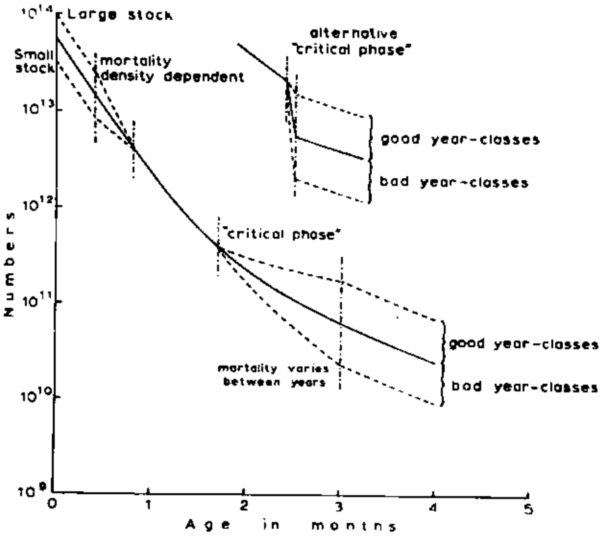

Fig. 6. Hypothetical mortality curves of eggs and young fish.

Hypothetical examples of the decline in numbers in the early stages and the differential mortality in the density-dependent and critical phases are shown in Fig. 6. Two possible critical phases are shown, one of short duration in which mortality for a good year-class is small, and much less than that for a poor year-class, and one of longer duration, in which the differences in mortality rate for good and poor year-classes is only slight. For simplicity the general mortality rate has been shown as fairly steady, but it is not denied that there may be certain stages (*e.g.* when larvae first start to feed) at which mortality may be very much higher than for older or younger stages. However, such a stage is not a critical stage, in the sense defined here, unless the mortality during this stage is different in good and bad year-classes.

Population dynamics of young stages

From the discussion in the preceding section it is clear that further advance in these studies requires the use of the same type of population techniques as have been used for commercial-sized fish; that is, the study of mortality rates (if possible split up between different causes), growth rates, etc. For young fish, mortality and growth are closely linked, poor growth not only being a sign of adverse conditions likely to increase mortality, but also directly affecting mortality by increasing the time during which the young fish are vulnerable to the smaller invertebrate predators.

Few surveys of eggs and young fish have been published in a form suitable for detailed population studies. Some of the best of these, *e.g.* that of the Atlantic mackerel (Sette, 1943), cover only one year or, though covering more than one year, include years in which conditions and also subsequent year-classes were nearly identical, *e.g.* the Pacific sardine (Ahlstrom, 1954). In neither case is it possible to observe differences in mortality which may be related to ultimate year-class strength, or to differences in the parent stocks.

Some other studies of young stages have been made, which though not so detailed and hence less suitable for direct estimation of mortality rates, etc., do enable comparisons to be made between years. Wiborg (1957) made studies of the Lofoten cod. He examined some hypotheses about year-class strength and found that there was no relation between numbers of eggs and early larvae and subsequent strength of year-class; in fact the outstanding year-class of 1950 corresponded to the lowest number of eggs and larvae observed in the period 1948-56. Data were also presented on the size of larvae caught each year, and the striking feature is that the years when large larvae (over 12 mm) were caught coincided with good year-classes (1948, 1949, 1950, 1954, 1956). The data cannot be used directly to give quantitative estimates of the mortalities of larvae, because of lack of information on growth and possible changes in growth from year to year, and because the drift of eggs and larvae through the area makes repeated samplings of the same group of eggs and larvae very difficult. They do suggest however that in the early months of life there is an observable difference in the size composition of the larval catches between years, corresponding to the differences in mortality and hence in ultimate year-class strength.

Saville has given such data for haddock in the North Sea (Saville, 1959), and at Faroes (Saville, 1956). For the North Sea, data on size of larvae are given for 1953, 1956 and 1957. The year 1956 had an outstandingly poor year-class, and in this year very few larvae of over 15 mm were caught, even though small larvae were abundant. However, there was no difference in abundance of larger larvae between 1953 and 1957, though the 1957 year-class was appreciably poorer than that of 1953. For the Faroes, length data for larvae caught in June are given for 1950, 1952 and 1953. The numbers of larvae of over 15 mm beneath 100 m^2 surface were 14, 21 and 27 respectively, which agree well with the indices of year-class strength obtained by research vessel surveys of I-group fish of 228, 488 and 490 per 10 hours fishing.

Simpson's (1959) surveys of the North Sea plaice were concentrated principally on the eggs, ut some data on larvae were also given. Sizes of larvae were not given, but taking his post-larvae *i.e.* those with the yolk-sac completely absorbed), it is possible to calculate the mean number aken per haul for each cruise. Taking the mean of the catch per haul for each cruise (omitting ecember cruises), one obtains indices of the abundance of later larvae of 0.95, 0.56 and 0.36 for he years 1947, 1948 and 1950 respectively. The corresponding year-class strengths, in terms of umbers of fish caught per hour's fishing as four-year-old fish by Lowestoft trawlers, are 46, 22 nd 23. These data do suggest that, in each of the stocks examined, the critical stage (in the ense defined above) occurs very early, and its effect can, at least to some extent, be measured. f this is so the study of the effect of environment on year-class strength will be greatly helped, ot only by defining more precisely the timing of the important critical step, and hence narrowing he range of possible factors, *i.e.* only those directly or indirectly operative at that time, but lso by increasing the number of possible comparisons above the one pair of year-class strength and nvironmental factor per year. That is, mortality rates may be calculated for different groups of arvae of the same year-class, *i.e.* those spawned at various times or in slightly different areas, nd these mortalities may be compared with the conditions affecting each group. Shelbourne (1957) ound two patches of plaice larvae in the Southern Bight of the North Sea; in one *Oikopleura* (the avourite food of larval plaice) was abundant, the larvae were in good condition, and late stage arvae were not uncommon; in the other food was scarce, the larvae were in poor condition, and late tage larvae were rare. This example does not give complete proof of poor feeding causing high ortality, because Shelbourne was not able to maintain continuous sampling on the same patch, so hat it is not certain whether the scarcity of larger larvae was due to high mortality, or to an riginally smaller number of newly hatched larvae. Even when there are no data on the relative bundance of different sizes, and hence probably of ages of larvae, many other less detailed pieces f information may be used to narrow down the possible factors or the timing of the critical phases ffecting larval survival or year-class strength. Fraser (1961) has suggested some differences beween types of water in the North Sea. This difference is reflected as relatively fewer larvae in he type of water, even though the numbers of eggs are much the same in the two water-masses. This ould be due to differential mortality at any time between the youngest eggs and quite late stage arvae. For cod and haddock, however, three stages or "age-groups" can be determined from the data - arly eggs (which for cod and haddock are indistinguishable), late eggs, and larvae. These data, aking the two species together, are summarized below, together with the survival from one stage o the next.

Cod + haddock	Type of water	
	S. elegans present	*S. elegans* present
Average No. per haul		
Early eggs	24.45	33.63
Late eggs	4.24	1.66
Larvae	1.24	0.38
Survival: %		
Early to late eggs	17	5
Late eggs to larvae	29	23

e big difference between the types of water is that the survival from early to late eggs is much ess when *Sagitta elegans* is absent; there is very little difference in the survival from late eggs larvae. The difference therefore lies somewhere in the egg stage, due to predation, or possibly isease, rather than to feeding.

Observations other than those on the relative numbers of different stages of eggs or larvae n often be of help. Thus food shortage affecting year-class strength, or indeed competition for food causing density-dependent mortality, is likely to affect growth first. Differential mortality, therefore, is unlikely to take place without some change in growth. Thus seaward migrating sockeye salmon smolts from Karluk River are longer in the more abundant broods (Rounsefell, 1958). Growth changes are rather easier to detect, either simply from size at a given time (when spawning is restricted to a short known season), or from the progression of modes in length composition, or as done by Shelbourne (1957) by the appearance of the larvae - robust when food is abundant, but thin when food is scarce. For the cod round Bear Island, Corlett (1958*a*) has suggested that the abundance of planktonic food in the summer influences the year-class strength. Corlett (1958*b*) gives some data on size of 0-group cod in October, *i.e.* at the end of the period to which the plankton data refer. These data are summarized below.

Year	1950	1951	1953	1954
Dry weight of plankton	54	15	26	46
Size of 0-group cod (cm)	11.25	11.5*	10.0	10.5

*Cod were caught in two areas; west of Bear Island and west of Spitsbergen; mean lengths 10.6 and 12.4 cm respectively.

There does not seem to be any relation between size of cod and abundance of plankton, nor are the years of good year-classes (1950, 1954) years of particularly good growth. While such analyses do help to get some insight into the causes of variations in larval survival and in year-class strength, and are far more satisfactory than mere correlations between annual pairs of values of year-class strength and some feature of the environment, they are a poor alternative to a thorough egg and larval survey designed to measure mortality directly.

Such surveys are however very time-consuming. If the form of the decrease in numbers is to be defined with any precision the individual surveys have to be quite frequent, *e.g.* at intervals of a week to ten days. This work is likely to need several research vessels if it is to be done satisfactorily, and it therefore appears to be a field where international cooperation, with several research vessels, is likely to be very productive. The stock to be investigated should be chosen with some care. It should be one in a small and fairly well defined area, so that the actual survey work taken as little time as possible. More important, the strength of year-classes should be very variable, so that say three years of surveys should give a good chance of including one year-class of unusual strength, from the data on which the critical phase might be determined fairly precisely. If possible, the abundance of the parent stock should also be variable, thus giving a better chance of observing any density-dependent effect. One stock that satisfies these conditions is the North Sea haddock, which has the advantage of being located not far from several laboratories, but there are several other suitable stocks.

REFERENCES

AHLSTROM, E.H. 1954. Distribution and abundance of egg and larval populations of the Pacific sardine. *Fish. Bull., U.S.,* 56: 83-140.

BARANENKOVA, A.S. 1960. The results of surveys on young cod and haddock in the Barents Sea during the period 1946-1959. *Soviet Fish. Invest. North European Seas.* Moscow, VNIRO and PINRO, p. 267-278. (MAFF Translation, 1961).

BEVERTON, R.J.H. 1962. Long-term dynamics of certain North Sea fish populations. In: *The Exploitation of Natural Animal Populations*, Eds. Le Cren and Holgate, Oxford. Blackwell Sci. Publs., 242-264.

BEVERTON, R.J.H. and S.J. HOLT. 1957. On the dynamics of exploited fish populations. *Fish. Invest., Lond.*, (2), 19, 533 p.

CARRUTHERS, J.N. 1938. Fluctuations in the herrings of the East Anglian autumn fishery, the yield of the Ostend spent herring fishery, and the haddock of the North Sea - in the light of relevant wind conditions. *Rapp. Cons. Explor. Mer*, 107(3): 10-15.

CARRUTHERS, J.N., A.L. LAWFORD, and V.F.C. VELEY. 1951. Fishery hydrography: brood-strength fluctuations in various North Sea fish, with suggested methods of prediction. *Kieler Meeresforsch.*, 8: 5-15.

CORLETT, J. 1953. Dry weight and fat content of plankton near Bear Island, 1949-1952. *Ann. biol., Copenhague*, 9: 8-9.

1958*a*. Plankton in the western Barents Sea and the year-class strength of the Arcto-Norwegian cod. *J. Cons.*, 23: 354-356.

1958*b*. Distribution of larval cod in the western Barents Sea. *Spec. Publ. int. Comm. Northw. Atlant. Fish.*, No. 1, p. 281-288.

1958*c*. Dry weight of plankton in the western Barents Sea, 1953-1956. *Ann. biol., Copenhague*, 13: 39-40.

1964. Winds, currents, plankton and the year-class strength of cod in the western Barents Sea. *This symposium, Contribution No. B-10.*

FRASER, J.H. 1961. The survival of larval fish in the northern North Sea according to the quality of the sea water. *J. mar. biol. Ass. U.K.*, 41: 305-312.

GULLAND, J.A. 1953. Correlations on fisheries hydrography. *J. Cons.*, 18: 351-353.

1964. The abundance of fish stocks in the Barents Sea. *Rapp. Cons. Explor. Mer*, 156.

HILL, H.W. and A.J. LEE. 1958. The effect of wind on water transport in the region of the Bear Island fishery. *Proc. Roy. Soc.*, Ser. B, 148: 104-116.

I.C.E.S. 1959. Second Progress Report of the Working Group on Arctic Fisheries. Copenhagen, 1959, Mimeo.

KISLYAKOV, A.G. 1961. The relation between hydrological conditions and the fluctuations in the abundance of cod year-classes. *Trudy Soveshch. ikhtiol. Kom.*, 13: 260-264. (MAFF Translation, 1963).

RADOVICH, J. 1962. Effects of sardine spawning stock size and environment on year-class production. *Calif. Fish Game*, 48: 123-140.

ROUNSEFELL, G.A. 1958. Factors causing decline in sockeye salmon of Karluk River, Alaska. *Fish. Bull., U.S.*, 58: 83-169.

SAVILLE, A. 1956. Eggs and larvae of haddock (*Gadus aeglefinus* L.) at Faroe. *Mar. Res. Scot.*, No. 4.

1959. The planktonic stages of haddock in Scottish waters. *Mar. Res. Scot.*, No. 3.

SETTE, O.E. 1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part 1: early life history, including the growth, drift, and mortality of the egg and larval populations. *Fish. Bull., U.S.*, 50: 149-237.

SHELBOURNE, J.E. 1957. The feeding and condition of plaice larvae in good and bad plankton patches. *J. mar. biol. Ass. U.K.*, 36: 539-552.

SIMPSON, A.C. 1959. The spawning of the plaice (*Pleuronectes platessa*) in the North Sea. *Fish. Invest., Lond.* (2), 22, (7).

WIBORG, K.F. 1957. Factors influencing the size of the year-classes in Arcto-Norwegian tribe of cod. *Fiskeridir. Skr. Havundersøk.*, 11 (8).

B-10

WINDS, CURRENTS, PLANKTON AND THE YEAR-CLASS STRENGTH OF COD IN THE WESTERN BARENTS SEA

By

John Corlett[1]

ABSTRACT

The early life history of the Arcto-Norwegian cod is described. The first few months of life are discussed in relation to winds, water transport and plankton abundance in the Bear Island area. The first reliable estimate of the year-class strength is from the commercial fishery when the fish are fully recruited at 5 years old. Correlations between year-class strength and wind and plankton indices are presented. It is suggested that wind and plankton data can be used as a basis for prediction of cod year-class strength 5 years in advance. Predictions for the year-classes of 1958 to 1963 in 1963 to 1968 are given.

INTRODUCTION

One of the aims of fishery research is to predict the size of a stock of fish as far ahead as possible. The ideal is to be able to estimate the size of a year-class soon after its birth and, from this estimate, to predict its strength when recruited to the fishable stock. In looking at the early life history of a fish stock and its environment in this context, we hope to find some factors which will help in making the predictions. This paper is a short account of the early life history of cod of the Arcto-Norwegian stock in the western Barents Sea, with a discussion of the possible influence of some environmental factors; from this a basis for early predictions of the size of a year-class is suggested. The discussion is confined to the western Barents Sea because most of the English work has been done there and because similar studies in the south-eastern Barents Sea are described by Russian scientists in Contributions B-7, B-15 and B-16 from this symposium.

LIFE HISTORY OF ARCTO-NORWEGIAN COD

The mature cod of the Arcto-Norwegian stock are found over most of the Barents Sea during summer and autumn and come together to spawn each spring off the Lofoten Islands. The main spawning is in the Westfjord, but spawning also takes place along the Norwegian coast to the north and south (Fig. 1). The spawning season is from late February to late April, with the peak usually in the second half of March. The distribution of eggs and larvae around the Lofoten Islands in spring has been described in several papers by Wiborg (*e.g.* 1950, 1952 and 1960*a*). From the spawning grounds many of the eggs and larvae are carried by the surface currents north-eastwards along the coast in the Atlantic Current, and when this divides to form the West Spitsbergen Current and the North Cape Current the larvae are separated; some are carried northwards towards the Bear Island, Hope Island and Spitsbergen Banks, and others are carried into the south-eastern Barents Sea (Corlett, 1958*a*; Wiborg, 1960*b*). Some of the eggs and larvae also find their way among the fjords and islands of the Norwegian coast. By late summer the young cod are beginning to descend towards the sea bed, and from late September onwards are found as 0-group cod on the nursery grounds all over the Barents Sea (Baranenkova, 1960; Corlett, 1958*a*). The codling grow up on these banks and eventually form the basis of extensive trawl fisheries. Many are caught when 4 years old, but they are not fully recruited into the fishery until they are 5 years old. Trout's (1957) work on otolith types has shown that yound cod tend to remain until they are mature in the area in which they begin their demersal life.

The numbers of eggs and young larvae near the spawning grounds have been estimated for many seasons by Norwegian scientists and the work has been summarized by Wiborg (1957). In spite of the difficulty of estimating the total production of eggs over a large area and throughout an extended spawning season, using only one ship, Wiborg could give estimates of egg numbers for several seasons.

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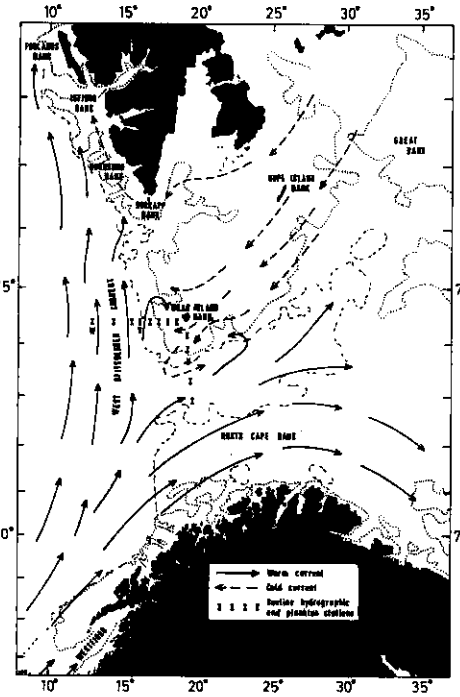

Fig. 1. Surface currents in the western Barents Sea.

But he could show no correlation between the abundance of eggs and young larvae and the subsequent strength of the corresponding year-classes.

During the early summer, when the larvae are larger and more widely dispersed, their numbers are very difficult to estimate, because of the inadequacy of the nets used and the large area that has to be covered. No full scale survey has yet been attempted.

When they are demersal from October onwards, 0-group cod can be caught in ordinary otter trawls using covered cod-ends. Some attempts to estimate numbers at that stage have been made by the *Ernest Holt* in the north-western Barents Sea in October in several years. But in the time available one ship was not able to cover adequately the large area involved. Russian workers using several ships during the autumn and winter in the southern Barents Sea have been much more successful in estimating the abundance of young cod (*e.g.* Baranenkova, 1960 and 1963).

Our first reliable estimate of the size of the year-class is obtained from market measurements of commercial catches. Four-year-old fish are not fully recruited and when caught are not always kept by the trawlers because they are too small for the market; so our earliest good estimate of abundance is at 5 years old. After this the abundance of the year-class is affected by fishing. What we would hope to predict as many years beforehand as possible, is the size of the year-class at 5 years old.

EARLY LIFE HISTORY AND ENVIRONMENT

The size of the year-class is generally considered to be decided in the first few weeks or months of pelagic life of the brood. After discussing the factors affecting the numbers and distribution of cod eggs and larvae on the north Norwegian coast, Wiborg (1957) concludes:- "the transport of eggs and larvae from the spawning areas to the nursery grounds in the Barents Sea and adjacent areas is probably of greatest importance for the abundance of a rich year-class. But in addition, other conditions, such as the number and kind of predators, the food organisms available, and the physical and chemical properties of the surrounding medium, are undoubtedly of great importance for the survival of the cod larvae". Of these other conditions the availability of food is probably most important; transport and food will now be considered further.

Cod larvae are carried to the banks of the western Barents Sea in the West Spitsbergen Currents and its various offshoots (Fig. 1). If the current is strong in spring and early summer the larvae should have a good chance of being widely distributed over the nursery grounds, and of not being carried westwards into the Norwegian Sea. During the period between 1949 - 59 the *Ernest Holt* regularly worked a line of hydrographic stations across the current west of Bear Island. Values of the volume transport above 400 m depth have been calculated for each crossing between stations "S" and "W" (Fig. 1). The values of this transport have been published by Hill and Lee (1958) and Lee (1961). In the spring and early summer the largest number of crossings was made in the month from mid-April to mid-May, and the values for these six years are given in Table 1. By this time the eggs have hatched and the young larvae are being carried between the Norwegian coast and Bear Island. Hill and Lee (1958) and Lee (1961) have discussed the relation between the wind and water transport in the eastern Norwegian Sea, and have shown that in the "non-summer" months of September to June, that is before thermal stratification occurs in the surface layers, there is a significant positive correlation between the southerly wind component and the volume transport between 2 and 20 days later. The correlation coefficient has its greatest significance around 10 days later, with $P<0.01$. The wind data are obtained from the records of the Bear Island Meteorological Station, and in Table 1 the mean southerly wind for April for each year from 1947 to 1959 is listed. Since we have the early summer transport values for so few years we have had to use the wind data instead to relate to the year-class strength.

TABLE 1.—ENVIRONMENTAL FACTORS AND YEAR-CLASS STRENGTH OF ARCTO-NORWEGIAN COD IN THE WESTERN BARENTS SEA.

Year	Southerly wind. April mph W	Water transport mid-April to mid-May km^3/hr	Summer plankton mg/m^3 P	0-group cod. October no. per hr	5-yr-old cod no. per hr Y
1947	-5.96				135.0
1948	-1.33				232.5
1949	-0.92		47		157.6
1950	-0.81		54		371.1
1951	-10.89	-0.2	15		139.7
1952	-5.94		22		30.0
1953	-7.11		26		93.4
1954	+0.66	8.4	46		237.3
1955	-4.63	0.3	24		119.2
1956	-2.30		29		210.8
1957	+3.28	3.6	34	3.8	203.5
1958	+3.75	4.1	45	9.9	
1959	+2.49	5.2	35	11.3	

Wiborg (1948 and 1960*b*) examined the food of cod larvae off the Norwegian coast and in the south-western Barents Sea between April and August and found that the main food organisms were copepods, with *Calanus finmarchicus* the most important. Other common foods are euphausiids, appendicularians and, locally, *Spiratella* and the larvae of bottom invertebrates. All these foods are planktonic and their frequency in cod stomachs is about the same as their frequency in plankton samples in the area. During the 11 years that the *Ernest Holt* was working in the western Barents Sea, plankton samples were taken on most cruises at fixed stations west and south of Bear Island (Fig. 1). Details of these stations and others in the Barents Sea and the quantity of zooplankton caught in each cruise, expressed as dry weight, have already been published (Corlett, 1953, 1958*b* and 1961). For each year a mean value has been calculated to represent the standing stock of zooplankton in the Bear Island area between mid-April and the end of September - that is, in the months when the cod larvae are pelagic. These indices of summer plankton are set out in Table 1.

The first regular index of year-class strength of cod in the western Barents Sea is obtained from the English commercial fishery when the fish are 5 years old. These indices are the numbers caught per hour's fishing and are published by the Ministry of Agriculture, Fisheries and Food (Great Britain, 1962). They are listed here in Table 1, with the addition of the previously unpublished value for the 1957 year-class in 1962. Also in Table 1 are the mean catches per hour of 0-group cod obtained during three October cruises of the *Ernest Holt*, using covered codends. Each estimate comes from between 30 and 40 stations on the West Spitsbergen Banks, Hope Island Bank and the south Bear Island Bank.

CORRELATIONS AND PREDICTIONS

The relation between the strength of the year-class when five years old and the wind and plankton indices, representing transport and food, have been examined to see whether year-class strengths can be predicted from either wind or plankton. All the indices are given in Table 1. The regressions of year-class strength on plankton and wind are shown in Fig. 2 (c and b). The formula for the regression of year-class on plankton for the 9 years 1949-57 is $Y = 5.63 P - 12$: the correlation coefficient, r , is 0.758, which is between the 1% and 2% levels of significance. The possible use of plankton data for predicting year-class strength was discussed in Corlett (1958*c*), but at that time no reliable indices of year-class strength were available.

For year-class on wind for the 11 years 1947 - 57 the regression line is Y = 13.27W + 219. *r* is 0.594, which is at the 5% level of significance.

The plankton abundance for any year is not independent of the wind and water transport. In years of strong southerly wind and increased transport in the West Spitsbergen Current, plankton is richer than average in the western Barents Sea. This is shown in the regression of plankton on wind for the 11 years 1949-59 in Fig. *2a*. The regression line is P = 1.93W + 38.24, and the correlation coefficient is 0.730, which is at the 1% level of significance.

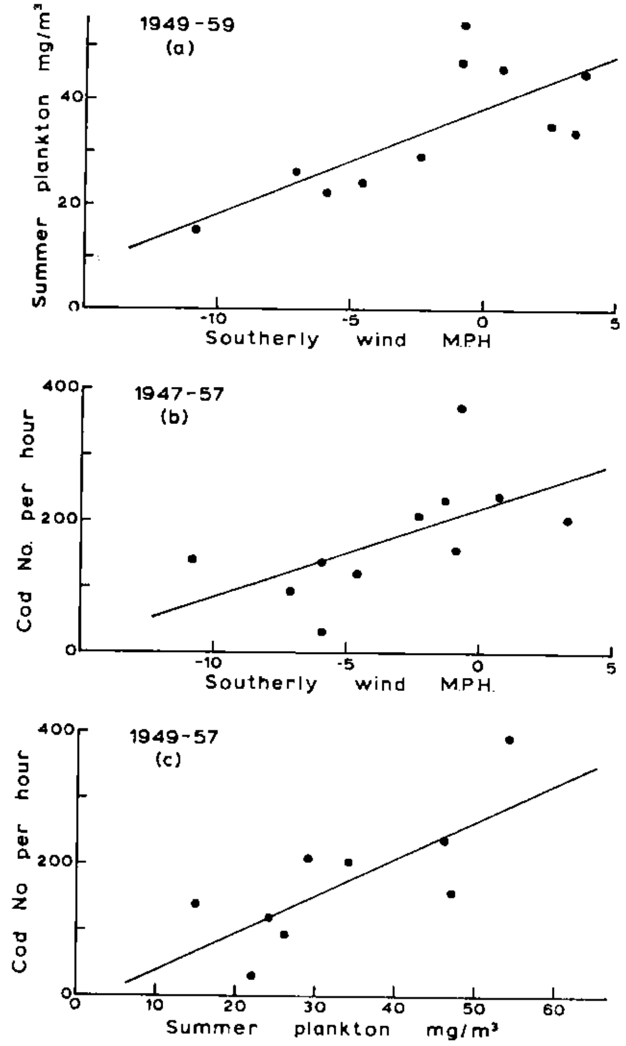

Fig. 2. Bear Island area:-

(a) Regression of summer plankton on mean southerly wind in April.

(b) Regression of cod year-class strength when 5 years old on wind in April.

(c) Regression of cod year-class strength when 5 years old on summer plankton.

Using the regression formulae the strength of the 1958 and 1959 year-classes of cod as five-year-olds in 1963 and 1964 can be predicted from both plankton and wind. These predictions are set out in Table 2, together with predictions for the 1960 - 1963 year-classes based on wind only.

TABLE 2.—PREDICTIONS OF COD YEAR-CLASS STRENGTH AT 5 YEARS OLD FROM WIND AND PLANKTON.

Year	Southerly wind mph	Predicted year-class strength	Summer plankton mg/m^3	Predicted year-class strength
	W	Y	P	Y
1958	+3.75	269	45	241
1959	+2.49	252	35	185
1960	+5.23	288		
1961	-2.69	183		
1962	-0.47	213		
1963	-0.76	209		

The estimate from plankton should be better than that from wind, because of the greater significance of the correlation. The estimates suggest that the 1958 and 1959 year-classes will be above the 1947-57 average of 175 fish per hour, and that the 1958 year-class will be stronger than that of 1959. The strong southerly wind in April 1960 should produce a particularly strong year-class. Baranenkova (1963) confirms this when she says that in October-November, 1960 "the 0-group was especially rich in the waters of West and North Spitsbergen and on the western slope of the Bear Island Bank. The occurrence of such high numbers of 0-group cod in these areas testifies to a significant drift in 1960 of fry from the spawning grounds....". She also suggests that "the 1960, 1959, 1958 and 1957 year-classes in the north-western part of the sea will not be below average".

Although the mean north-south wind component in April in each of the years 1961, 1962 and 1963 was northerly, all were less northerly than the average for the years

1947-57: so the 1961, 1962 and 1963 year-classes of cod may be expected also to be above average.

Attempts to relate year-class strengths to wind data have been made in several fisheries (Hela and Laevastu, 1961) and will no doubt continue to be made, because wind data can be obtained regularly and without any use of valuable research ship time.

POSTSCRIPT

In another paper in this section of the Symposium (p. 363-371), Gulland discusses the difficulties in the use of correlations to establish a connection between the environment and year-class strength. He quotes this paper and then, using different estimates of year-class strength and the same plankton values, obtains a correlation coefficient for the years 1949-56 of only 0.56. Gulland's estimates of year-class strength are based on the percentage age composition of the catches between 1929 and 1960 and estimates of fishing mortality during those years on fish between 4 and 9 years old. His estimates for the year-classes for 1949-51 are thus based on 6 years (4-9 years old) and for subsequent year-classes on successively fewer ages, until that of 1956 is based only on four-year-old fish. Thus his estimates are less direct than the catch of fish at 5 years old used in this paper, and, for the years in question, cannot be considered any better.

It has also been suggested that cod are not always fully recruited to the fishery at five years old. Using the catch per hour of six-year-old fish for the year-classes 1949-56 a correlation with summer plankton gives $r = 0.805$ (which is between the 1% and 2% levels of significance), compared with 0.758 for the 1945-57 year-classes as five-year-olds. In view of the controversy over estimation of year-class strengths perhaps it is best to say only that these correlations are between summer plankton and the subsequent catch per effort of five- and six-year-old fish in the Bear Island - Spitsbergen area.

REFERENCES

BARANENKOVA, A.S. 1960. The results of surveys on young cod and haddock in the Barents Sea during the period 1946-1959. *Soviet Fish. Invest. North European Seas.* Moscow. VNIRO and PINRO. p. 267-275. In Russian, with English summary.

1963. Soviet investigations on young cod in the Barents Sea. *Ann. biol., Copenhague*, 18: 105-107.

CORLETT, J. 1953. Dry weight and fat content of plankton near Bear Island 1949-1952. *Ann. biol., Copenhague*, 9: 8-9.

1958*a*. Distribution of larval cod in the western Barents Sea. *Spec. Publ. int. Comm. Northw. Atlant. Fish*, No. 1, p. 281-288.

1958*b*. Dry weight of plankton in the western Barents Sea 1953-1956. *Ann. biol., Copenhague*, 13: 39-40.

1958*c*. Plankton in the western Barents Sea and the year-class strength of the Arcto-Norwegian cod. *J. Cons. int. Explor. Mer*, 23: 354-356.

1961. Dry weight of plankton in the western Barents Sea 1957-1959. *Ann. biol., Copenhague*, 16: 68-69.

GREAT BRITAIN. 1962. Ministry of Agriculture, Fisheries and Food and Department of Agriculture and Fisheries for Scotland. *Fish Stock Record 1961.*

HELA, I. and T. LAEVASTU. 1961. *Fisheries Hydrography.* London. Fishing News (Books) Ltd. 137 p.

HILL, H.W. and A.J. LEE, 1957. The effect of wind on water transport in the region of the Bear Island fishery. *Proc. roy. Soc. (B)*, 148: 104-116.

LEE, A.J. 1961. The effect of wind on water movements in the Norwegian and Greenland Seas. *Proc. Symp. Mathematical-Hydrodynamical Methods of Physical Oceanography*, p. 353-383. Institut für Meereskunde der Universität Hamburg.

TROUT, G.C. 1957. The Bear Island cod migrations and movements. *Fish. Invest., Lond., Ser.2*, 21 (6): 1-51.

WIBORG, K.F. 1948. Investigations on cod larvae in the coastal waters of northern Norway. *Fiskeridir. Skr. Havundersøk.*, 9(3): 1-27.

1950. The occurrence of fish eggs and larvae along the coast of northern Norway during April-June 1948 and 1949. *Ann. biol., Copenhague*, 6: 12-16.

1952. Fish eggs and larvae along the coast of northern Norway during April-June 1950 and 1951. *Ann. biol., Copenhague*, 8: 11-16.

1957. Factors influencing the size of the year-classes in the Arcto-Norwegian tribe of cod. *Fiskeridir. Skr. Havundersøk.*, 11 (8): 1-24.

1960*a*. Investigations on eggs and larvae of commercial fishes in Norwegian coastal and offshore waters in 1957-58. *Fiskeridir. Skr. Havundersøk.*, 12 (7): 1-27.

1960*b*. Investigations on pelagic fry of cod and haddock in coastal and offshore areas of northern Norway in July-August 1957. *Fiskeridir. Skr. Havundersøk.*, 12 (8): 1-18.

B-11

ON THE LIFE CYCLE OF LABRADOR COD

By

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EDITORIAL NOTE:

This paper reports on data collected on cod in the Labrador area (ICNAF Subarea 2) during the ICNAF NORWESTLANT Surveys, April-June 1963. It will be published *in extenso*, in ICNAF Special Publication Number 7 (Report of the NORWESTLANT Surveys).

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B-12

CHANGES IN RECRUITMENT TO THE STOCK IN RELATION TO THE ENVIRONMENT, WITH REFERENCE TO MATHEMATICAL MODELLING

By

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ABSTRACT

The factors governing the size of a fish stock are considered briefly. It is argued that the causes of annual fluctuations of a stock must be clearly understood before planning the regulation of a fishery. For the most part, such fluctuations are related to changes in survival rates during the early stages of the life history of the fish.

By means of illustrations taken from Russian work, it is shown that the abundance of planktonic food organisms influences the survival of young fish.

It is emphasized that the effects of the biotic and abiotic environment on brood strength should be included in mathematical models of the dynamics of fished stocks.

The efficiency of regulation of a fishery and accuracy of prediction depend in some cases on the extent of our knowledge of the causes of fluctuations in the stock. The task facing ichthyologists is to assess the quantitative effect of each factor on the dynamics of the population, and particularly the role of governing factors. Among other causes affecting the stock, the governing factor may be one which, under certain conditions, has a direct effect on the abundance of the population at one or another stage of development.

A fish population becomes specific while dwelling in a water body. This is the result of a relative consistency of the governing factors affecting the survival of the population. The governing factors may be replaced by some others only if fairly sharp changes take place in the hydrologic regime or food resources, or new fishing methods are introduced, aimed at the intensification of the fishery.

Among the main factors, it is necessary to distinguish those which bring about long-range fluctuations in the abundance of the stock, and those affecting annual fluctuations in the sizes of the year-classes. No clear distinction can be established between them due to their close relation. Nevertheless, an approach should be differently chosen to gain some knowledge of their role as a factor governing either long-term or short-term fluctuations in the stock in each case.

The annual recruitment size varies greatly, and thus the relation between recruitment and the remainder of the fishing stock also varies, particularly in fishes with a short or medium span of life, bringing about changes in the relation between catches and abundance of fish.

Consequently, it is quite obvious that the causes of annual fluctuations in recruitment should be clearly elucidated. In most species the annual fluctuations are closely related to the survival of embryos and the food supply for early larvae. It is at this time that the heaviest mortality in fish is known to occur. Great fecundity of fish is an adaptive ability to compensate for the early mortality, so that the abundance of the species can be maintained. If the early mortality was reduced even by a very small amount, it would lead to a considerable increase in the abundance of the species, assuming favourable conditions. This conclusion can serve as a basis for fishing management in the sea by increasing the food supply for larvae, and in this way increasing the

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survival rate and fishery yield (Shelbourne *et al.*, 1963).

Let us consider some results obtained in the USSR during the recent decade, supporting the existence of a direct relation between the abiotic and biotic factors and the survival of young fish at the early stages.

There are many data on the relation between the availability of food plankton and survival of larvae when they begin active feeding, which undoubtedly indicate that this factor should be considered as a governing factor for the abundance of a year-class.

Lisivnenko (1961), studying material collected in the period 1955-59 on the abundance of zooplankton in the Gulf of Riga and that of larvae of the Baltic spring spawning herring, found a quite clear, quantitative, relation shown in Fig. 1 as an S-shaped curve. In some years, when the larvae of the Baltic herring began active feeding, the small plankton was poor (1 organism in more than 100 cc of water), so a shift in the normal feeding conditions could be observed and the year-classes were usually poor. On the other hand, in years when the small plankton was relatively rich, the frequency of occurrence of larvae and plankton organisms increased. If one organism occurs in less than 100 cc of water, the feeding conditions for larvae become normal and survival is high.

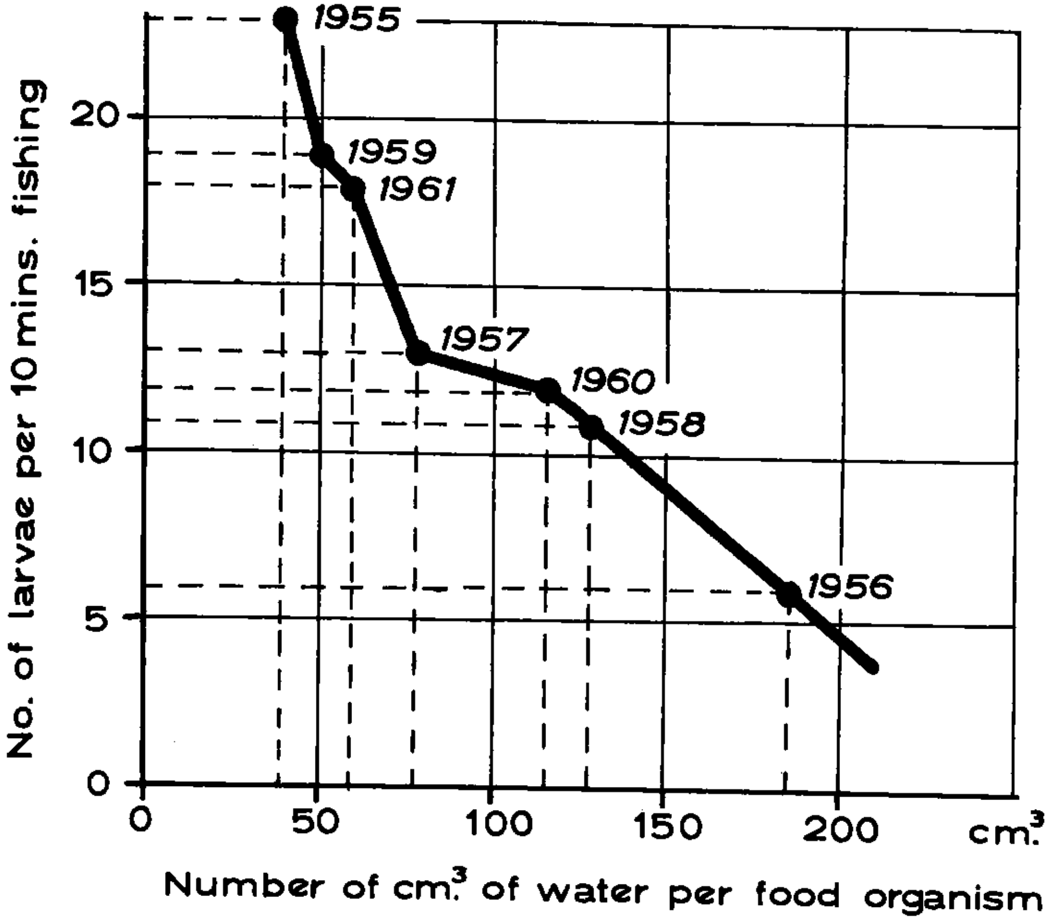

Fig. 1. The relation between the abundance of herring larvae and their food organisms (Lisivnenko, 1961). Herring larvae are shown as numbers per 10 minute haul; food as cm^3 of water per organism.

The same relation is found for the Black Sea anchovy (Pavlovskaya, 1961). As shown in Fig. 2., there is almost a direct relation between the survival of the young fish and biomass of food zooplankton in the period 1949-58. The largest generations are observed with a concentration of more than 10,000 organisms or 500 mg per m^3 of water for 4-10 mm fish larvae. Of great importance is the development of food plankton at the time when the anchovy larvae appear in large numbers.

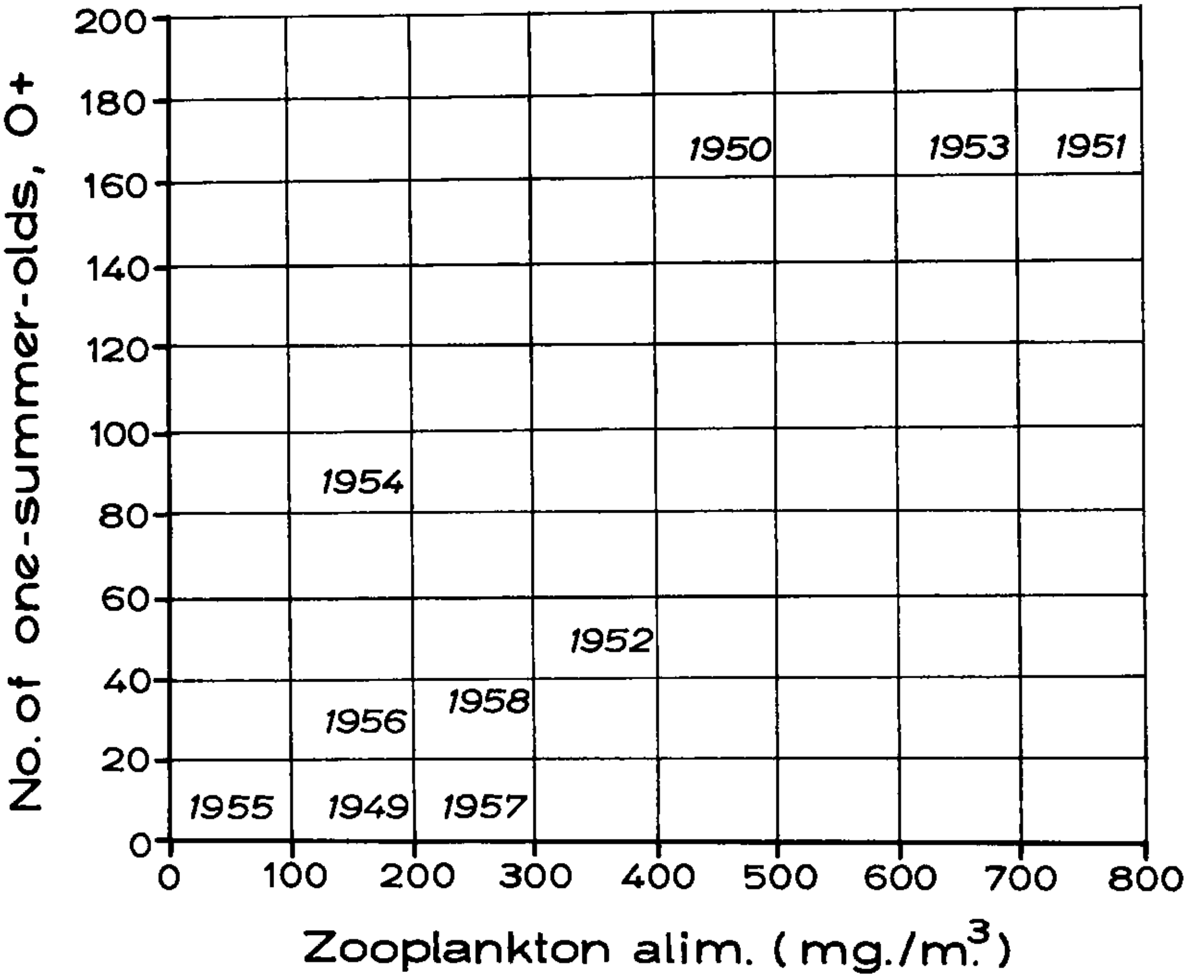

Fig. 2. The relation between the abundance of young stages of anchovy and the biomass of their planktonic food in the north-western Black Sea, during the years 1949-1958 (Pavlovskaya, 1961).

For the Baltic cod a direct relation was found between the salinity and oxygen content of off-bottom waters in the deeps (spawning places for cod) and the survival of eggs. The fluctuations in the abundance of embryos are in compliance with the fluctuations in the mean catches of one-summer-olds and catches of adult fish at corresponding ages. For the Barents Sea cod the relation between the abundance of year-classes and temperature, which seems to affect the food supply for the cod larvae, was established (Kislyakov, 1959).

In all the inland seas there is a direct relation between the abundance of the migratory and semi-migratory fishes and the volumes of the river discharges which provide suitable spawning areas and food supply for the fish at early stages. Specific research in this field was carried out by

L.A. Rannak on the Baltic herring, S.G. Kryzhanovsky on Sakhalin herring, V.I. Vladimirov on Danube herring, E.G. Boiko on bream and perch pike of the Azov Sea, T.F. Dementyeva, V.S. Tanasiychuk, A.G. Kuzmin on sea bream, perch pike and *Rutilus rutilus* of the Caspian Sea, A.A. Ostroumov on bream of the artificial Rybinsk water body and other workers, the results being similar.

The interrelation between the spawning of fish and the abiotic and biotic environment is so distinctly expressed that it enables us to work out methods of calculating the stock population by using characteristics of environmental factors (Izhevsky, 1961) in view, of course, of the fishing mortality.

Because of the above-mentioned effects, the wide range of the annual fluctuations in recruitment to the fishery stock should be included in models of the dynamics of fished populations. Calculations of the recruitment size and possible changes can be obtained from the quantitative counts of the young fish at various stages of development. For this purpose annual observations on spawning should be carried out, the result of which can be assessed in various ways, as follows:

1. By mean catches of spawned eggs at various stages of development in view of the percentage of living embryos and environmental conditions;

2. by mean catches of larvae at the stage of development after turning to the active feeding;

3. by mean catches of one-summer-olds to assess the density of their distribution per unit of area;

4. by mean catches of young age-groups (prior to maturation) per commercial or research fishing gear.

The method of counting one-summer-olds is probably most important because it enables us to assess the young fish at the stage when the heaviest mortality of eggs and larvae has already occurred. The evidence can be supported by a correlation between the fishery returns and mean catches of one-summer-olds of a certain year-class. Using this relation this index can be applied to calculations of the recruitment size to the fishing stock.

The counts of eggs and larvae may also be promising in assessing differences in the strengths of year-classes; however, the data obtained are, to a lesser extent, useful for mathematical calculations. In most cases they only indicate trends of fluctuations in the strength of the year-classes and may be suggestive in the studies of the causes conditioning the survival of embryos and larvae at early stages of development.

SUMMARY

The efficiency of measures for the regulation of fisheries and the precision of fishery forecasts depends in a number of cases on adequate knowledge of the factors affecting fish stock fluctuations.

For the majority of fish species, annual fluctuations of stock depending on the value of recruitment are noted. These fluctuations depend upon the conditions for survival of eggs and on the provision of food for larvae at the stage of their transition to external feeding. When the conditions for species are optimal, the decrease in larval mortality, even by a very small fraction, results in a considerable increase in a fish population.

During the recent decade a great number of papers were published showing a direct relationship between abiotic and biotic factors and the survival of young fish at early stages. In particular, some data on the relationship between the abundance of food plankton and the survival of larvae, allow us to consider this factor (which is not dependent on the population density) to be of extreme importance when determining recruitment abundance. The data also show that, in the case of species for which a critical period is that of transition to active feeding, there is a certain level of plankton density at which an abundant year-class survives.

Thus, to estimate an abundant year-class of the Baltic herring, it is necessary to have less

than 100 cc of water per one food organism (Lisivnenko, 1961); the density of plankton which is necessary to estimate an abundant year-class of the Black Sea anchovy is expressed in another form; such year-classes were observed when the density of food plankton for the larvae 4-10 mm long was above 10,000 organisms or 500 mg per m^3 (Pavlovskaya, 1961). These data allow us to look for ways to assess the strength of a stock of consumers on the basis of the value of plankton biomass.

Taking into consideration the wide range of fluctuations of annual recruitment to commercial fish stocks, as a result of the factors mentioned above, it is considered extremely necessary to show these fluctuations when making models expressing the dynamics of a fished population.

REFERENCES

IZHEVSKY, G.K. 1961. Oceanologic bases for fishing productivity of the seas. *Pishchepromizdat*, Moscow, p. 1-215.

KISLYAKOV, A.G. 1959. Temperature regime and yield of the year-classes of cod spawning off the north-western Norway. *Nauchno-Tech.Bull., PINRO*, No. 1 (9), p. 22-26.

LISIVNENKO, L.N. 1961. Plankton and feeding of larvae of the Baltic herring in the Riga Gulf. *Trud. nauch.-issled. Inst. ryb. Khoz., Latvian SSR*, 3: p. 105-138.

PAVLOVSKAYA, R.M. 1961. La survie des larves de l'anchois de la Mer Noire en fonction de leur alimentation. *Rapp. Comm. int. Mer. Médit.* XVI (2), p. 345-350.

SHELBOURNE, J.E., J.D. RILEY, and C.T. THACKER, 1963. Marine Fish Culture in Britain. *J. Cons.*, Vol. XXVIII, No. 1, p. 50-90; No. 2, p. 246-261.

B-13

ON PRIMARY FOOD SUPPLY - THE BASE OF PRODUCTIVITY IN THE NORTHWEST ATLANTIC

By

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EDITORIAL NOTE:

This paper reports on data collected during the ICNAF NORWESTLANT Surveys, April-June 1963. It will be published *in extenso*, in ICNAF Special Publication Number 7 (Report of the NORWESTLANT Surveys).

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B-14

THE EFFECT OF TEMPERATURE AND CURRENTS ON THE DISTRIBUTION AND SURVIVAL OF COD LARVAE AT WEST GREENLAND

By

Frede Hermann[1], Paul M. Hansen[2] and Sv. Aa. Horsted[2]

ABSTRACT

The distribution of cod larvae off West Greenland is compared with the surface currents. It is shown how the westerly branch of the West Greenland Current carries great numbers of larvae away from the Greenland banks.

A comparative measure of the strength of cod year-classes between 1924 and 1951 is calculated. The year-class strengths are correlated with the water temperature during the larval stage. Significant correlation was found between year-class strength and mean temperature, surface to 45 m over Fylla Bank in June.

The number of cod larvae caught off West Greenland in different years is compared with water temperature in June and July.

The onshore wind component during the larval stage is correlated with year-class strengths. No significant correlation is found.

COD SPAWNING GROUNDS OFF WEST GREENLAND

At West Greenland the most important cod spawning grounds seem to be along the western slopes of the banks, mainly at depths between 200 and 600 m in the relatively warm water of the Irminger Current. The map (Fig. 1) which shows the distribution of these spawning grounds, is based on information from Faroese fishermen and from German, Norwegian and Russian research vessels. In addition, some spawning takes place in coastal waters and in the inner parts of some fjords, but these spawning grounds are supposed to be of lesser importance for the recruitment of the West Greenland cod stock.

DISTRIBUTION OF COD LARVAE

The distribution of cod larvae off West Greenland has been investigated for many years by R/V *Dana* taking hauls with stramin nets at a number of stations on standard sections. Figure 2 shows, as an example, the number of cod larvae caught in July 1957 (Hansen, 1958). It is seen that most of the larvae are found north of the spawning grounds, mainly in the area between Fylla Bank in the south and the southern part of Store Hellefiske Bank in the north. Furthermore it is remarkable that a great concentration of larvae is found more than 100 nautical miles west of Fylla Bank. These larvae have drifted so far westward that they are probably lost for the Greenlandic cod stock. They can possibly contribute to the recruitment of the Labrador cod stock.

In the year 1957, which was used as an example here, the number of cod larvae caught was greater than the average, but the distribution seems to be typical for the month of July, with very few larvae south of 64°N.lat, one concentration being over the West Greenland banks between 64°N. and 67°N. and another concentration far west of Fylla Bank.

CURRENTS OFF WEST GREENLAND

The surface currents off West Greenland are illustrated in Figure 3. It is well known that the main direction of the West Greenland Current is northwestward along the coast, but a branch of the current turns westward between 64°N. and 65°N. These features explain the distribution of the cod fry. From the spawning grounds the eggs and larvae are carried northward by the current. Some of the larvae are carried westward by the westerly branch of the current and, as mentioned, are probably lost for the Greenland cod stock. The fraction of the eggs and larvae which is carried away from Greenland waters is expected to have some influence on the size of the year-class of the year in question.

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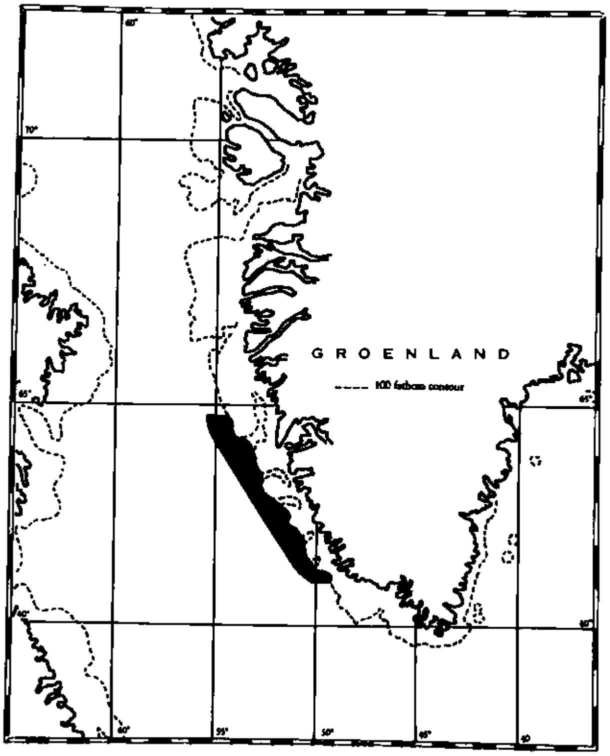

Fig.1. Offshore spawning grounds of West Greenland cod stock.

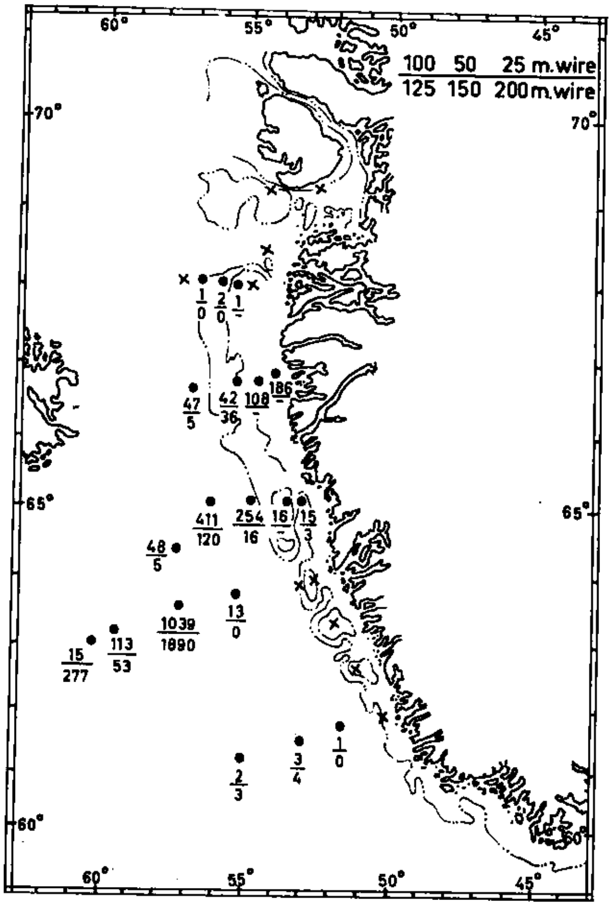

Fig.2. Number of cod larvae caught in stramin net hauls, July 1957.

The West Greenland Current is a mixture of two currents: the Polar component, which is a continuation of the East Greenland Polar Current and an Atlantic component which is a continuation of the warm Irminger Current. Off the middle part of West Greenland a considerable mixing has taken place so that the temperature differences between the two components are smaller than in the Cape Farewell region.

The water temperature over the banks and their western slopes, where the cod eggs and larvae are found, depends very much on the relative strength of the two current components.

The cod in West Greenland waters lives near its northern limit and it is therefore reasonable to assume that even small temperature variations will have great effect on the survival of the eggs and larvae. The correlation between the strength of the cod year-classes and the water temperature during the larval stage will be investigated in the following sections.

STRENGTH OF COD YEAR-CLASSES AT WEST GREENLAND

The basic material for calculating a comparative measure of the stremgth of the cod year-classes is the record of *the total catch of the Greenlanders* in the different years and *the age distribution in the single years* calculated from age determinations on samples. From this material the total catch of each year-class between age-group V and XI is calculated for all the year-classes from 1924 to 1951. In the present contribution only the catch from Godthåb district and more northern districts is considered since the cod off the southernmost part of West Greenland is

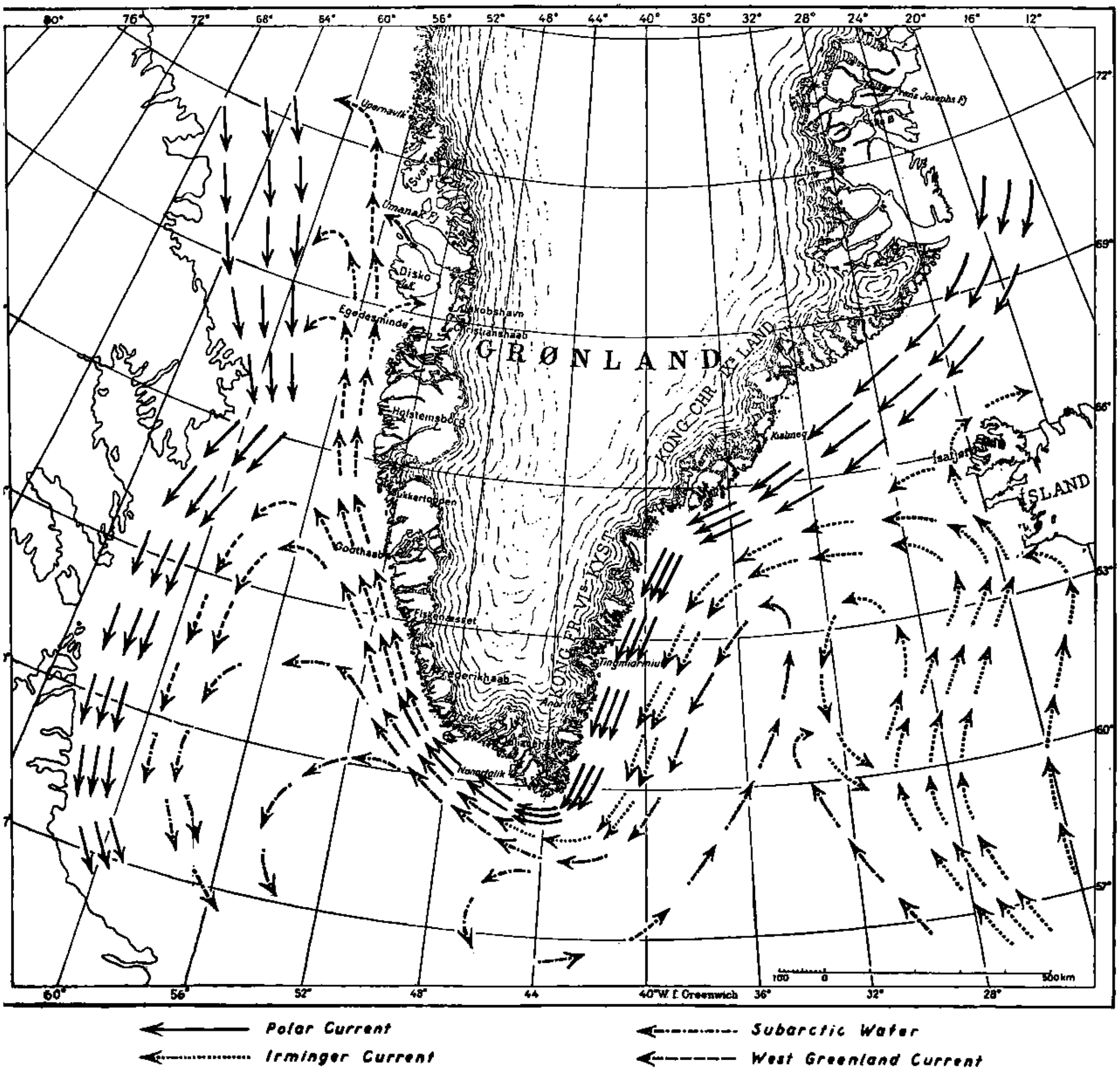

Fig.3. Surface currents in Greenland waters. (From Hansen and Hermann: Fisken og Havet ved Gronland)

supposed to be a mixture of stocks of different origin.

Had the Greenlanders' fishing effort been constant during the years, their total catch could have been used as comparative measure of the year-class strength; but, in view of the great development of the Greenlanders' fishery, especially in the years after the war, it is necessary to correct for the variation of their fishing effort. A rough measure of the relative fishing effort is obtained from the percentage of recaptures of tagged cod in different periods and from the number of boats in the Greenlanders' fishery. Table 1 gives the number of cod tagged in the Godthåb and Sukkertoppen districts (between 63°N. and 66°N. approximately) and the number and percentage of recaptures taken by Greenlanders in all districts in the year of tagging and the following three years. The mean year has been calculated with the number of cod tagged as a weighting factor for the two periods 1924-39 and 1948-58. Cod tagged in the Godthåb Fjord are not included in Table 1 as this fjord is inhabited by a local stock.

TABLE 1.

Period	Mean yr.	Cod tagged No.	Recaptures No.	Recaptures %	Fishing effort relative to 1932
1924-39	1932	2374	66	2.78	1.0
1948-58	1954	2738	251	9.17	3.3

It appears that the percentage recaptured for the period 1948-58 was a factor 3.3 greater than the percentage recaptured for the period 1924-39.

Table 2 gives the number of rowing boats and motor boats in the Greenlanders' fishery for different years. Each motor boat has been calculated as equivalent to five rowing boats. The factor five has partly been estimated from information from fishermen, but it has also been taken into account, that with this factor the fishing effort calculated from number of boats will fit with the fishing effort calculated from tagging experiments.

TABLE 2.

Year	Rowing boats	Motor boats	Motor boats x 5	Equivalent total no. of rowing boats	Fishing effort relative to 1932
1932	1210	30	150	1360	100
1939	1410	70	350	1760	129
1945	1650	75	375	2025	149
1950	1950	360	1800	3750	276
1952	1620	450	2250	3870	285

Assuming that the fishing effort of the Greenlanders is proportional to the total number of boats as given in Column 5 of Table 2 and to the percentage recapture of tagged cod, the fishing effort of each year relative to the effort in 1932 can now be calculated. This is done in the last column in Tables 1 and 2 and plotted in Fig. 4.

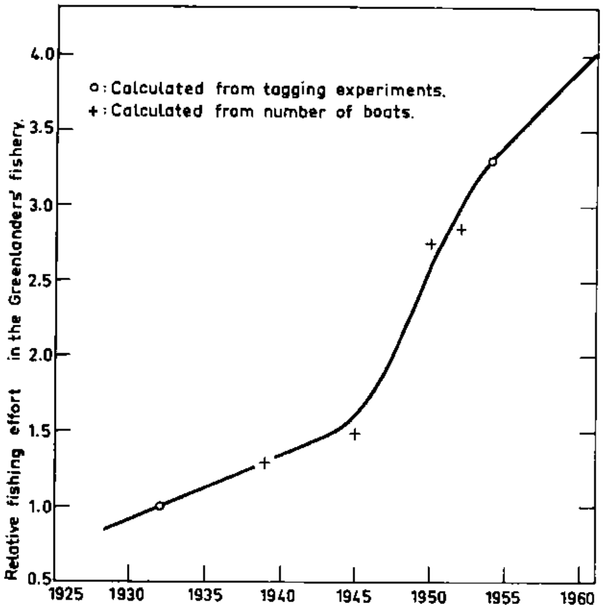

Fig. 4. Variation in relative fishing effort in the Greenlanders' Cod fishery.

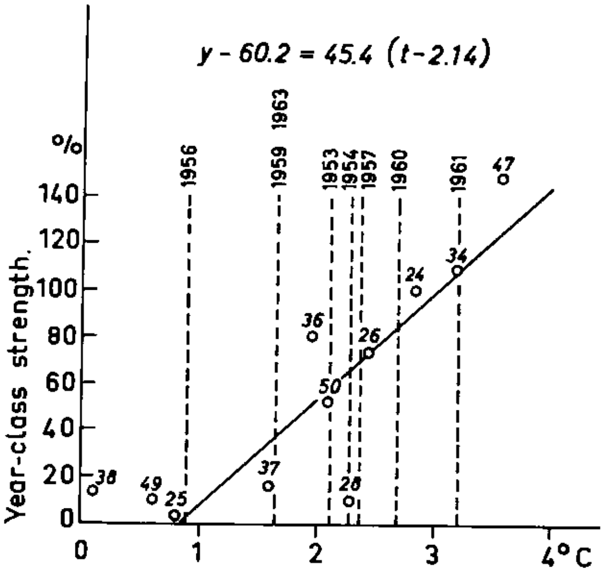

Fig. 5. Year-class strength plotted against mean temperature, surface to 45 metres over Fylla Bank in June.

The relative strength of the year-classes is now calculated in the following way: the number of cod of a certain year-class caught by the Greenlanders is divided by the relative fishing effort for the mean year of the period in which the year-class in question has been fished, *i.e.* when the year-class was 8 years old. The year-class strength is then calculated as the percentage of the strength of the 1924 year-class. The results are given in Table 3.

TABLE 3. RELATIVE STRENGTH OF THE YEAR-CLASSES 1924 - 1951

Year-class	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936	1937
Number caught in age groups V to XI in thousands	1787	57	1425	248	190	516	401	999	866	454	2741	872	2355	487
Relative fishing effort	1.00	1.03	1.08	1.12	1.17	1.22	1.25	1.29	1.33	1.37	1.41	1.47	1.56	1.66
Relative strength	100	3	74	12	9	24	18	43	36	18	109	33	81	16

Year-class	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951
Number caught in age groups V to XI in thousands	433	977	1008	1349	3950	1411	1236	3337	748	9044	1297	733	3433	1163
Relative fishing effort	1.81	1.98	2.15	2.34	2.58	2.81	2.98	3.17	3.30	3.40	3.50	3.60	3.70	3.80
Relative strength	13	28	28	32	86	28	23	59	13	148	21	11	52	17

CORRELATION BEWEEN YEAR-CLASS STRENGTH AND SEA TEMPERATURE

Table 3 shows that there is wide variation in the year-class strengths. In this section we will try to see whether this variation can be explained as an effect of the temperature conditions during the egg and early larval stage. The temperature data from West Greenland waters consist partly of surface observations from commercial vessels (collected by the Danish Meteorological Institute and published by Jens Smed, 1958, 1959 as monthly temperature anomalies for large areas) and partly of subsurface observations from research vessels.

The year-class strengths are correlated with Smed's surface temperature anomalies for Area A_1 (West Greenland waters) for the years 1924 - 39 and 1946 - 51, for the months April to July. The correlation coefficients, r, are given in Table 4.

TABLE 4.

Month	April	May	June	July	Mean temperature anomaly, April-July
r	0.14	0.53	0.15	0.42	0.38

Only the correlation coefficient for May is significant within the 0.02 probability limit. One reason for these low correlation coefficients could be that the surface temperature is not sufficiently representative of the temperature in the water layers where the cod eggs and larvae are found.

In June the cod larvae are mainly found over Fylla Bank and Lille Hellefiske Bank in the upper 50 m. The hydrographic station in this area which has been worked most frequently in June is the international station r-2 over the shallow part of Fylla Bank (63°58'N.52°44'W.). Observations have been made in June at this station in the following years: 1924,25,26,28,34,36,37,38,47,49,50,53,54, 56,57,60,61 and 1963. Thus for 11 years between 1924 and 1950 we have observations of temperature as well as strength of year-classes. In Fig. 5, year-class strength is plotted against mean temperature in June in the upper 45 m on Fylla Bank. The index numbers at the points indicate the year-classes. At the lowest temperatures it looks as though the year-class strength lies at a constant low value, but from a certain temperature the year-class strength seems to increase linearly with the temperature.

The correlation coefficient between year-class strength and the mean temperature over Fylla Bank in June is found to be $r = 0.85$. As the relationship cannot be linear over the total temperature range the correlation coefficient was also calculated omitting the observations from the "coldest" year 1938 and was found to be $r = 0.87$. Both correlation coefficients are significant ($P<0.01$). Still omitting the 1938 observations the regression line for year-class strength on temperature was found to be: $y - 60.2 = 45.4\ (t - 2.14)$. The standard deviation of the points around this regression line is equal to 25 year-class units, (25% of the 1924 year-class). This gives a measure of the accuracy with which year-class strength can be predicted from temperature observations over Fylla Bank in June.

The year-class strengths have earlier been compared with the temperatures off Fylla Bank (Hermann, 1953 and 1961). In these papers the Greenlanders' total catch of the different year-classes up to the year 1946 was used as a measure of the year-class strength and only the year-classes up to 1938 were studied. In the present paper some of the more recent year-classes have been included and, after correction for variationa in the fishing effort, they show a close relationship between year-class strength and temperature.

The mean temperatures for the water column 0 - 45 m in June for the years between 1953 and 1963 in which observations are available are indicated on Fig. 5 by hatched lines. Judging from the temperatures we would expect to get good year-classes from the years 1957, 1960 and 1961, the year-classes 1953 and 1954 should be fairly good and only small year-classes would be expected from the years 1956, 1959 and 1963.

CORRELATIONS BETWEEN NUMBER OF COD LARVAE AND SEA TEMPERATURES IN JUNE AND JULY

In 1950 and in the years 1952 - 1959 four standard sections have been worked out by the *Dana* in July in the area from Fylla Bank to Egedesminde with stramin net hauls and hydrography. From the four easternmost stramin net stations in each section and from two stations between Lille and Store Hellefiske Banks the total number of cod larvae caught has been calculated. The values for the few missing stations have been interpolated using the average percentage of the number of larvae found at stations mentioned. The catches at the westernmost stations were not included because the larvae found here will probably not benefit the West Greenland cod stock. Table 5 shows the calculated number of cod larvae.

TABLE 5.

Year	1950	1952	1953	1954	1955	1956	1957	1958	1959
Number of cod larvae	554	90	474	78	64	37	1629	187	77

It is doubtful whether these numbers are a good representation of the total mass of cod larvae off West Greenland. The larvae are not evenly distributed over the area. Thus in 1950, 554 larvae were caught on the 18 stations. Of these 319 (58%) were caught on one single station.

These numbers of larvae have been correlated with July temperatures from surface, 20 m and 40 m over both Fylla Bank, Lille Hellefiske Bank and Store Hellefiske Bank, but no significant correlations have been found. Unfortunately temperatures in June over Fylla Bank are only observed in five of these years but in these five years the number of cod larvae generally increases with increasing mean temperature (surface to bottom) over Fylla Bank in June. This confirms the hypothesis that it is during the early larval stage that the temperature conditions influence the survival of larvae.

CORRELATION BETWEEN YEAR-CLASS STRENGTH AND BAROMETRIC PRESSURE DIFFERENCES

As already mentioned a great part of the cod larvae are carried westward towards Labrador with he westgoing branch of the West Greenland Current and thus are probably lost from the West Green- and cod stock.

It is reasonable to assume that the relative strength of the two branches of the West Greenland urrent will depend to some degree on the wind conditions and specially on the onshore wind compon- nt. As a measure of this wind component, the difference in barometric pressure between Ivigtut t 61°N. lat and Jakobshavn at 69° N. lat is used. The barometric pressure differences were com- uted from the monthly means published in the Danish "Meteorologisk Årbog" for the months March to uly and correlated with the strength of cod year-classes for the years 1924 - 1951. The corre- ation coefficients found were, however, very small and very far from being significant.

Thus it looks as though the onshore wind component has no influence on the survival of the od larvae.

REFERENCES

HANSEN, P.M. 1958. Danish Research Report, 1957. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 8: p. 27.

HERMANN, F. 1953. Influence of Temperature on Strength of Cod Year-Classes. *Ann. biol., Copenhague*, Vol. IX, p. 31.

1961. Some Considerations about Correlations between the West Greenland Stock of Cod and Environmental Factors. *Annu. Meet. int. Comm. Northw. Atlant. Fish.*, 1961. Doc. No. 34, Serial No. 844 (mimeographed).

SMED, J. 1948 to 1963. Monthly Anomalies of the Surface Temperature in Areas of the Northern North Atlantic. *Ann. biol., Copenhague*, Vol. II to XVIII.

B-15

NOTES ON THE CONDITION OF FORMATION OF THE ARCTO-NORWEGIAN TRIBE OF COD OF THE 1959-1961 YEAR-CLASSES DURING THE FIRST YEAR OF LIFE

By

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ABSTRACT

The paper deals with the peculiarities found in the conditions of formation of the Arcto-Nor-egian tribe of cod of the 1959, 1960 and 1961 year-classes during the first year of their life.

INTRODUCTION

Every year-class of cod is formed under specific conditions because of great yearly changes n the abiotic and biotic environment. It is known that the natural conditions most strongly affect he strength of year-classes during the early period of their life. A characteristic feature of od biology is that the pelagic eggs and later, the extruding larvae are immediately exposed to the ffect of local conditions on the spawning grounds. The nature of water masses (temperature and alinity, water movement and biological characteristics) determines the area of distribution of the arvae, the density of their concentrations, the feeding conditions and the predators. The direc-ion and speed of currents result in transport of eggs, larvae and pelagic fry into various parts f the sea, thus determining the conditions of their subsequent life. The attention of investi-ators has long been drawn to studies of the causes of fluctuations in the strength of cod year-lasses. Hjort (1914) and later, Wiborg (1957) failed to find any correlation between the numbers f liberated eggs, hatched larvae and abundance of the year-class of cod in commercial catches. rom the data collected for a number of years, Wiborg (1957) concluded that the formation of rich ear-classes in the Arcto-Norwegian tribe of cod was favoured by prolonged spawning, large area of pawning grounds, extension of the central spawning area to the north, prolonged period of hatching nd by more rapid transport of eggs and larvae by currents to the areas of fattening of fry. The uthor also does not exclude such additional factors as the number of predators, availability of ood and the physical and chemical characters of the environment. Wiborg assumes that the abundance f a year-class is determined during the drift of pelagic larvae or just after the fry descend to he bottom. Studying the plankton in the area of Bear Island and the western part of the Barents ea in 1949-56, Corlett (1958) showed a relationship between the stock of plankton from mid-April to ate September (*i.e.* during the pelagic larval phase) and the strength of the corresponding year-lasses of cod. He also pointed out that survival of larvae and the size of the plankton stock were ffected by water temperature and transport. Hill and Lee (1958) demonstrated a correlation between he volume of water transported by the West Spitsbergen Current, the strength of the south wind in pril-May and the strength of corresponding year-classes of cod in the area of Bear Island. Examin-ng the abundance of 1946-58 year-classes in the Arcto-Norwegian tribe of cod in relation to hydro-ogical conditions, Kislyakov (1959, 1961) came to the conclusion that there is a close relationship etween the yields of the year-classes and the average temperature of water masses on the spawning rounds during the spawning period. He is of the opinion that rich year-classes are associated with igh intensity of atmospheric circulation, higher intensities and velocities of currents, high heat upply in water masses, dilution by coastal water, early timing of biological spring and greater epth of the 27.5-27.6 isopicnal. In warm years, due to the greater depth of the 27.5-27.6 isopicnal, ggs are found in deeper waters and are less subject to the mechanical effect of waves as compared ith cold years. According to Rollefsen (1930), a number of the cod eggs are killed by mechanical amage caused by stormy weather.

In 1959-61, the Polar Institute of Marine Fisheries and Oceanography carried out special nvestigations on the drift of eggs and larvae of various species of fish from the spawning grounds f the north-west Norwegian coast into the Barents Sea and the area of the Bear and Spitsbergen

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Islands. The investigations were conducted in the area limited by the latitude of Bear Island in the north, and the Lofoten region in the south, by the meridian of the Kola Gulf in the east and 5° to 10°E in the west (Fig. 1). The main routes of the drift of eggs and larvae of the Arcto-Norwegian tribe of cod pass this area. Two cruises were performed every year: one in the last ten-day period of April and in May and the other in June and early July. Standard hydrological sections were worked. The time of working the sections varied in different years, but the difference, as a rule, did not exceed two days or, occasionally, several days. Sampling of eggs and larvae of fish was accompanied by measurements of water temperature, sampling of water for hydrochemical analysis and collections of plankton. In the winters of these years the amount of "demersal" cod fry in the 0-group was estimated in the southern and north-western parts of the Barents Sea, including the areas of the Bear and West Spitsbergen Islands. The gear used for sampling plankton and ichthyoplankton during spring-summer surveys were plankton nets (gauze No. 38), egg nets (gauze No. 140) and ring trawls of perlon (3 mm mesh).

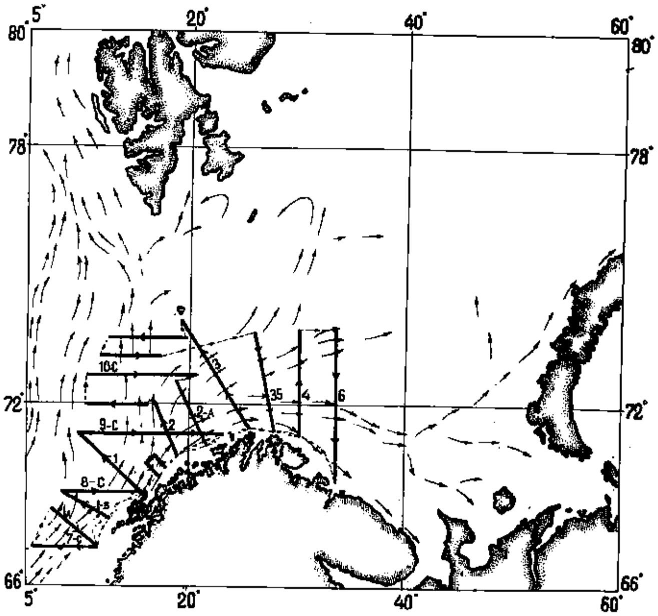


Fig. 1. Sketch map of currents and location of sections, worked during April-May and June-July 1959 and 1961. (The data on currents are taken from the works of A.I. Tantsura (1959), and A.P. Alekseev and B.V. Istoshin (1956).

For estimating the abundance of the 0-group cod, a commercial bottom trawl with a fine-mesh (10 mm) cotton net inserted into the trawl cod-end was used. Feeding of larvae (Sysoeva and Degtereva, this symposium) and "demersal" fry (Ponomarenko, this symposium) of cod of the year-classes in question was thoroughly studied.

SPAWNING OF COD

Observations on sexual maturity, stages of development of the eggs and sizes of the larvae showed a slight variation in the timing of the mass spawning of cod during these years. In 1959 and 1961, individual specimens in the area of the Rost Bank spawned in the third ten-day period of January. In January of 1960 no observations were made but in February 1960, the percentage of fish nearing the ripe and post-spawning stages was higher than in 1959 and particularly than in 1961. During these three years mass spawning started in the period from late March and April. The latest spawning period was observed in 1959. In 1960 spawning of the bulk of cod in the area of the north-west coast of Norway started and ended earlier than in 1959 and 1961. According to observations made by Wiborg (1961), mass spawning of cod in Westfjord in 1960 took place three weeks earlier than in 1959. Our analysis of material showed that mass spawning of cod in 1960 had two peak periods. This was indicated by the sizes of larvae (Table 1) and the greater percentage of eggs in early stages of development in April-May as against the same periods of 1959 and 1961. In June 1960, a group of 6-11 mm larvae was notable along with large larvae (16-26 mm). It is assumed that the second peak period of mass spawning in 1960 was caused by the approach of younger fish to the spawning grounds. In 1961 spawning was the most prolonged and ended later than in the two previous years.

DISTRIBUTION OF EGGS, LARVAE AND "DEMERSAL" FRY OF COD

The greatest numbers of eggs in April-May were found on the banks (Malang, Vesterolen and Rost banks). The distribution of eggs and larvae in the area investigated varied somewhat from year to year (Figs. 2, 3, 4). In 1961 eggs and larvae occupied a much more extensive area than in the two previous years. In 1959 the greatest drift of eggs and larvae was to the southern part of the Barents Sea. In 1960 they were carried away in great quantities to the north-west areas of the Sea. In 1961 drift was observed to the north-west areas of the Sea as well as to the southern part of the Barents Sea in the coastal branch of the current. Annual changes in the direction of

TABLE 1.

SIZES OF COD LARVAE IN mm (PERCENTAGE FREQUENCY)

Year and Month	Fishing gear	3-5	6-8	9-11	12-14	15-17	18-20	21-23	24-26	27-29	30-32	33-35	Total number	Mean size
1959 April-May	egg net	92.5	6.2	1.5									536	4.43
1960 " "	egg net	40.0	50.0	10.0									10	6.65
1961 " "	egg net	92.4	6.2	1.5									117	4.87
1959 June-July	egg net	2.2	17.8	24.5	26.6	17.8	6.7	2.2	2.2				45	12.45
1959 " "	ring trawl			2.1	22.9	31.3	28.1	5.2	4.2	1.0	4.2	1.0	96	17.70
	Combined:	0.7	5.8	9.3	23.5	27.0	21.4	4.4	3.6	0.7	2.9	0.7	141	16.02
1960 June	egg net		25.8	27.0	6.8	6.7	11.2	7.9	6.7	3.4	3.4	1.1	89	14.52
1960 "	ring trawl		3.2	3.3	-	6.4	25.8	6.5	22.5	9.7	19.4	3.2	31	23.37
	Combined:		20.0	20.9	5.0	6.6	15.0	7.5	10.8	5.0	7.5	1.7	120	16.74
1961 June-July	egg net	7.8	23.6	22.2	23.0	14.0	5.7	2.3	0.6	0.8			487	11.48
1961 " "	ring trawl			2.5	24.1	34.2	21.6	11.2	4.7	1.4	0.3		663	17.11
	Combined:	3.3	10.0	10.8	23.7	25.7	14.7	7.6	2.9	1.1	0.2		1150	14.70

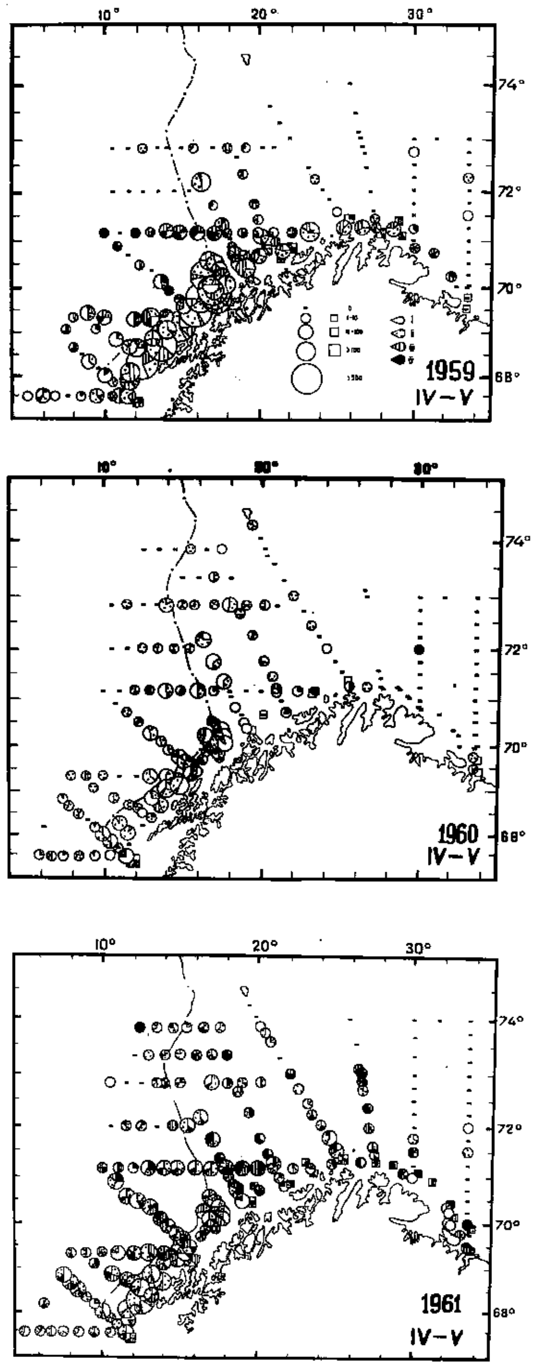


Fig. 2. Distribution of cod eggs of different stages of development in April-May 1959-1961 based on catches taken with egg net. Sizes of circles and squares indicate average amount of eggs per haul. Squares represent catches taken during second visit to the station along the paths of the route. The I-IV sectors represent the stages of development of eggs.

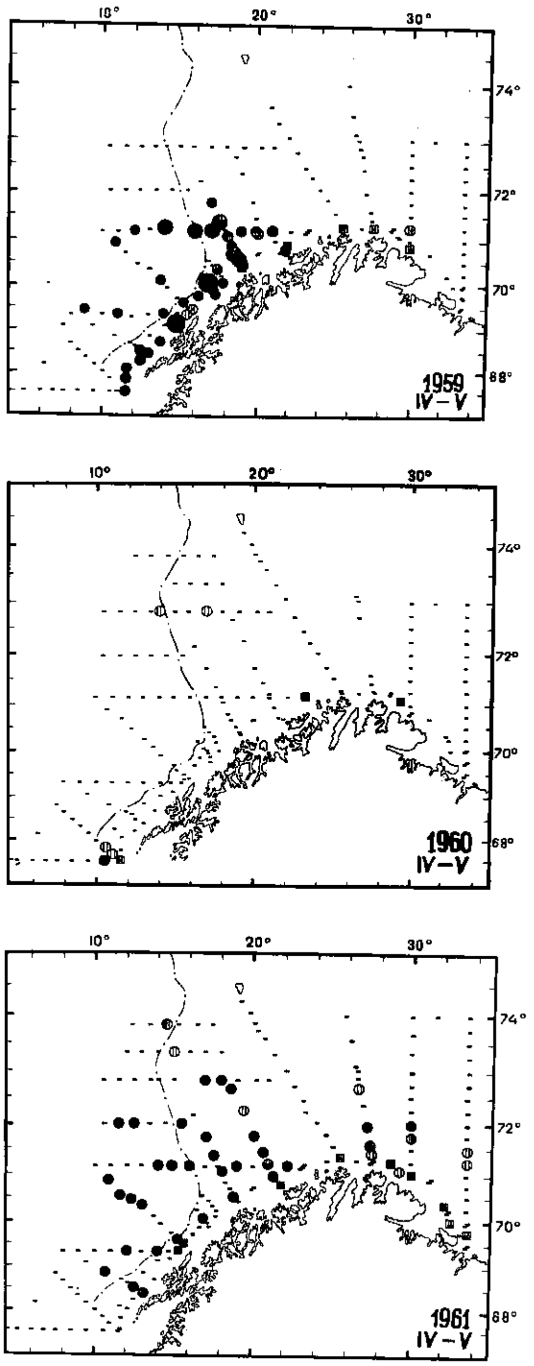
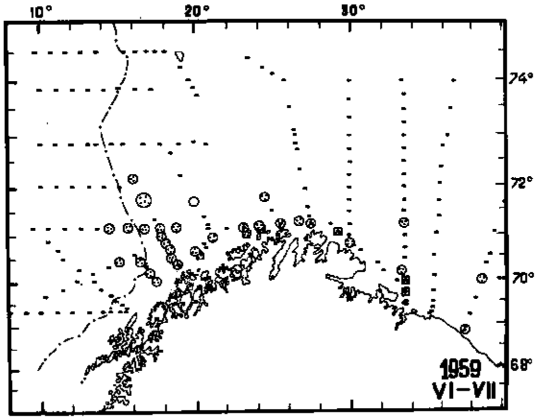
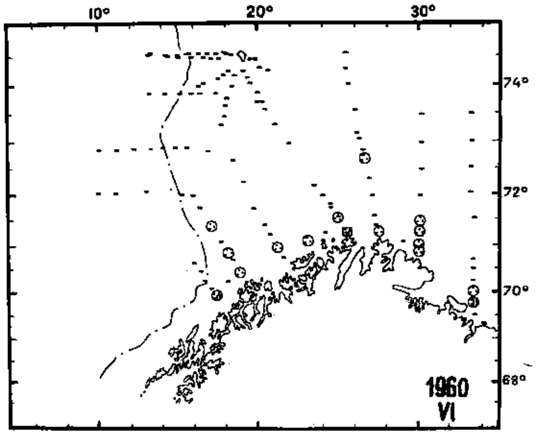


Fig. 3. Distribution of cod larvae of different sizes in April-May 1959-1961, based on catches taken with egg net.
Circles and squares indicate average amount of larvae per haul. Squares represent catches taken during second visit to the stations along the paths of the route. The key to the map is shown in Fig. 4.

the drift of eggs and larvae were confirmed by the distribution and catch per hour of trawling of "demersal" fry of the 0-group in winter season (Figs. 5, 6, 7: Table 2).





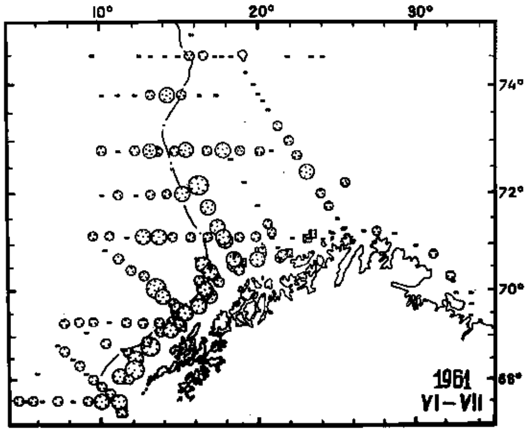


Fig. 4. Distribution of cod larvae of different sizes in June-July 1959-1961 based on catches taken with ring trawl. Circles and squares indicate the number of larvae per haul. Squares represent catches taken during second visit to the stations along the paths of the route. Sectors represent larvae sizes from 5 mm up (black) from 6 to 10 mm (shade), over 11 mm (points).

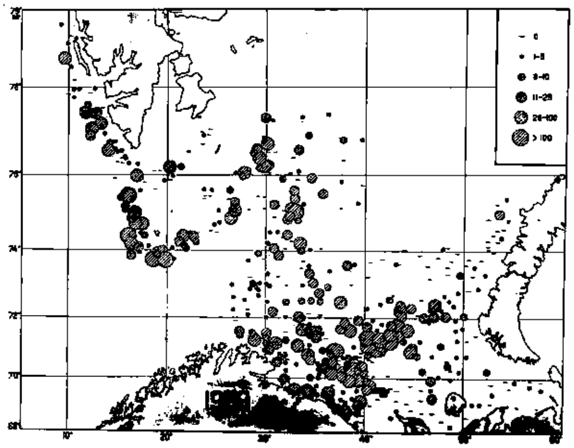


Fig.5. Distribution of the 0-group cod of the 1959 year-class. Sizes of circles indicate the number of specimens in catches per hour of trawling.

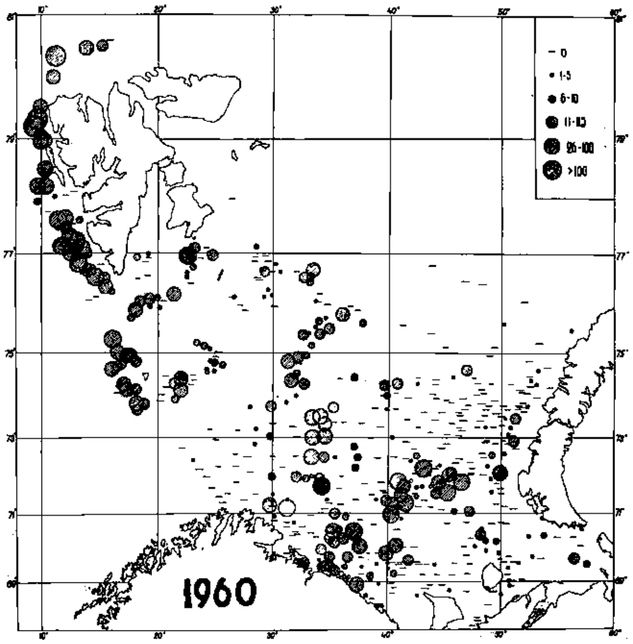


Fig. 6. Distribution of 0-group cod of 1960 year-class. Sizes of circles indicate the number of specimens taken per hour of trawling.

TABLE 2.

AVERAGE CATCHES OF 0-GROUP COD IN VARIOUS AREAS OF THE BARENTS SEA DURING THE WINTER (NUMBERS PER HOUR USING A BOTTOM TRAWL WITH COVER)

Areas	1961-1962		1960-1961		1959-1960	
	no. of hauls	no. of specimens	no. of hauls	no. of specimens	no. of hauls	no. of specimens
Southern part of the Barents Sea						
Central	111	4	108	9	168	18
West	132	2	84	10	247	8
Coastal	26	6	27	5	68	10
East	42	3	41	2	45	2
North-east	42	2	38	1	27	1
Central elevation	67	2	27	10	29	14
Total:	420	3	325	7	584	11
North-west areas of the Barents Sea						
Bear Island						
South slope	33	16	18	14	34	33
East slope	21	10	18	5	21	9
West slope	37	12	15	35	49	21
Total:	91	13	51	17	104	23
North Spitsbergen	17	141	5	39	-	-
West Spitsbergen	48	30	49	66	59	9
Zuyd Cape trench	32	7	37	14	30	30
Hope Island	23	7	19	1	27	8
Persues Elevation	44	7	14	6	17	4
Total:	255	22	175	29	137	16
West trench	-	-	-	-	11	4
Whole Sea	675	10	500	15	832	12

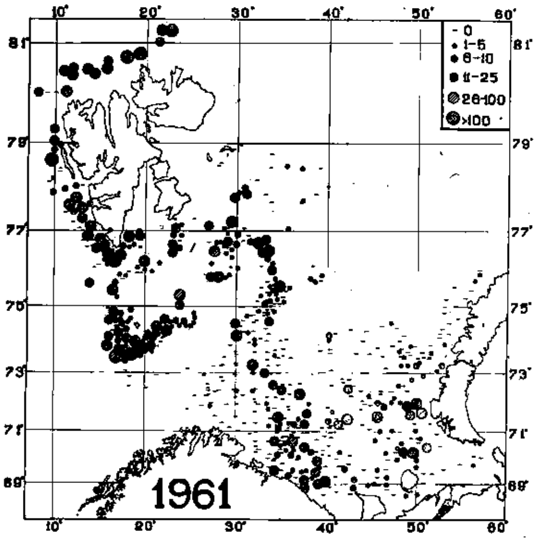


Fig.7. Distribution of 0-group cod of 1961 year-class. Sizes of circles indicate the number of specimens taken per hour of trawling.

ABUNDANCE OF EGGS, LARVAE AND "DEMERSAL" FRY OF COD

Table 3 shows average numbers of eggs and larvae per haul during the three years under review. The abundance of eggs and larvae in April-May does not correspond to that in June-July. The highest abundance of pelagic eggs and larvae in April-May was observed in 1959 (95.9 specimens per haul) and the lowest in 1960 (23 specimens). The greatest number of larvae in the period June-July was observed in 1961 (1.1 specimens per haul) and the least in 1959 (0.19 per haul). Also, the average number of eggs and larvae per haul did not correspond to the average catch of "demersal" fry per hour of trawling (Table 2). On the contrary, the number of eggs and larvae was the least in 1960 and the total number of "demersal" fry all over the Sea was the greatest (15 specimens per hour's trawling against 12 in 1959 and 10 in 1961). Such a discrepancy could be accounted for by a number of factors, particularly by different rates of survival of specimens in various years. But very likely it is to be explained by the fact that

TABLE 3.

AVERAGE NUMBERS OF COD EGGS AND LARVAE PER HAUL

Year		April-May						June - July		
		Egg net								
		Eggs			Larvae	Eggs + larvae		Larvae		
		Stages 1 and 2	Stages 3 and 4	Total		Stages 1 to 4 + larvae	Stages 3 and 4 + larvae	Egg net	Ring trawl	Egg net + Ring trawl
1961	Specimens	19.22	5.34	24.56	0.24	24.80	5.58	0.63	3.97	1.11
	%	78.30	21.70	100						
	No. of hauls	426	426	426	426	426	426	440	74	514
1960	Specimens	8.64	0.64	9.28	0.02	9.30	0 66	0.31	0.11	0.26
	%	93.10	6.90	100						
	No. of hauls	393	393	393	393	393	393	275	105	380
1959	Specimens	80.42	14.09	94.51	1.41	95.92	15.50	0.08	0.50	0.19
	%	85.09	14.91	100						
	No. of hauls	374	374	374	374	374	374	334	118	452

the area of distribution of eggs and larvae was not fully covered by our investigations. Wiborg (1961) found that the number of eggs and larvae in the coastal waters of Norway, in Westfjord, was higher in 1960 than in 1959 whereas on the outside of the Lofoten Islands, near Eggum, it was lower. According to our data, the number of eggs and larvae in the open part of the Sea, near the north-west coast of Norway, was also much higher in 1959 than in 1960. The difference in the numbers of eggs and larvae in coastal waters and in open areas of the Sea has been noticed previously in my own work (unpublished) on the 1948 and 1949 year-classes. According to Wiborg (1949), the number of larvae in the Westfjord was greater in 1949 than in 1948, whereas according to our data, the number of larvae on the outside of the Lofoten Islands in the high sea was greater in 1948 than in 1949.

The average catch of the 0-group varied during these years in different areas. In the southern part of the Sea and in the area of Bear Island, a decrease in the average catch of fry per hour of trawling was observed from 1959 to 1961, whereas the average catch of fry in the areas to the north of Bear Island was the highest in 1960 (29 specimens) and the lowest in 1959 (16 specimens).

According to the estimates of the young of various ages, the 1959 year-class can be evaluated as an average one. On the basis of total catches of the 0-group fry over the whole area, it can be assumed that the 1960 and 1961 year-classes also approximate to the average, with only this difference, that the 1960 year-class is somewhat more, and the 1961 year-class somewhat less, abundant than that in 1959.

The survival rate also varies by years. The ratio of the number of larvae caught during the second survey (in June-July) to the number of eggs and larvae caught during the first survey (April-May) may be expressed as a percentage: from this, the survival rate of eggs and larvae in the interval between the two surveys can be estimated. This ratio is shown in Table 4. On the left side of the table the eggs of all stages of development are presented: on the right side of the table, only the eggs of the third and fourth stages of development, when their identification as cod was undoubted. The stages of development of cod eggs are given according to Rass (1949). For 1959 the percentage is quite low. In this year, a high mortality rate during the early stages of development of eggs appeared to be due to weather conditions: in the spring of 1959 there were more stormy days than in 1960 and 1961.

TABLE 4.

PERCENTAGE RATIO OF COD LARVAE DURING JUNE-JULY TO EGGS AND LARVAE IN APRIL-MAY (BASED ON EGG NET SAMPLES IN BOTH PERIODS AND RING TRAWL SAMPLES IN JUNE AND JULY)

Year	To the eggs of all stages of development and to larvae			To the eggs of the 3rd and 4th stages of development and larvae		
	egg net	ring trawl	egg net + ring trawl	egg net	ring trawl	egg net + ring trawl
1961	2.54	16.00	4.47	11.29	71.15	19.89
1960	3.33	1.17	2.79	46.97	16.66	39.39
1959	0.08	0.52	0.19	0.52	3.23	1.22

In 1960 and 1961 the percentage of the number of larvae caught in June was higher than the percentage of the number of eggs and larvae caught in April-May, which indicates a higher survival rate. The high indices (3.33 and 46.97%) obtained with the egg net in 1960 (Table 4) can be explained by the presence of the second peak in mass spawning which resulted in the appearance of many eggs in early stages of development in April and May, and of small larvae which are easy to catch by egg net in June. The indices obtained for ring trawl catches reflect the changes in the number of larvae which took place during the first peak period of spawning. These indices evidently lie between those of 1959 and 1961. A great reduction in the abundance of the 1960 year-class in the southern part of the Sea took place, apparently, at an older age. This assumption is confirmed by the data published by Ponomarenko (this symposium) which indicate that a great number of the fry of the 1960 year-class had been eaten by young cod of the II and III age groups in the winter season of 1960-1961. Greater numbers of fry of this year-class than of the 1959 and 1961 year-classes were eaten.

The survival rate of eggs, larvae and pelagic fry of the 1961 year-class was the highest of the three year groups studied. However, the number of "demersal" fry in almost all areas, except North Spitsbergen, was found to be the lowest. It can, therefore, be assumed, that a high mortality rate of this year-class took place in the pelagic stage before "settling" of fry or during their transition to the near-bottom way of life. "Demersal" fry in the southern part of the Sea during winter season were eaten by older young of cod in inconsiderable amounts which, in the opinion of Ponomarenko (this symposium), was due to their low abundance.

The effect, on the total abundance of the 1961 year-class, of extensive transportation of fry to such a distant area as North Spitsbergen will be studied further. The estimates of the young in the north-western part of the sea in autumn of 1962 showed a great reduction in catches of the young of the 1961 year-class per hour of trawling (less than one specimen on the average).

THE CONDITION OF DRIFT OF COD EGGS AND LARVAE

The years investigated were characterized by different temperature and salinity conditions, intensity of various branches of the warm current, periods of development and plankton biomass.

The year 1961 was characterized by an average temperature regime: 1959 was warmer and 1960 was the warmest of the three (abnormally warm for the Norwegian Sea). The average temperatures in the sections investigated in 1959-1961, and changes in temperature in these sections from year to year, (Kislyakov and Borovaja, 1963) are shown in Tables 5 and 6. As seen from the Tables, temperature conditions during a year and in different years changed in different ways in various parts of the area, on the routes of drift of eggs and larvae. The years 1959, and particularly, 1960 were characterized by an intensive inflow of Atlantic water into the Norwegian Sea. Beginning in the spring of 1961 a reduction in advection of heat by the current was observed in the Norwegian Sea (Alekseev *et al.*, 1963).

The intensity of the branches of warm currents varied: for example, the eastern branch of the Norwegian Current and the West Spitsbergen Current were the most intensive in 1960. Because of

TABLE 5.

AVERAGE TEMPERATURE IN THE 0-200 m LAYER AND IN STANDARD SECTIONS DURING APRIL-MAY OF 1959, 1960 AND 1961 (ACCORDING TO KISLYAKOV, 1963)

Sections	1959	1960	1961
7-c	6.38	7.12	6.79
8-c	6.20	6.27	6.44
9-c	6.34	6.26	5.95
72°00'	5.44	5.92	5.31
10-c	5.62	5.63	4.99
73°50'	-	5.30	4.93
1A	6.61	6.31	6.55
1B	6.87	6.45	6.05
1	6.15	6.96	6.01
2	6.10	6.34	5.81
2A	5.63	6.10	5.54
3	4.82	5.03	4.60
35	4.43	4.58	4.27
4	4.16	4.32	3.85
6	3.59	3.84	2.96

TABLE 6.

CHANGE IN AVERAGE TEMPERATURE BETWEEN YEARS IN SECTIONS OF THE 0-200 m LAYER DURING APRIL-MAY (ACCORDING TO KISLYAKOV, 1963)

Sections	Change in temperature from 1959 to 1960	 from 1960 to 1961	 from 1959 to 1961
7-C	+0.74	-0.33	+0.41
1A	-0.30	+0.24	-0.06
1B	-0.42	-0.40	-0.82
8C	+0.07	-0.17	+0.24
1	+0.75	-0.70	-0.14
9C	-0.08	-0.31	-0.39
72°N	+0.48	-0.61	-0.13
10C	+0.01	-0.64	-0.63
73°50'N	-	-0.37	-
2	+0.24	-0.53	-0.29
2A	+0.47	-0.56	-0.09
3	+0.21	-0.43	-0.22
35	+0.15	-0.31	-0.16
4	+0.16	-0.47	-0.31
6	+0.25	-0.88	-0.63

this, the temperature in the West Spitsbergen Current was higher in 1960 than in 1959 and 1961. In 1959 the intensities of the branch of the North Cape Current and of the branch of the Murmansk Coastal Current were higher than in 1960 and 1961. Throughout the year, positive temperature anomalies were observed in the Murmansk Coastal branch. Kondratsova (1961) is of the opinion that the year 1959 in the Coastal branch was one of the warmest in the period from 1953 to 1960.

The intensity of the main branch of the Murmansk Current in 1959 was low. The north branch of the North Cape Current was characterized by a lower intensity as compared with the Murmansk branch. In 1960 the intensity of the main branch of the Murmansk Current was high, and the intensity of the Murmansk Coastal Current was low (Kondratsova, 1962). In 1961 the north branch of the North Cape Current was characterized by a particularly high intensity of all the branches in the Barents Sea. In the second half of the year the temperature in this branch was abnormally high (Kislyakov and Borovaja, 1963).

The salinity of water masses in the area of the north-western and north coasts of Norway was highest in 1960, somewhat lower in 1959 and lowest in 1961. In 1961 the salinity in the east branch of the Norwegian Current was several hundredths of parts per mille lower than in 1960. The 35.2% isohaline extended 200 miles farther to the south as compared with 1960 (Kislyakov, 1963). The most distinctive feature of the year 1961 was the extension of coastal diluted waters from Fugloy and Sarö Islands far to the north and their mixing with the Bear Isle Current which was also greatly diluted by fresh water in 1961. As a result of this, waters with salinity over 35 °/oo could not penetrate into the surface layer of the Barents Sea. In the spring of 1959 and 1960 such a wide spreading of coastal waters was not observed. In June and July of 1961 there was further dilution of coastal waters flowing outwards from the area of the north-west coast of Norway towards the north and from the Bear-Spitsbergen region towards south-west. These distributions of waters influenced the distribution of cod larvae and plankton (Figs. 8, 9).

As a result, in that year, no close relation was observed between the distribution of larvae and the abundance of "settled" cod fry on the one hand, and the intensity of branches of the warm currents on the other. Such a relationship, between the distribution of larvae and the intensity of current branches, was quite obvious in 1959 and 1960 and was reported earlier by Kislyakov (1961) for the fry of the 1946-58 year-classes in the Arcto-Norwegian cod. The transport of a great number of fry into the Spitsbergen area in 1961, when the intensity of the West-Spitsbergen Current

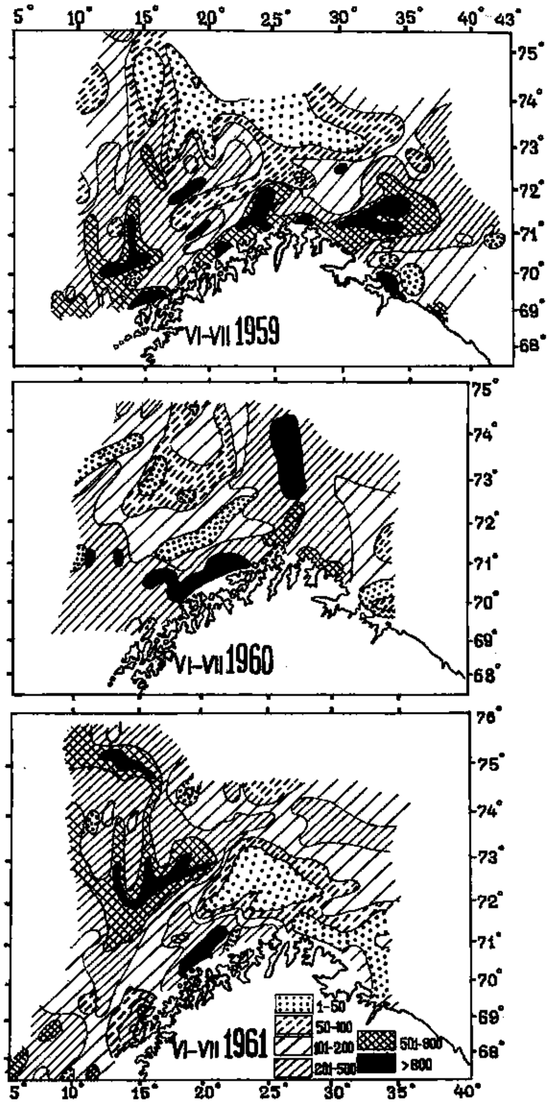


Fig. 8. Plankton biomass (in mg/m^3) in June-July of 1959-61 (according to A.A. Degtjareva).
1 — 1-50
2 — 51-100
3 — 101-200
4 — 201-500
5 — 501-800
6 — > 800

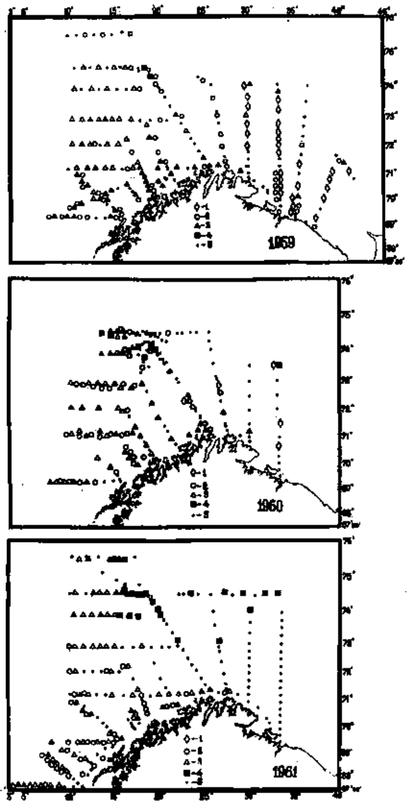


Fig. 9. Distribution of warm water (white) and cold water (black) organisms in June-July of 1959-61 (according to A.A. Degtjareva).
1 — *Physophora*
2 — *Limacina retroversa*
3 — *Collozoum*
4 — *Limacina helicina, Aeginopsis*
5 — not present in the catch

was reduced (as compared with 1960) can be explained, Kislyakov believes, by the presence in 1961 of a peculiar watershed in the area between the north coast of Norway and Bear Island. The appearance of this watershed was caused by a high water level in this part of the Sea, which obstructed penetration of the Antarctic waters into the Barents Sea and resulted in driving away a great number of eggs and larvae with freshened waters from the coastal zone of Norway into the high seas. The existence of such hydrological conditions in this area is considered by Adrov (1957) as quite normal. In May and June, northern and eastern winds predominate there: these impede the North Cape Current and carry away greatly freshened waters into the open Sea. Just such an intensive outflow of freshened waters from coastal areas was observed in 1961.

From the data obtained by A.A. Degtereva, who studied the plankton in these years, the biological spring (beginning of the *Calanus* spawning) off the north-west coast of Norway began earlier in 1960 (late March) than in 1959 and 1961 (the first ten-day period of April). The development of phytoplankton and the spawning of *Calanus* in the years 1959 and 1960 were observed earlier in the coastal zone, and somewhat later in deep water areas located outside the continental slope. In 1961, unlike the two previous years, spawning of *Calanus* off the coasts and in the high seas took place at the same time. As a result, the development of *Calanus* in the eastern branch of the Norwegian Current began earlier in 1961 than in 1959 and 1960. In 1961 the period of spawning of *Calanus* was more prolonged as was shown by the simultaneous presence in plankton samples of great quantities of eggs, nauplii and various copepodite stages of plankton. In 1959, and particularly in 1960, the period of *Calanus* spawning was considerably shorter. All this affected the abundance of plankton as well as its biomass. As a result the highest abundance for the spring season (late April-May) was observed in 1961, and the highest biomass in 1960 (Table 7). The high abundance of *Calanus* in 1961 has to be accounted for by the presence of great amounts of nauplii and early stages, whose proportion by weight was inconsiderable.

TABLE 7.

ABUNDANCE OF *Calanus* AND BIOMASS OF PLANKTON, 1959-1961.

Calanus IS SHOWN AS NUMBERS UNDER 1 m^2 IN THOUSANDS ALONG 4 SECTIONS (67°31'N, 71°10'N, NORTH CAPE TO BEAR ISLAND AND KOLA SECTION TO 33°30'E) BIOMASS IS EXPRESSED IN mg/m^3 IN THE WHOLE AREA OF THE INVESTIGATIONS

Year	Abundance of *Calanus*						Plankton biomass	
	April-May			June-July				
investigated	nauplii	copepods	total	nauplii	copepods	total	April-May	June-July
1961	62.6	32.2	94.8	1.8	14.9	16.7	182.1	255.3
1960	21.9	40.7	62.6	6.2	28.4	34.6	228.7	455.3
1959	24.3	34.3	58.6	7.2	46.5	53.7	112.7	443.9

In 1960, because of earlier spawning of *Calanus* in the coastal zone at the time when observations were made, they had reached later stages of development (III, IV and even V). Small crustaceans in these stages were comparatively scarce but, because of their size, they resulted in a very high biomass. The only exception was the North Cape - Bear Island section, where in 1960, due to delayed spawning of *Calanus*, the abundance and biomass of plankton were lower than in the years 1959 and 1961.

In the summer season (June-July) the bulk of plankton was represented by *Calanus finmarchicus* of copepodite stages IV and V, the so-called "Red *Calanus*". The most extensive spreading of Red *Calanus* towards the east in the coastal zone was observed in 1959 (Fig. 8), less extensive in 1960: in 1961 the border of the area of their distribution was found in the region of the North Cape-Bear Island section. In 1961 in the south-west part of the Barents Sea between the North Cape and the Kola sections, *Calanus* were almost absent, and the main components of zooplankton were represented by *Oithona similis* and *Oncaea borealis*. This distribution of *Calanus* resulted in an abrupt reduction of their abundance and biomass in the south-west part of the Barents Sea (Fig. 8), which affected the total biomass (Fig. 7). In the Eastern branch of the Norwegian Current, however, plankton biomass was rather high.

These data show the existence in the period reviewed of a close relationship between the distribution and direction of the drift of eggs, larvae and pelagic fry of cod, the plankton organisms and the movement of water masses. Annual changes are also clearly revealed by the data on distribution of warm water organisms (Fig. 9). The main drift of these organisms in June-July of 1961 took place in the eastern branch of the Norwegian Current, whereas their transport to the southern part of the Barents Sea was not observed.

Most interesting data on the life of larvae in various branches of current are reported by ysoeva and Degtereva in a paper presented to this symposium (see p. 412). A study of feeding f larvae and pelagic fry of cod by these authors showed that the distribution of the larvae was elated to the greatest concentrations of their main food - *Calanus finmarchicus*. Thus, better onditions for the feeding of larvae and pelagic fry existed in those branches of the currents here their main drift was observed. In the branches of the currents where the abundance of *'alanus* was not high, as in 1961 in the southern part of the Barents Sea, large larvae had to feed n other numerous, but smaller organisms (in particular, *Oithona similis* and *Evadne nordmani*), which nfluenced their weight.

SUMMARY

. As a result of the three years' investigations some peculiarities were found in formation of the Arcto-Norwegian tribe of cod of the 1959, 1960 and 1961 year-classes during the first year of life. These years differed in relation to the temperature and salinity of the water, the intensity of different branches of the currents, the periods of development and plankton biomass.

Variations were observed in the timing of the mass spawning and the total duration of cod spawning, in the distribution and abundance of eggs, larvae and "demersal" fry of cod and in the conditions for the feeding of larvae. For every year-class, there was a characteristic period when greatest decrease in abundance occurred.

. A close relationship was observed between the biological processes and the annual changes in the dynamics of water masses.

The main drift of eggs and larvae of cod, the highest biomass of plankton and the most favourable conditions for the feeding of cod larvae were found mainly in those branches of the currents which were more intensive in the given year.

. The distribution of cod larvae in the branches of the currents coincided with that of warm water plankton organisms. An absolute conformity was observed between the periods of spring development of plankton and spawning of cod.

. The investigations showed the complexity of the problem of revealing the factors determining the strength of individual year-classes of the Arcto-Norwegian tribe of cod.

REFERENCES

ADROV, N.N. 1957. "Hydrological investigations in the Kopytov area". *Trudy PINRO*, 10: 198-211, Fig. 12, Table 1.

ALEKSEEV, A.P. and B.V. ISTOSHIN. 1956. "Scheme of constant currents of the Norwegian and Greenland Seas". *Trudy PINRO*, 9: 62-68, Fig. 4.

ALEKSEEV, A.P., B.V. ISTOSHIN, and L.P. SHMARINA. 1963. Soviet Hydrological Investigations in the Norwegian and Greenland Seas in 1961. *Ann. biol. Copenhague*, 18 (1961): 24-26, Fig. 30-33.

CORLETT, J. 1958. Plankton in the western Barents Sea and the year-class strength of the Arcto-Norwegian Cod. *J. Cons.* 23 (3): 354-356.

HILL, H.W. and A.J. LEE, 1958. The effect of wind on water transport in the region of the Bear Island fishery. *Proc. roy. Soc. Edinb.* (B), 148: 104-116.

HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in light of biological research. *Rapp. Cons. Explor. Mer*, 20: 1-228.

KISLYAKOV, A.G. 1959. "Temperature conditions and yields of year-classes of the cod, spawning off the north-west coast of Norway". *Scientific and Technical Bulletin PINRO*, No. 1/9, p. 22-26, Fig. 3, Table 5.

KISLYAKOV, A.G., 1961. "The relation of hydrological conditions to fluctuations in the abundance of cod year-classes". Transactions of the meeting of the Ichthyological Commission of Academy of Sciences of the USSR, 13: 260-264, Fig. 3, Table 2.

1962. Hydrographic conditions in the Norwegian Current and the North Cape Current in the spring of 1960. *Annu. biol. Copenhague*, 29 (1960): p. 25, Fig. 2, Table 1.

1963. Hydrological Conditions in the north-eastern part of Norwegian Sea and the adjacent areas of the Barents Sea in April-June 1961. *Ann. biol. Copenhague*, 28 (1961): 26-29, Fig. 6, Table 2.

KISLYAKOV, A.G. and L.X. BOROVAJA, 1963. Hydrological Conditions in the Barents Sea in 1961. *Ann. biol. Copenhague*, 28 (1961): 29-33, Fig. 37-42, Table 3.

KONDRATSOVA, O.F. 1961. "The characteristics of temperature conditions of the Murmansk coastal waters in 1959". Transactions of the Murmansk marine biological institute (MMBI), 3/7, p. 5-14, Fig. 7, Table 4.

1962. "Heat conditions in the south part of the Barents Sea in 1960". Transactions of MMBI, 4/8, p. 3-10, Fig. 9, Table 1.

PONOMARENKO, I.Ja. 1964. "Comparative characteristics of some biological indices of the bottom stages of 0-group cod belonging to the 1956, 1958-1961 year-classes". *This symposium Contribution No. B-7.*

RASS, T.S. 1949. "Composition of ichthyofauna of the Barents Sea and systematical indications of fish eggs and larvae of this reservoir". Materials on fish reproduction and development in the North Seas. *Trudy VNIRO*, 27: 9-65, Fig. 32, Table 5, bibliography.

ROLLEFSEN, G. 1930. Observations on cod eggs. *Rapp. Cons. Explor. Mer*, 65: 31-34, Fig. 2.

SYSOEVA, T.K., and A.A. DEGTEREVA, 1964. "The Relation between the Feeding of Cod Larvae and Pelagic Fry and the Distribution and Abundance of their Principal Food Organisms". *This symposium Contribution No. B-16.*

TANTSURA, A.I. 1959. "Currents of the Barents Sea". *Trudy PINRO*, 11: 35-53, Fig. 7, Table 1, bibliography.

WIBORG, K.F. 1949. The occurrence of fish eggs and larvae along the coast of Northern Norway during April-June 1948 and 1949. *Ann. biol. Copenhague*, 6: 12-16, Fig. 15.

1957. Factors influencing the size of the year-classes in the Arcto-Norwegian tribe of cod. *Fiskeridir. Skr. Havundersøk.*, 11, No. 8.

1961. Forekomst av egg og yngel av fisk i vest of nordnorske kyst og bankfarvann våren 1960. *Fiskets Gang* No. 9, p. 190-195, Fig. 8, Table 4.

B-16

THE RELATION BETWEEN THE FEEDING OF COD LARVAE AND PELAGIC FRY AND THE DISTRIBUTION AND ABUNDANCE OF THEIR PRINCIPAL FOOD ORGANISMS

By

T.K. Sysoeva and A.A. Degtereva[1]

ABSTRACT

This paper summarizes 3 years' investigations (1959-1961) on the feeding of larvae and pelagic ry from the Arcto-Norwegian cod stock. .

The main food item of larvae and pelagic fry in the first three months of their life is *Calanus* *inmarchicus*. The larvae and fry feed on *C. finmarchicus* in different periods of life and at dif- erent stages of development, such as nauplii, younger and older copepodites. The close relation f the life of cod larvae and pelagic fry with that of *Calanus finmarchicus* is supported by the fact hat, in June of all the years studied, coincident quantitative occurrences of larvae and fry of cod d *C. finmarchicus* were observed in different branches of the currents.

Oithona similis, Pseudocalanus elongatus, Acartia cluasi, Evadne nordmanni and other species ch smaller than *Calanus finmarchicus* serve as secondary food for larvae and fry of cod. They ecome especially important when there is a lack of *Calanus finmarchicus* in the plankton. The mini- m abundance of *Calanus finmarchicus* in the plankton when the intensity of feeding of cod larvae d fry decreases is from 5,000 to 18,000 specimens under 1 m^2.

Investigations into the problem of the formation of rich and poor year-classes were carried t regularly from 1959 to 1961. The present paper deals with the analysis of the material relating the feeding conditions of larvae and pelagic fry of cod. The authors used the data on spawning, undance and distribution of eggs, larvae and fry which are published by Baranenkova (this sympo- ium). Some data on the food composition of larvae and pelagic fry of cod as well as on their se- ective ability were obtained previously by Wiborg (1948, 1960).

Our material permitted us to get a generalized picture of the regular changes in the feeding young cod during the three months of their life, from the moment when they begin to feed freely til they reach a length of 42 mm. This part of cod ontogenesis can be divided into four periods the basis of characteristics of the feeding and morphology of larvae and pelagic fry (Fig. 1).

FIRST PERIOD. The larvae, just beginning active feeding, feed on minute slow moving plankton, inly on nauplii of *Calanus finmarchicus*. Their length is 3.2-7.0 mm. A characteristic morpho- gical feature of larvae in this period is an undifferentiated fin fold.

SECOND PERIOD. The larvae gradually begin to take more active and, with increasing length, rger organisms, such as Copepoda in different copepodite stages. Nauplii and copepodites of *lanus finmarchicus* and *Oithona similis* prevail. The larvae are 7.0-19.0 mm in length. During is period paired and unpaired fins, stomach, pyloric caeca and barbel are formed. Thus, by the ginning of the third period the larvae are already transformed into the fry.

THIRD PERIOD. The fry consume comparatively large organisms, mainly *Calanus finmarchicus* at e IV - V copepodite stages ("red *Calanus*"). The length of fry ranges from 19.0 to 35 mm. They e gradually acquiring their characteristic "chess" pigmentation.

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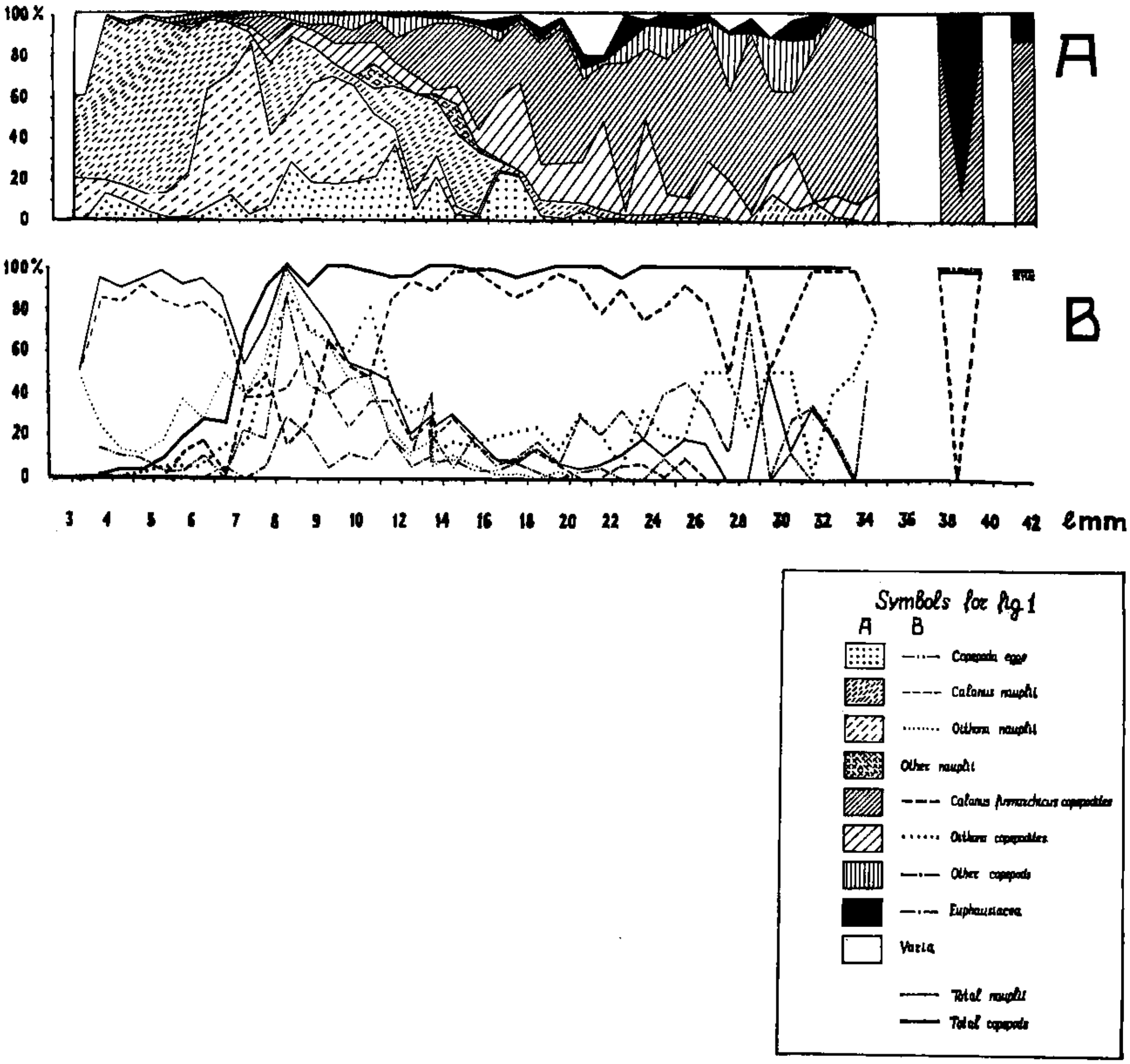

Fig. 1. Changes in the composition of the food of larvae and pelagic fry of cod with increasing length.
A. Importance of the main food organisms (numbers in %).
B. Occurrence of the main food objects (numbers of digestive tracts containing food in %).

FOURTH PERIOD. This period is characterized by a transition of fry to the consumption of young Euphausiacea. According to Wiborg (1960) and Ponomarenko (this symposium), Euphausiacea become the main food of cod fry and, as was observed by Ponomarenko, influence the indices of fullness, fatness and nutritional condition of fingerlings.

Each period consists of several stages characterized by changes in feeding and morphology. These stages cannot be discussed in this short paper. The size limits of these stages are designated in Fig. 2(B).

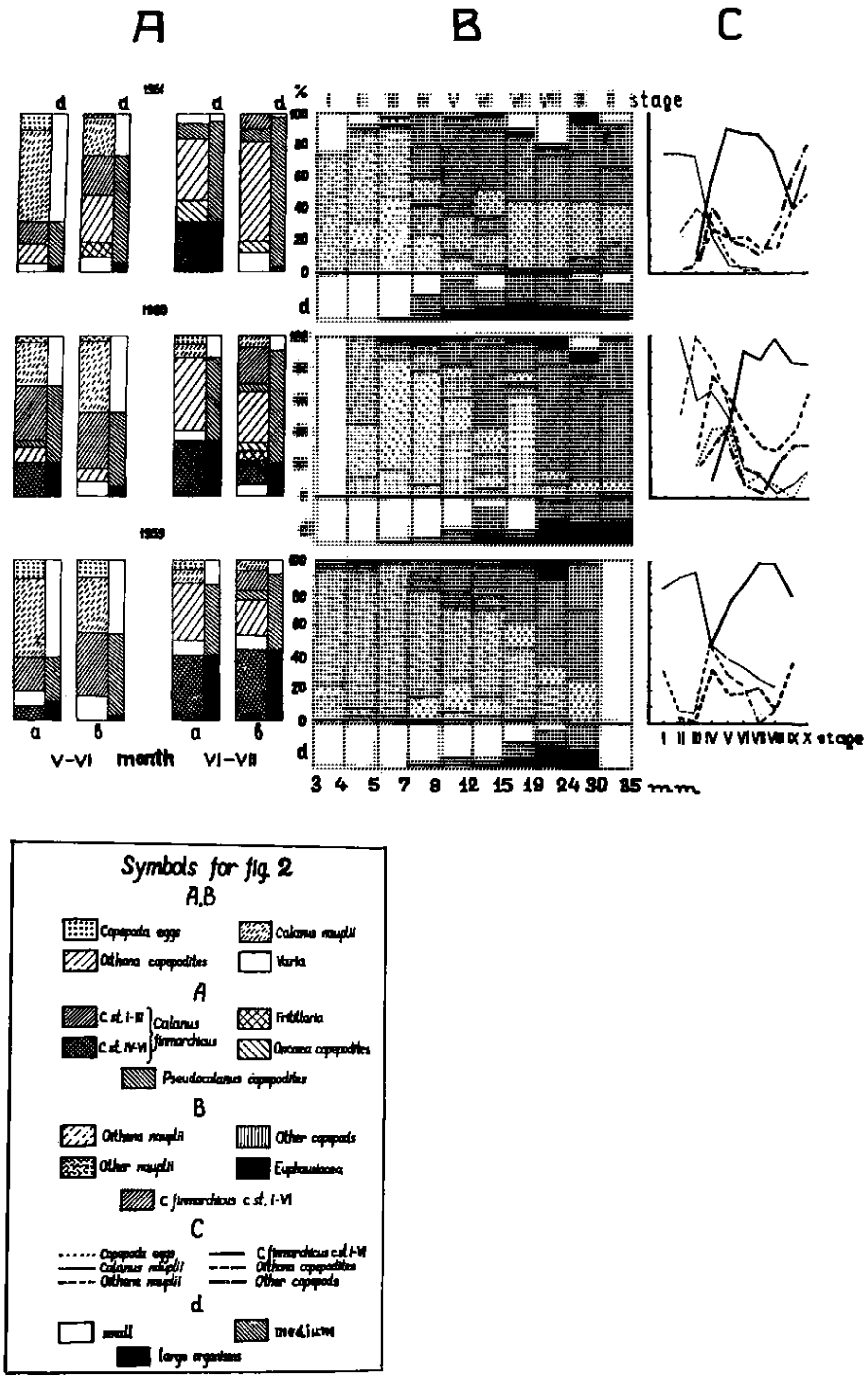

Fig. 2. Plankton composition in the sea (A) and composition of food of larvae and pelagic fry of cod (B,C) in different years.

A. Number of organisms as a percentage of the total. (a — Norwegian Sea; b — Barents Sea.)

B. Number of organisms as a percentage of the total.

C. Percentage occurrence.

D. Importance of small, medium and large organisms in plankton and in the food of larvae and pelagic fry (number of organisms in %).

It is clear from the above summary, that the life of cod larvae and fry is closely related to the life cycle of *C. finmarchicus*, the most numerous zooplankter in the Barents and Norwegian Seas. In the second half of April, when active feeding of cod larvae starts, nauplii of *C. finmarchicus*, the basic food of larvae at the first stages of development, occur in the plankton in great quantities. In late May, the larvae become more active (second period) and can take more active food organisms, namely *Calanus finmarchicus* of the I-III copepodite stages, which appear by this time in the plankton. In June, most of the larvae reach a length of about 20 mm and feed on "red *Calanus*" which develops at this time over a large sea area.

In June, a coincidence of the quantitative distribution of cod larvae with that of *C. finmarchicus* was observed in separate branches of the currents in all the 3 years investigated. In 1959, the main mass of larvae was carried into the southern part of the Barents Sea. The abundance of *C. finmarchicus* in 1959 was also higher in the southern part of the Barents Sea where great biomasses of this organism were recorded over large areas (Fig. 2A and Fig. 8 in the paper by Baranenkova, this symposium). In 1961, most of the larvae drifted into the area of Bear Island and Spitsbergen where greater abundance and biomass of *C. finmarchicus* was observed (Fig. 2A and Fig. 8 in the paper by Baranenkova, this symposium). The year 1960 was intermediate in respect to the abundance of larvae and distribution of plankton biomass in June in the area investigated. Such a coincidence of the quantitative distribution of *C. finmarchicus* with that of the larvae and fry of cod is evidently the consequence of the general factors influencing the distribution both of the food organism and of its consumer. A similar phenomenon was recorded by Ponomarenko (this symposium) for demersal fry of 0-group cod in the southern part of the Barents Sea, feeding on Euphausiacea: the fewer fry in the southern part of the Barents Sea, the more scarce was their food. The larvae and pelagic fry of the 1961 year-class, being the least numerous in the southern part of the Barents Sea, could not feed on *C. finmarchicus* (their main food item) due to its scarcity. In 1959, however, the larvae and fry were transported mainly into the southern part of the Barents Sea and fed there freely on *C. finmarchicus*.

Oithona similis took second place in the food of larvae and pelagic fry (Fig. 1). It was more often encountered in the food of cod larvae in June, in the period of its mass appearance in the plankton, and provided the food for recently hatched cod larvae. In 1960, the spawning of cod had two peaks. The food of larvae appearing in April consisted mainly of nauplii of *C. finmarchicus*. The more numerous larvae of the second peak, which reached a length of 6-12 mm in early June, fed mainly on nauplii of *Oithona* in the coastal zone in 69°20'N (Fig. 2B and C). Due to the early spawning in that year, *Calanus finmarchicus* reached copepodite stages IV and V in the coastal zone in early June, too large to be eaten by such small larvae. In the area beyond the continental slope, the larvae lived on nauplii of *Oithona* and eggs and nauplii of *Calanus finmarchicus* which were available in those waters.

Copepodites of *O. similis* are important in the food of fry and large larvae when *C. finmarchicus* occurs in small numbers. For instance, in 1961, when *C. finmarchicus* was very scarce in the southern part of the Barents Sea (Table I, Fig. 2A), *Oithona similis* was most important in the food of larvae and fry of 15-35 mm (Fig. 2B, C, Table 2). Together with *O. similis*, the importance of other planktonic organisms (such as *Evadne nordmanni*, *Pseudocalanus elongatus*, *Acartia clausi*) also increased, although, because of the predominance of *C. finmarchicus* in the plankton, the importance of these species in the diet of larvae and pelagic fry is quite insignificant.

TABLE 1. THE ABUNDANCE OF *Calanus finmarchicus* (COPEPODITE STAGES) UNDER 1 m^2 IN THE UPPER 50 m, JUNE-JULY, IN THOUSANDS OF SPECIMENS.

Year	Section 69°20'N	Section 71°10'N	Section North Cape Bear Island	Section along the Kola Meridian
1959	31.6	25.8	53.1	75.3
1960	9.6	15.6	83.8	4.4
1961	20.3*	18.8	18.0	2.6

* This figure represents the abundance of *Calanus* on the section 67°30'N.

The food objects were grouped by sizes: (1) small organisms (eggs and nauplii of Copepoda), (2) medium organisms (small copepoda including *O. similis* and *C. finmarchicus* at the I-III copepodite stages) and (3) large organisms (*C. finmarchicus* at the IV-V copepodite stages, Euphausiacea, Tunicata, fish larvae). The importance of each group both in the diet of larvae and in the plankton is shown in Fig. 2d.

As is evident from Fig. 2B, C, d, the larvae of cod up to the VI-VII stages, belonging to the 1959 and 1960 year-classes, lived for a relatively long period of time on small organisms: nauplii of *C. finmarchicus* in 1959 and nauplii of *Oithona* in 1960. In 1961, the larvae as early as the IV stage ate medium and even large organisms. In 1959 and 1960, the pelagic fry fed on large organisms (*C. finmarchicus* in the IV-V copepodite stages), whereas in 1961, medium-sized organisms prevailed in their food (*O. similis*, other Copepoda, *Evadne nordmanni*).

It was found that the qualitative composition of food influences the increment in weight. To illustrate this, we present diagrams showing the changes in the body weight of larvae and fry in different years (Fig. 3). Larvae and fry up to 29 mm of the 1959 and 1960 year-classes, living for a long time on small organisms when in the larval phase, had a lower body weight than larvae and fry of the same length in the 1961 year-class which started feeding on medium and large organisms earlier. Fry of over 29 mm in the 1959 and 1960 year-classes, feeding freely on *C. finmarchicus* in the IV-V copepodite stages, had a higher body weight than the fry of the 1961 year-class of the same length feeding on the great quantities of *O. similis* and *E. nordmanni*.

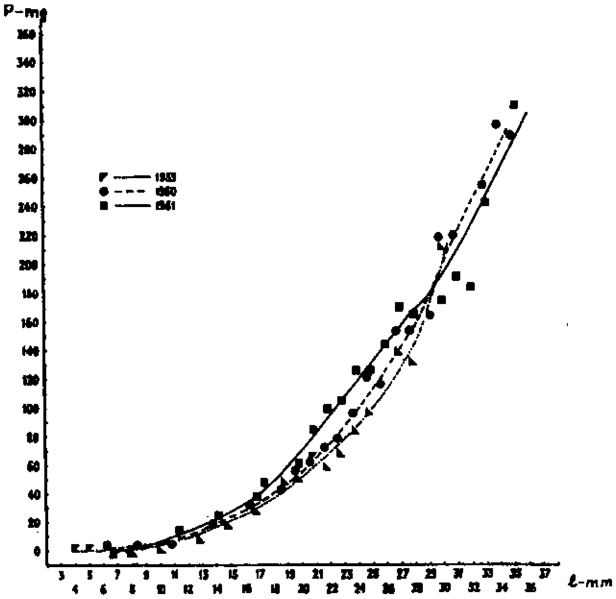

Fig. 3. Change of the weight of larvae and pelagic fry with linear growth.

The material on the feeding of pelagic fry in the southern part of the Barents Sea enabled us to judge at what concentration of *C. finmarchicus* fry start living on the secondary food organisms. It can be seen from the material for 1961 (Table 1) that the abundance of *C. finmarchicus* of 2,600 specimens under 1 m^2 in the 50 m surface layer, observed on the section along the Kola Meridian, was not sufficient for fry feeding. This is evidenced by the data on the food consumption of cod fry in the area eastwards of the section North Cape-Bear Island (Table 2). The abundance of *C. finmarchicus* of 4,400 specimens under 1 m^2, observed on the section along the Kola Meridian in 1960, seemed to be very low too: the stomachs of fry, 17 and 27 mm long, caught on this section contained no *Calanus*. As in 1961, the food of fry consisted of *O. similis, E. nordmanni* and *Fritillaria* which

TABLE 2. IMPORTANCE OF THE MAIN COMPONENTS IN THE FOOD OF LARVAE AND PELAGIC FRY IN 1961 IN DIFFERENT PARTS OF THE AREA (NUMBER OF SPECIMENS AS PERCENTAGES OF THE TOTAL NUMBER).

Region	Food components	Stage VII. 15.0 to 19.0 mm	Stage VIII. 19.0 to 24.0 mm
Southern part of the Barents Sea to the east of the Section North Cape-Bear Island	*Calanus finmarchicus*	2.4	
	Oithona similis	76.3	65.7
	Other Copepoda	1.2	3.5
	Evadne nordmanni	17.5	30.6
Southern part of the Barents Sea, Inshore Station.	*Calanus finmarchicus*		1.8
	Oithona similis	63.6	12.5
	Other Copepoda		30.4
Section North Cape Bear Island	*Calanus finmarchicus*	68.9	77.8
	Oithona similis	6.7	
	Other Copepoda	22.2	7.4
Section 72°50'N.	*Calanus finmarchicus*	100	85.4
	Oithona similis		
	Other Copepoda		3.7

were abundant in this area. The abundance of *C. finmarchicus* of about 18,000 specimens under 1 m^2 provides sufficient food supply for cod fry, as is seen from the data for 1961 obtained on the section North Cape-Bear Island (Tables 1 and 2).

REFERENCES

BARANENKOVA, A.S. 1964. Notes on the Condition of Formation of the Arcto-Norwegian Tribe of Cod of the 1959-1961 Year-Classes During the First Year of Life. *This symposium, Contribution No. B-15.*

PONOMARENKO, I.Ja., 1964. Comparative Characteristics of Some Biological Indices of the bottom Stages of 0-Group Cod Belonging to the 1956, 1958, 1959, 1960 and 1961 Year-Classes. *This symposium, Contribution No. B-7.*

WIBORG, K.F. 1948. Investigations on cod larvae in the coastal waters of northern Norway. *Fiskeridir. Skr. Havundersøk.*, 9 (3): 1-27.

1960. Investigations on pelagic fry of cod and haddock in coastal and offshore areas of northern Norway in July - August, 1957. *Fiskeridir. Skr. Havundersøk.*, 12 (8): 1-18.

B-17

THE BREEDING AND LARVAL DISTRIBUTION OF REDFISH IN RELATION TO WATER TEMPERATURE

By

A. Kotthaus[1]

ABSTRACT

This paper deals with the larval redfish material collected on board the R/V *Anton Dohrn* on the occasion of a joint Icelandic-German survey in the central North Atlantic carried out in April-May 1961. Reference is made to the results of a similar survey during the ICNAF Environmental Survey (NORWESTLAND 2) in 1963.

Larval redfish distribution along with the water temperature conditions are considered, and the "breeding" places of the redfish are located from the occurrence of new born larvae. The question of the depths at which redfish larvae are liberated is discussed.

INTRODUCTION

Tåning (1949) summarized the known facts about the distribution of redfish larvae in the North Atlantic. His paper, however, left some questions unanswered. Tåning considered that the area in which larvae were found corresponded to the breeding area. We know, however, that there are strong currents in the North Atlantic which may displace the larvae for considerable distances from the breeding areas within a relatively short time. We may also assume that the larvae were no longer at the original spawning places at the time when most of the Danish investigations were carried out (at the end of June and the beginning of July). It would seem, therefore, that Tåning's views are not necessarily correct.

From the hydrographic conditions at the time of the investigations, Tåning concluded that the liberation of larvae occurs at temperatures of 3° to 5°C and at depths between 300 and 500 m. When the larvae ascend to the upper layers, they need a temperature of 8° to 9°. Consequently the question remains as to whether or not these temperatures occur at the time of the main spawning, *i.e.*, in April and May, because the hydrographic conditions may change very quickly.

Tåning gives no details of geographical variation in the size of larvae. It is necessary to know this in order to discover the location of the breeding areas; the smaller the larvae are, the nearer the breeding places will be.

To study these problems, Iceland and Germany decided to make a special survey of redfish larvae together with hydrographic observations. It was not possible, of course, for these two nations to survey the whole distributional area of redfish larvae shown by Tåning. Therefore, the first investigations were restricted to the central North Atlantic, including the Irminger Sea and the Denmark Strait. This area was chosen because it seemed to be the most important breeding area of the oceanic stocks of redfish and may perhaps be important in studies of the Icelandic and Greenlandic stocks.

The Icelandic-German survey was carried out from the end of April to the beginning of June, 1961. Icelandic scientists aboard the R.V. *Aegir* investigated Denmark Strait and the Irminger Sea north of 60° N. lat., and German scientists aboard the R.V. *Anton Dohrn* investigated the southern and eastern parts between the longitude of 42°W and the Iceland-Faroe Ridge and southwards to the northern border of the Gulf Stream. The results of these two cruises were submitted separately as preliminary reports to the ICES Meetings in 1961 (by A. Kotthaus) and 1962 (by J. Magnusson).

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GEAR AND METHODS

The Nansen closing net was used for vertical hauls. Horizontal tows were made using three Icelandic High Speed samplers (IHSS), at different depths, on a few occasions when the sea conditions were too bad to use the Nansen net. Fish larvae were separated from the whole catch, and not, as is usually done in bigger plankton catches, from a part of it. The water temperature was measured at every station by a hydrographic series to 500 m or by the bathythermograph from the surface to 270 m.

RESULTS AND DISCUSSION

a) The distribution of redfish larvae.

Figure 1 shows that redfish larvae were found over most of the area (square symbols) with the exception of the relatively warm waters of the Gulf Stream. Two main areas of distribution, separated by some stations without redfish larvae (open circles), may be distinguished (apart from a third in the south of Iceland, which shall not be considered here): a) a small area to the south-south-east of Cape Farewell, which probably extends farther westwards, and b) a very extended area on both sides of the Middle Atlantic-Ridge (MAR), which continues to the north and north-east along the Reykjanes Ridge as indicated by Magnusson's (1962) simultaneous investigations. These areas are characterized by distinct water temperatures at a depth of 30 m: in the western area the temperature ranged from 4° to 5.5°C, and in the central area along the MAR, from 6° to 8°C (south of Iceland in the eastern area we found still higher temperatures of 8° to 9.5°C). No larvae were found in waters with temperatures higher than 9.5°, *i.e.*, in Gulf Stream waters. These areas of distribution correspond well with Henderson's (1961) distribution chart, although the areas in his charts are not so well defined, probably because of the combination of material from several months.

b) Abundance of redfish larvae.

The abundance of redfish larvae may be seen from Fig. 1 which shows the total number caught at each station. The highest density of larvae, more than 10 specimens per sample, was found along the western slope of the MAR. Somewhat smaller concentrations, 6 - 10 specimens, were encountered in the western area south-south-east of Cape Farewell. In all other regions the number per station was less than 6.

As indicated by divided vertical hauls with the Nansen closing net and by catches with the IHSS, larval redfish prefer the upper layers between 15 and 50 m in depth. No larvae were found below 60 m or in the upper recorder of the IHSS which was fishing at 5 m.

c) Breeding places of the redfish.

In order to find out where the redfish larvae were born, all larvae were measured. From measuring pre-extrusion larvae, we know that these range from about 5 to 7 mm in length; in only a few cases were there larvae measuring up to 7.5 mm. Such small and doubtless new-born larvae with the remains of the yolksacks still visible were found only at very restricted places. These correspond with the highest concentrations of larvae along the western slope of the MAR and south-south-east of Cape Farewell. Outside these areas the new-born fish were extremely scarce.

We must conclude from this that the hatching of larvae is restricted to special areas, although some redfish may occasionally spawn (if this expression may be allowed for the ovo-viparous redfish) outside these areas. These observations show that the area of occurrence of redfish larvae is not at all identical with the breeding area of the adult fish.

Figure 2, which is based on the Icelandic material (Magnusson, 1962) as well as the German samples (Kotthaus, 1961 and 1962), shows the spawning areas in the central North Atlantic. The intensity of spawning in the area west of Iceland slowly decreases to the south and ends at about 52°N. The spawning area to the south-south-east of Cape Farewell, is clearly separated from the central area but is of no significance when compared with this.

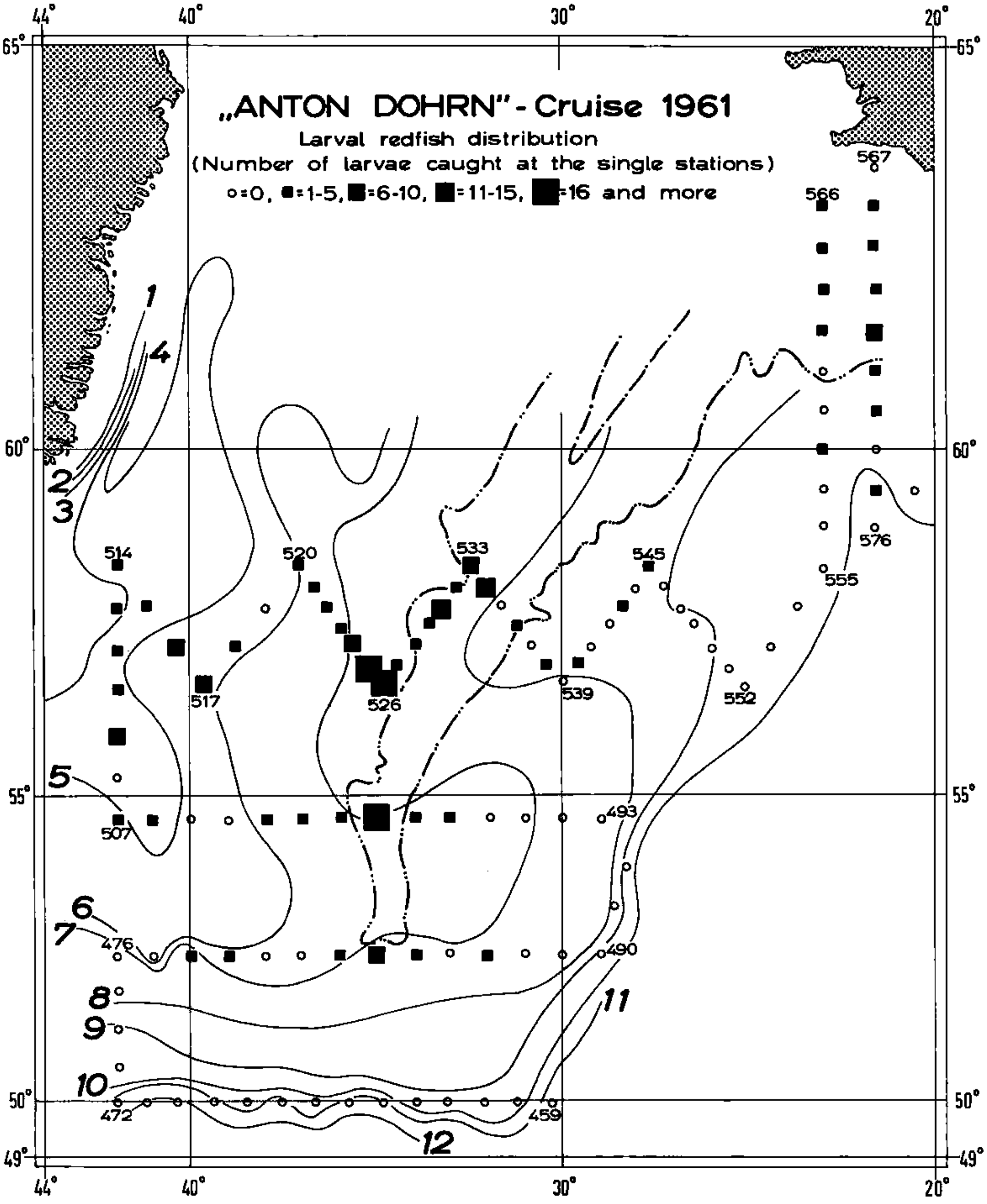

Fig. 1. The abundance of redfish larvae at each station during the cruise of the *Anton Dohrn* in 1961 (see key above). The position of the Middle Atlantic Ridge and the Reykjanes Ridge are indicated by the 1,000 m and 2,000 m depth contours. The isotherms are based on observations at 30 m depth. Small figures show station numbers.

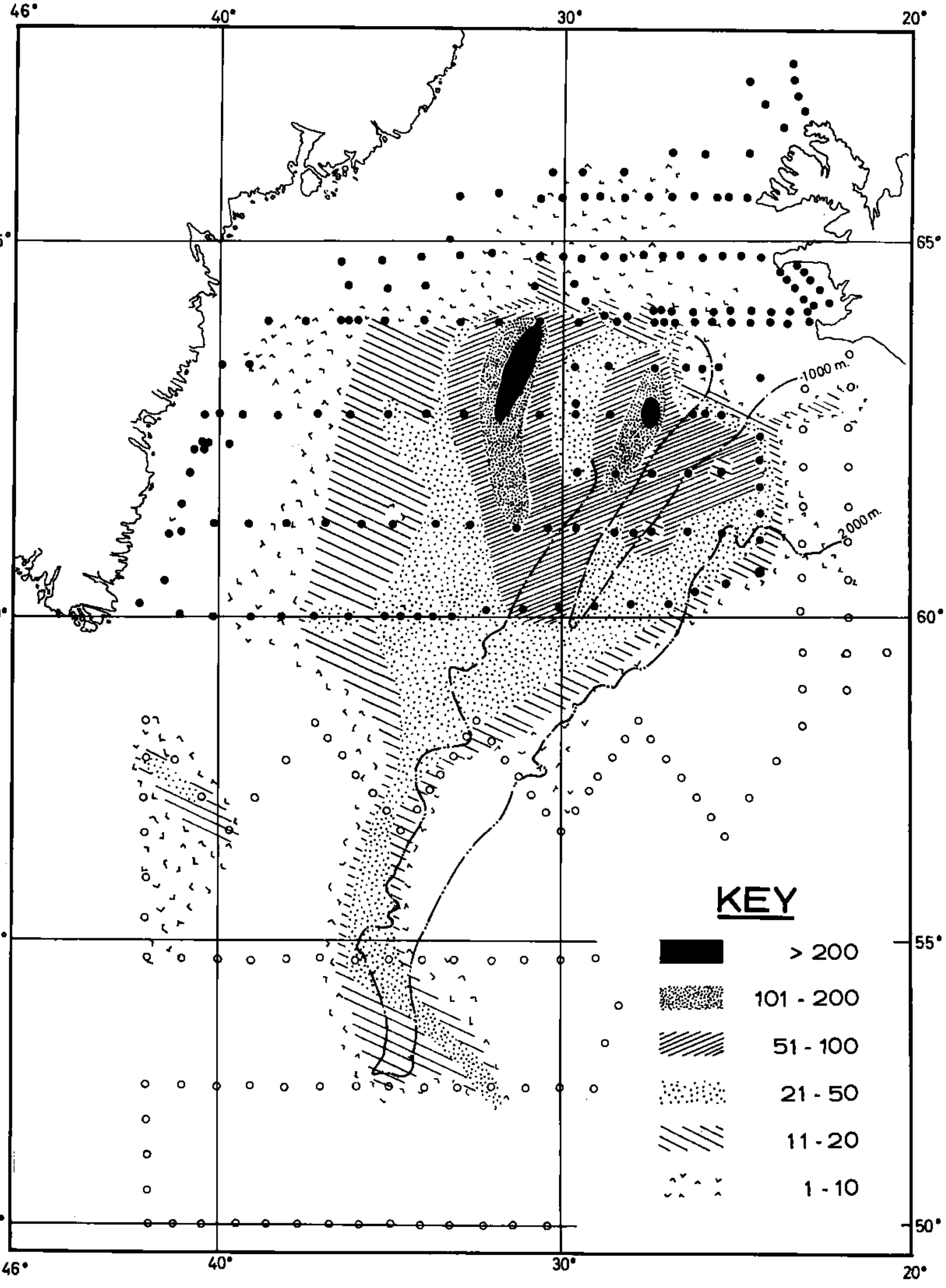

Fig. 2. Spawning areas of the redfish; based on the German *Anton Dohrn* and Icelandic *Aegir* cruises in 1961. The key shows numbers of redfish larvae of less than 7 mm length. The positions of the Middle Atlantic Ridge and the Reykjanes Ridge are indicated by the 1,000 m and 2,000 m depth contours.

d) Spawning depth of the redfish.

The depths at which redfish larvae are extruded have been uncertain until now. Einarsson (1960) doubts whether redfish fry are born at depths of 200-500 m as Tåning and others had supposed. He believes that the young hatch at depths of between 500 and 800 m, and he has evidence to show that temperature conditions at these depths, at least to the west of Iceland, are not necessarily in opposition to Tåning's hypothesis that the redfish require a temperature of 3° to 5°C in order to spawn.

Our observations in 1961 tend to agree with those of Einarsson. The fishing we did in the open ocean at depths of up to 450 m by longline and floating trawls as well as echo soundings never indicated the presence of pelagic redfish in the area. From these observations it is easy to believe that the ripe redfish females are living in much deeper water at spawning time.

The fact that adult redfish have been caught at different localities in the open ocean at depths of less than 300 m does not conflict with the possibility of spawning in deep water. We have never heard, so far, that running females have been caught at these depths. It could well be that these fish caught by line are either spent fish (having ascended from the deep spawning places to the upper layers and are migrating, using the currents at these depths, to their feeding places on the Icelandic slope) or else they are fish belonging to an oceanic stock of redfish generally living in these levels, whose breeding places, however, are far deeper. That males were also caught leads us to suggest this probability. This problem might be solved by racial investigations.

The question now arises as to whether or not the temperature conditions at these depths of 500 - 800 m fulfil the temperature requirements of 3° to 5°C for spawning. Einarsson (1960) states that, in the areas west of Iceland which he believed to be breeding grounds, the temperatures at depths of 500 - 800 m were within the range of 4° to 6°C.

The hydrographic measurements carried out on our cruise only cover depths down to 500 m. However, we may conclude from the trends of the isotherms (Fig. 3) that at least along the MAR the required temperatures must exist at depths of more than 500 m. Our diagrams show this fact clearly: water masses of relative high temperature of 4° to 6°C push down in a wedge-like form to remarkable depths. In the northernmost section the 5°-isotherm dipped below the 500 metre-line at one point. This downward sweep of warm water masses seems to be common in that season along the Reykjanes Ridge and the MAR as indicated in the diagrams of Tåning (*loc. cit.*, p. 89, Fig. 2) and from the investigations on *Anton Dohrn* during the IGY in 1958 and later (Dietrich, 1960, p. 14, 20, 26 and 32). It is easy to believe that the ripe female redfish are carried by the relatively small and deep-reaching wedge of warm water running from the south-west coast of Iceland to their breeding places along the submarine ridges. This supposition is supported by the observations in April of several years that ripe female redfish are concentrated in considerable numbers off the south-west coast of Iceland in depths of 450 m and more at the base of the Reykjanes Ridge. (This is the *marinus* type redfish, which lives at other times at depths of no more than 350 m). If the hypothesis of deep-sea spawning of the redfish should prove to be correct, the larvae would be able to ascend to the surface in more or less isothermal waters.

In 1963, as part of the NORWESTLANT survey, the *Anton Dohrn* made a cruise off south-east Greenland from 24 May to 30 June. Detailed results will be published in ICNAF Special Publication No. 7, as part of the NORWESTLANT series of papers, but a brief summary is given here.

The area covered by the NORWESTLANT survey in 1963 overlapped partly with the 1961 cruise but lay further to the north-west, extending to the coast of Greenland. In general the NORWESTLANT survey provided confirmation of the results based on the earlier cruise. There were three areas in which redfish larvae were found, two of these corresponding to those found previously (the central area, west of the MAR, and the region south-south-east of Cape Farewell). The other region was an area along the east coast of Greenland with temperatures of 5° to 6.3°C. The smaller larvae were found in the south-west and western parts of the survey and there was an irregular gradient of increasing sizes to the east and north-east. It is assumed that this pattern resulted from the current systems carrying the larvae from their birth places and towards the Icelandic shelf where they can descend to the bottom.

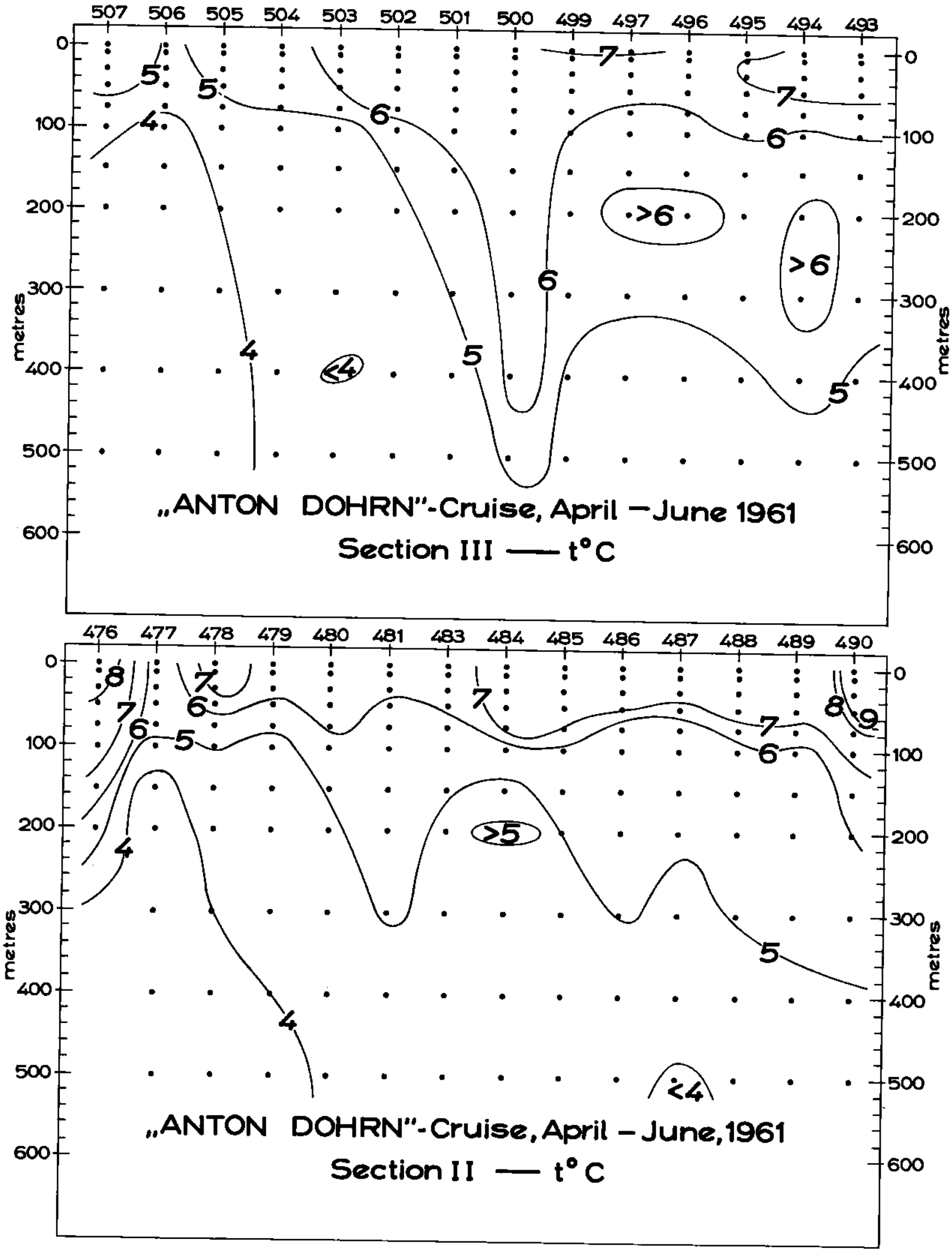

Fig. 3. The vertical distribution of temperature in two sections of the 1961 cruise. Station numbers are indicated above the sections as in Fig. 1.
Above — 50°40'N : 42°00'W to 29°00'W
Below — 52°30'N : 42°00'W to 29°00'W

One difference between the surveys in 1961 and 1963 was noticed in the vertical temperature distributions. The downward sweep of the isotherms which was a feature of the 1961 results (Fig.3) was not apparent in 1963. From our hypothesis on breeding conditions, it would seem likely that the conditions were unfavourable for breeding in June 1963. Only at the southern part of the MAR did we find a slight hint of the downward sweep of the isotherms and it was only in this region that we found young larvae.

SUMMARY

Though our investigations are preliminary, we feel there is evidence for the following statements:

1) There are three main areas of occurrence of redfish larvae in the central North Atlantic covered by the *Anton Dohrn* cruises of 1961 and 1963 each showing different thermal conditions; these are:

   a) a central area along the Middle Atlantic Ridge having temperatures of about 6° to 8°C (at 30 m depth).

   b) a western area south-south-east of Cape Farewell with temperatures of about 4° to 5.5°C.

   c) an area along the east coast of Greenland with temperatures of 5° to 6.3°C.

2) The main spawning area in the waters surveyed by *Anton Dohrn* runs along the western slope of the Middle Atlantic Ridge, only extending to the eastern slope in the south. Some spawning of less importance also occurs in the other two areas.

3) The spawning of the redfish probably occurs at depths of more than 500 m and at water temperatures of between 4° and 6°C. This, however, concerns only the main spawning area. In the others the breeding conditions may differ from these.

4) Since the spawning areas were found to be restricted, the area of occurrence of redfish larvae cannot be considered to correspond with the breeding places of the adult fish.

REFERENCES

DIETRICH, G. 1960. Temperatur-, Salzgehalts- und Sauerstoffverteilung auf Schnitten von FFS *Anton Dohrn* und VFS *Gauss* im Internationalen Geophysikalischen Jahr 1957/58. *Dtsh. Hydrogr. Z.*, Ergänzungsheft Reihe B, 4.

EINARSSON, H. 1960. The fry of *Sebastes* in Icelandic waters and adjacent seas. *Rit Fiskid.* 2 (7): 1-67.

HENDERSON, G.T.D. 1961. Continuous plankton records: The distribution of young *Sebastes marinus*(L). *Bull. Mar. Ecol.*, 5, 46: 173-193.

KOTTHAUS, A. 1961. Redfish larvae investigations in the central North Atlantic in 1961 (preliminary report). ICES-C.M., 1961, paper no. 4.

1962. Rotbarschbrut im zentralen Nordatlantik. *Inform. Fischw.*, 1/2: 7-14.

MAGNUSSON, J. 1962. Redfish larvae in the Irminger Sea in May, 1961. ICES-C.M.,1962, paper no. 90.

TÅNING, Å.V. 1949. On the breeding places and abundance of the redfish (*Sebastes*) in the North Atlantic. *J. Cons.*, 16: 85-95.

B-18

SOME RESULTS OF SOVIET RESEARCH WORK ON ICHTHYOPLANKTON IN THE NORTHWEST ATLANTIC: EGGS AND LARVAE OF COD

By

V.P. Serebryakov[1]

ABSTRACT

The distribution and abundance of cod eggs and larvae are considered in relation to the sur- ace water temperatures and current systems off the Labrador and Newfoundland regions. Spawning n the spring months started at very low, and sometimes negative, temperatures. It is shown that emperature, through its effect on the rate of development of larvae, determines the length of time hat larvae are transported by the currents and, therefore, the subsequent distribution of the oung cod.

In 1959-62 the Soviet research and scouting vessels collected ichthyoplankton in the northwest art of the Atlantic Ocean. The samples were taken with conical egg nets with a diameter at the pening of 80 cm and gauze 140) in 15-20 min oblique hauls; 1,674 samples were taken. Collections overed the waters of Labrador (ICNAF Subarea 2), Newfoundland (Subarea 3), Nova Scotia (Subarea 4) nd Georges Bank (Subarea 5). Cruises were conducted during the spring and summer, from March to ugust. The material included eggs and larvae of 37 fish species belonging to 18 families (Appendix). ost numerous were the eggs and larvae of gadoids, *Pleuronectes*, scorpionfishes, and *Ammodytes*. Pre- iminary data have been published previously (Serebryakov, 1962 and 1963). The present paper con- ains the results of investigations of cod only.

The distribution of eggs and larvae of cod in the waters of Nova Scotia, Gulf of Maine, Georges ank, Saint Pierre and Green Bank was given in the works of Dannevig (1918), Bigelow and Schroeder 1953). In addition, our investigations cover the more northern areas, which had not been inves- igated earlier.

In March, ichthyoplankton was collected only in the waters of Flemish Cap, on the slopes of rand Newfoundland Bank (GNB) and in the area to the east of the Avalon Peninsula (Fig. 1A). Indi- idual cod eggs were observed over the oceanic depths to the east of Flemish Cap Bank, on the north- ast and southwest slopes of the Grand Bank over the depths of 150-375 m; and in somewhat greater uantities (up to 11 specimens per vertical haul) in the area of the Grand Bank east of the Avalon eninsula over depths of 74 to 160 m (Fig. 1A). In March the surface layer temperature in these reas was as follows: 0.35°C near Avalon Peninsula along the section 47°00N; 1.8°C in the Flemish ap area; and 0.52°C on the southeast slope of the Grand Newfoundland Bank. In all cases 90% of he eggs were at the first stage of development, according to the stages defined by Rass (1949). he scarcity of eggs and the predominance, amongst them, of eggs in the first stage of development, oupled with the small numbers of post-spawners amongst the adult fish (Table 1), suggest that spaw- ing began in March when only occasional individuals were spawning.

In April and May collections were made in almost all the investigated areas. The distribution f cod eggs during the spring period in the Labrador area is most interesting.

From 14th to 18th April, 1962 large quantities of eggs were found on the boundary between cen- ral and north Labrador waters on the slope of the shelf over depths from 380 to 450 m; more than ,000 eggs were hauled at two stations (Fig. 1B). More than 600 eggs were also caught on 24 April t two stations in the area of South Labrador. The catch composition of eggs of North and South abrador differed with respect to the ratio of development stages (Table 2).

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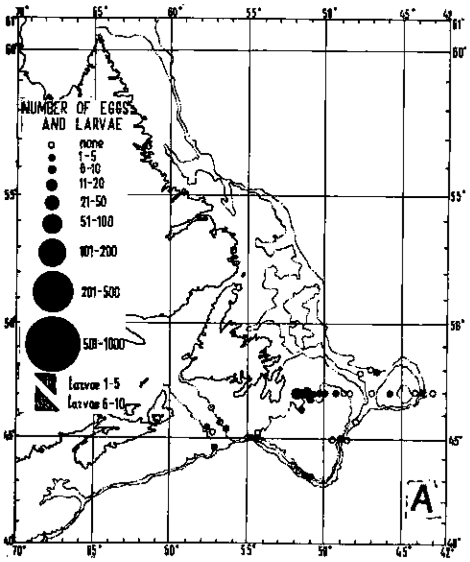

Fig. 1A. Distribution of eggs (circles) and larvae (triangles) of cod (*Gadus m. morhua*): A — in March.

TABLE 1. MATURITY OF GONADS OF ADULT SPAWNERS CAUGHT IN MARCH DURING 1957-61 IN THE WATERS OF GRAND NEWFOUNDLAND BANK (30 AND 3N) (AS PERCENTAGES OF THE NUMBER OF DISSECTED FISH).

Areas	Gonad maturation stages							Total number of dissected fish
	II	III	IV	IV-V	V	VI	VI-II	
3N	34.3	12.0	46.0	0.4	0.4		6.9	525
30	50.0	12.0	29.0	5.0	4.0			565

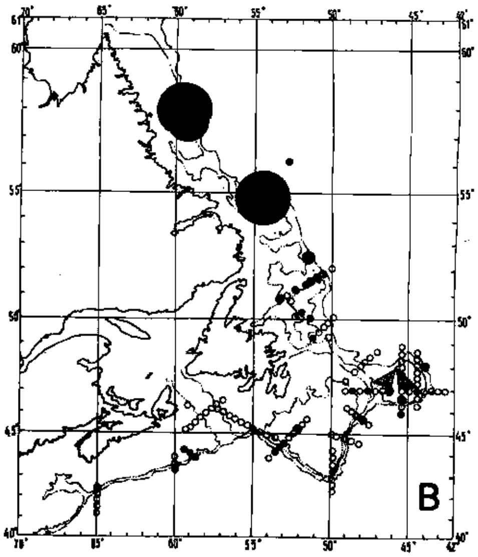

Fig. 1B. Distribution of eggs (circles) and larvae (triangles) of cod (*Gadus m. morhua*) : B — in April.

TABLE 2. COMPOSITION OF EGG CATCHES IN THE LABRADOR AREA BY THE STAGES OF DEVELOPMENT APRIL 1962, AS PERCENTAGES OF THE TOTAL CATCH OF EGGS IN THE AREA.

	Stages of egg development				
Areas	I	II	III	IV	Total number of eggs
North Labrador	76	33	0	0	1020
South Labrador	26	57	13	4	650

Gonad maturation stages of adult fishes in these areas were also different (Table 3).

TABLE 3. GONAD MATURATION STAGES OF COD CAUGHT IN THE LABRADOR AREA IN APRIL 1962, AS PERCENTAGES OF THE NUMBER OF DISSECTED FISH IN THE AREA.

Areas	Stages of maturity					Total number of dissected fish
	IV	IV-V	V	VI	VI-II	
North Labrador			20	80		180 specimens
South Labrador	26		10	19	45	726 specimens

In May the material was collected in the waters off North and Central Labrador as well as to the north of Hamilton Bank, on the boundary of Central and South Labrador. Catches of cod eggs during this period were considerably poorer than in April: at two stations in the North Labrador area only 6 eggs were caught at the temperature -1.0°, whereas in the Central Labrador area 88 specimens were caught at the temperature -0.1°, and at the boundary of Central and South Labrador Area - 129 eggs at the temperature + 0.9°. The proportions of the development stages of eggs in the samples off Central Labrador are different from that in samples from the northern part of Hamilton Bank (Table 4).

TABLE 4. COMPOSITION OF EGG CATCHES IN THE LABRADOR AREA BY THE DEVELOPMENT STAGES IN MAY 1962, AS PERCENTAGES OF THE TOTAL CATCH OF EGGS IN THE AREA.

	Stages of egg's development				Total number of eggs
Areas	I	II	III	IV	
Central Labrador	95	0	2.5	2.5	88
Boundary of Central part of Southern Labrador	1	14	28	57	129

Almost all the adult cod caught in these areas were post-spawners, only a few specimens having gonads at the fifth stage of maturity. The first larvae were taken in May, when larvae, 3.5 mm and 3.6 mm long, were found on the boundary of Central and South Labrador.

At the end of June there were very few eggs in the area of South Labrador (Fig. 1C); no samples were taken from the north. Only a few eggs were caught (not more than 10 per egg net haul). A total of 12 larvae of 4.5 - 5.7 mm long was encountered in the area of South Labrador and to the north of the Newfoundland Bank.

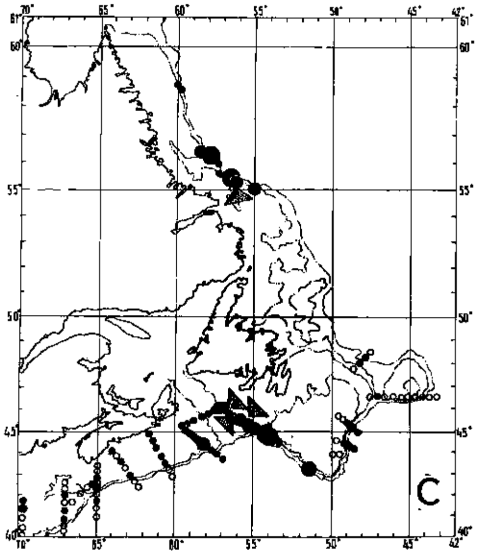

Fig. 1C. Distribution of eggs (circles) and larvae (triangles) of cod (*Gadus m. morhua*): C — in May.

The analysis of the distribution of cod eggs and larvae and the condition of gonads of adult spawners during spring months in the waters of Labrador allows us to describe some of the characteristics of cod reproduction in these areas. The presence of a large number of eggs and spawning cod in the areas of North, Central and South Labrador is a clear indication that the spawning of cod on the slopes of the Labrador Shelf takes place in April-May. However, the character of spawning in the areas of North and South Labrador is different. In the waters of North Labrador the spawning period is shorter and proceeds on a larger scale than in the waters of South Labrador. This is confirmed by the fact that in April adult cod off North Labrador were represented only by spawners, while off South Labrador spawners make up only about 30% (Table 3). Spawning off North Labrador takes place in April and in the first ten-day period of May, whereas in mid-May only post-spawners are found in the area. Off South Labrador spawning is extended from April to July: spawning cod and eggs of the first stages of development are encountered there in April, May, late June and July.

The presence of eggs in the first stages of development (I and III) as well as the absence in the samples of cod in the late stages in the North Labrador area in April (Table 2) is explained by the fact that the extruded eggs in this area are driven away from the spawning areas to the areas of Central and South Labrador by the Labrador Current where they reach later stages of development during the drift (Table 2 and Table 4).

In April the temperature of the surface layer where eggs were distributed was very low: -1.5°C off North Labrador, and -0.1°C off South Labrador; in May the temperature was -0.1°C in the Central Labrador area and +0.9°C in South Labrador. Low temperatures of the surface layer of about 100 m thick and deeper are characteristic of the Labrador Current (Buzdalin, Elizarov, 1962). Development of cod eggs in the Labrador areas takes place at very low temperatures, sometimes negative, influencing both the rate of development and duration of drift of eggs and larvae. Thus, at a temperature 0.0°C, the period of egg development from fertilization to hatching takes about 43 days, and at a temperature -1.0°C about 50 days (Apstein, 1909). Within this time the eggs would be driven about 280-300 miles away from the spawning grounds by the Labrador Current, its velocity being 10 cm/sec off North and Central Labrador and 14-20 cm/sec off South Labrador (Küllerich,1943), *i.e.* they would cover the distance equal to the distance from North to South Labrador. If the actual pattern of drift and development of eggs corresponds to the described one, then the larvae hatched from the eggs spawned near North Labrador would be expected to appear in Central and South Labrador only 40-50 days after the commencement of spawning, *i.e.* in mid-May (the beginning of spawning falling on late March-early April). It was in mid-May when the larvae of cod, 3.5 to 3.6 mm long, were discovered on the boundary of Central and South Labrador.

The larvae hatched from the eggs in Central Labrador are likely to drift further to the south, to the areas of South Labrador and northern Newfoundland Bank. This is shown by the increasing size of larvae as they move to the south. Thus, in May the length of larvae in the Central Labrador area was 3.5 to 3.6 mm; in June in the South Labrador area, 4.2 to 5.7 mm; in July in the northern Newfoundland Bank, 9.0 mm; in August in the northern Newfoundland Bank and southern Labrador, 12.7 to 13.9 mm.

In the more southern areas the number of cod eggs was considerably smaller. Only individual eggs were observed in the egg-net catches in the northern Newfoundland Bank. In April, the eggs were found on the northeast, south and southwest slopes of the Flemish Cap Bank, over depths of 290-450 m. In the area southwest of Flemish Cap, some eggs at the first stages of development were found over a depth of 2,200 m. Individual specimens of cod eggs were observed in the central part of the bank over depths less than 100 m (Fig. 1B). In May only a small number of cod eggs were observed in the area: only on the west slope of the Bank, five eggs at the first stages of development were found. In April larvae of cod (17 specimens) were found in this area in the central part of the Bank over a depth of 150-255 mm where the temperature of the surface layer was +4.35°C; the length of the larvae was from 4.0 to 5.5 mm.

The presence of larvae in the central part of the Bank is most probably explained by the drift of eggs and larvae from the south and southwestern slopes, where cod spawn in March (Mankevitch and Prochorov, 1962) with cyclic currents or rather with their branches flowing from the slopes to the central part of the Bank (Buzdalin and Elizarov, 1962). It is possible that larvae of cod could be brought from the Northern Newfoundland Bank or from the northeast slope of the Great Newfoundland Bank. However, in this case larvae would have probably been larger owing to the longer duration of the drift.

In April very few cod eggs were found in the areas of the Grand Newfoundland Bank. Only a few eggs were observed in the northeast and southwest areas of the Bank (Fig. 1B). In May, cod eggs appeared on the northeast and southeast slopes, but in very small numbers; not over 5-6 specimens per vertical haul. In May, considerably more eggs were found on the southwest slope of the Grand Bank as well as in the areas of Saint-Pierre and Green Banks - up to about 50 specimens of cod eggs per vertical haul. All stages of development were represented in the catches of egg-nets with the first stage dominating (Table 5).

TABLE 5. COMPOSITION OF CATCHES OF COD EGGS IN THE AREAS OF SAINT-PIERRE BANK, GREEN BANK AND SOUTHWEST SLOPE OF THE GRAND NEWFOUNDLAND BANK BY THE DEVELOPMENT STAGES AS PERCENTAGES OF THE TOTAL CATCH OF EGGS IN THESE AREAS.

Stages of development				Number of eggs
I	II	III	IV	
55	19.5	19.5	6	325

Larvae of cod, 4.0 to 5.5 mm long occurred in these areas in May. The temperature of the surface water layer in these areas was from 1.8 to 2.8°C. Of the cod caught by trawl in these areas, 70% consisted of spawners or postspawners (see Table 6).

TABLE 6. MATURITY OF GONADS OF COD CAUGHT IN THE AREAS OF SAINT-PIERRE BANK, GREEN BANK AND SOUTHWEST SLOPES OF THE GRAND NEWFOUNDLAND BANK AS PERCENTAGES OF THE TOTAL NUMBER OF DISSECTED FISH.

Stages of maturity						Total number of dissected fish
II	III	IV	V	VI	VI - II	
22	0.1	7.2	33.9	20.2	16.4	670

Distribution of cod eggs and adult spawners shows that spawning of cod in these areas takes place during the first ten days of May. However, the abundance of spawning concentration was not so great, as the cod catches by trawl with vertical opening 8.5 m did not exceed 100 kg per one hour of hauling. This fact can, probably, explain the small number of eggs in plankton samples.

In April and May there were very few cod eggs in the areas of Nova Scotia and Georges Bank (Fig. 1C).

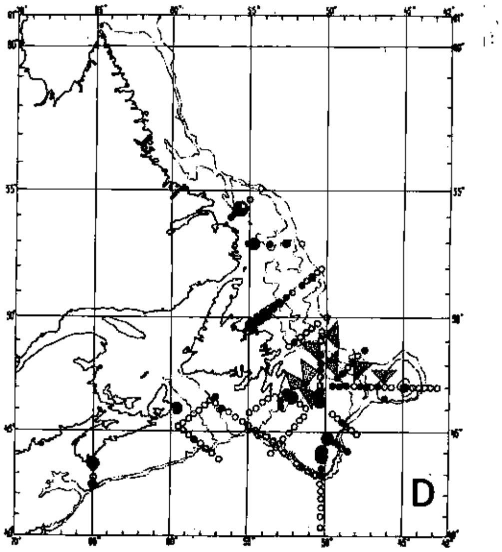

Fig. 1D. Distribution of eggs (circles) and larvae (triangles) of cod (*Gadus m. morhua*): D — in July-August.

In July-August, eggs of cod were distributed over lesser depths than during spring months. The main mass of eggs was discovered close to the coast or in the shallow areas of the banks (Fig. 1D). In August, eggs were distributed close to the coast over depths of about 150 m and at a temperature of +2.8°C, and in the shelf area at the latitude of Belle-Isle. In the area of the Northern Newfoundland Bank, eggs were also distributed mainly in the coastal waters. The main mass of the eggs in the waters of Grand Newfoundland Bank was distributed near the shores of Newfoundland Island over depths 48-150 m; in the northeastern part of the Bank over the depths 150-190 m; in the central part of the Bank and in the shallow waters of the southern part of the Bank. Individual eggs are driven away from the slopes of the Bank to the areas of oceanic depths. Individual eggs were found in the central part and on the southwest slopes of the Flemish Cap Bank. In August larvae of cod were distributed both near Avalon coast in the northern, northeastern and central parts of the Grand Newfoundland Bank. The larvae were 4.0-9.5 mm long. Only single larvae were found in the catches of egg-nets.

In August, eggs of cod were encountered over small depths in the area of Nova Scotia Shelf and the Great Newfoundland Bank. In July-August, the temperatures of waters where eggs and larvae of cod were distributed were, naturally, much higher than in April-May. If in April surface layer temperature near Labrador was 1.5 to 1.0°C, on the east and southeast slopes of GNB +0.50°C, on the south slope of GNB +4.0°C, on Flemish Cap Bank +4.38°C, Saint-Pierre and Green Banks +1.8 to +2.8°C, then in July-August the temperature of the surface layer near Labrador was +2.98° to +4.6°C, on the north and northeast slopes of GNB +7.70° to +8.78°C in the south of GNB +8.37° to +10.40°C and near the Newfoundland coast +7.0°C. In July-August the development rate of cod embryos owing to the higher temperatures, was considerably faster than during the spring months. In the area of South Labrador the duration of development from fertilization to the hatching stage at the temperature +2.88 - +4.60°C was about 18-23 days (Apstein, 1909), *i.e.* less than half what it was in April-May. In other areas the period of development in July-August was about 11-14 days. Owing to the increased rate of development, the time of pelagic life during the summer season is reduced, so it is possible to suppose that the duration of drift both with regard to time and distance must be much shorter in the summer period than in April-May.

CONCLUSIONS

1. Ichthyoplankton of the investigated areas is represented by eggs and larvae of 37 fish species from 18 families.

2. In April-May spawning of cod takes place in the waters of Labrador (Northern, Central and Southern parts). In Northern Labrador, spawning was observed to begin in April and end in the first ten days of May. In the waters off South Labrador spawning is more extended, in April, May, June and early August.

3. Development of cod eggs and larvae in the areas of Labrador in the spring months was observed at very low, sometimes negative temperatures, so the rate of development was very slow. This extends the period of passive pelagic life which is directly related to the duration of drift migration.

4. In the areas of Labrador drift of eggs and larvae was observed from the spawning grounds. Direction and velocity of the drift is determined by the Labrador Current. Eggs from North Labrador drift from Central to South Labrador. In May larvae appeared in the Central Labrador area and drifted to the south towards South Labrador and North Newfoundland Bank.

5. Drift of cod eggs and larvae was observed within the area of Flemish Cap. It was directed rom the south and southwest slopes towards the central part of the Bank, where the spawning grounds f cod were situated (Mankevitch and Prochorov, 1962). Direction of drift is determined by the cirular current which is directed from the southwest slope to the centre of the Bank in this area.

6. General trends of spawning of commercial fish species of Labrador and Newfoundland make it ossible to conclude that the extrusion of cod eggs takes place on the slope of the continental helf in the near-bottom slope waters with positive temperatures, *i.e.* in those waters which are ormed by the Irminger Current. But, their drift takes place in the waters of Labrador Current with hich the eggs and larvae are driven from their spawning grounds to the areas of banks located much ore to the south from the spawning grounds. So, it is possible to suppose that the formation of tocks of commercial fishes in these areas is largely determined by the character and conditions of he drift migrations during the period of early stages of development.

REFERENCES

APSTEIN, C. 1909. Die Bestimmung des Alters pelagisch lebende Fischeier. Mitteilungen des Deutschen Seefischerei-vereins. Bd. XXV, p. 364-373.

BIGELOW, H.B. and Wm. C. SCHROEDER. 1953. Fishes of the Gulf of Maine. *U.S. Fish and Wildl. Serv., Fishery Bull.* 74, 53: 577 p.

BUZDALIN, Ju. I. and A.A. ELIZAROV. 1962. Hydrological conditions in the areas of Newfoundland Banks and Labrador, 1960. *Soviet Fisheries Investigations in the North-West Atlantic. VNIRO-PINRO,* p. 155-171.

DANNEVIG, A. 1918. Canadian fish-eggs and larvae. Canadian fishery Expedition, 1914-1915. Ottawa.

KIILERICH, A. 1943. The hydrography of the West Greenland Fishing banks. *Medelelser fra Kommissionen for Danmarks Fiskeri og Havundersøgelser, Serie: Hydrogr.III, No.3,* p. 3-15.

MANKEVICH, E.M. and V.S. PROCHOROV. 1962. Size-age composition and spawning of cod on the southwest slope of Flemish-Cap Bank. *Soviet Fisheries Investigations in the North-West Atlantic. VNIRO-PINRO,* p. 355-360.

RASS, T.S. 1949. Composition of ichthyofauna and taxanomic classification of eggs and larvae of fishes of the Barents Sea. *Trudy VNIRO,* 17: 9-65.

SEREBRYAKOV, V.P. 1962. Some aspects of the ichthyoplankton studies in the areas of Labrador and Newfoundland. *Soviet Fisheries Research in the Northwest Atlantic Ocean. VNIRO-PINRO,* p. 227-234.

1963. Distribution of pelagic eggs and larvae of commercial fishes in the Northwest Atlantic area. *Annu. Meet. int. Comm. Northw. Atlant. Fish. 1963.* Doc. No. 56, Serial No. 1107 (mimeographed).

APPENDIX

SPECIAL COMPOSITION OF ICHTHYOPLANKTON IN THE AREAS OF
LABRADOR (2), NEWFOUNDLAND (3), NOVA SCOTIA (4), GEORGES BANK (5).

		Areas				Total number	
	Species	2	3	4	5	eggs	larvae
	I. Clupeidae						
1.	*Clupea harengus harengus* Linné	-	-	-	+	-	52
	II. Osmeridae						
2.	*Mallotus villosus villosus* (Müller)	-	+	-	-	-	162

	Species	Areas				Total number	
		2	3	4	5	eggs	larvae
	III. Bathylagidae						
3.	*Bathylagus* sp.	-	+	-	-	-	4
	IV. Myctophidae						
4.	*Benthosema glaciale* (Reinhardt)	+	+	+	+	-	14
5.	Genus sp.	+	+	+	+	-	176
	V. Gadidae						
6.	*Brosme brosme* (Muller)	-	-	+	+	426	-
7.	*Enchelyopus cimbrius* (Linné)	-	+	-	-	5	7
8.	*Urophycis* sp.	-	-	+	+	11	5
9.	*Molva molva* (Linne)	-	-	+	-	4	-
10.	*Merluccius bilinearis* (Mitchill)	-	+	+	+	467	20
11.	*Pollachius virens* (Linné)	-	+	-	-	2	12
12.	*Melanogrammus aeglefinus* (Linné)	-	+	+	+	390	6
13.	*Gadus morhua morhua* (Linné)	+	+	+	+	11759	110
	VI. Macruridae						
14.	Macrurus sp.	-	-	-	+	-	1
	VII. Syngnathidae						
15.	Genus sp.	-	-	+	-	-	1
	VIII. Anarhichadidae	-	+	+	-	-	3
16.	*Anarhichas lupus* (Linné)						
17.	*Anarhicas minor* (Olafson)	-	+	+	-	-	1
	IX. Stichaeidae						
18.	*Chirolophis ascanii* (Walb.)	-	-	+	+	-	57
	X. Lumpenidae						
19.	*Leptoclinus maculatus* (Fries)		+	-	-	-	1

Species	Areas				Total number	
	2	3	4	5	eggs	larvae
XI. Annodytidae						
20. *Ammodytes americanus* DeKay	-	+	+	-	-	12500
XII. Scombridae						
21. *Scomber* sp.	-	-	-	+	-	2
22. *Scomber scombrus* Linné	-	-	+	+	-	1
XIII. Thunnidae						
23. Genus sp.	-	-	-	+	-	2
24. *Katsuwonus pelamis* (Linné)	-	-	-	+	-	2
XIV. Scorpaenidae						
25. *Sebastes* sp. (*S. mentella* Travin)	+	+	+	+	-	2725
XV. Cottidae						
26. Genus sp.	-	-	+	-	-	24
27. *Mioxocephalus octodecim spinosus* (Mitchill)	-	+	+	-	-	1
XVI. Agonidae						
28. *Leptagonus decagonus* (Bloch et Schneider)	-	+	+	-	-	6
29. *Aspidophoroides monopterygius* (Bloch)	-	-	+	-	-	3
30. *Ulcina olriki* (Lutken)	-	-	+	+	-	3
XVII. Liparidae						
31. *Neoliparis atlanticus* (Jordan et Everman)	-	-	+	-	-	51
32. Genus sp.	-	-	+	-	-	1
XVII. Pleuronectidae						
33. *Hippoglossus hippoglossus hippoglossus* (Linné)	-	-	+	-	10	18
34. *Hippoglossoides platessoides limandoides* (Bloch)	+	+	+	+	2090	18
35. *Limanda ferruginea* (Storer)	-	+	+	+	1250	3
36. *Microstomus microcephalus* (Donovan)	-	+	+	-	74	-
37. *Glyptocephalus cynoglossus* (Linné)	-	+	+	-	405	10

SECTION

C

C-1

REMARKS ON EFFECT OF FOOD ANIMALS ON COD BEHAVIOUR

By

Sv. Aa. Horsted and Erik Smidt[1]

ABSTRACT

In Greenland waters cod make long spawning and feeding migrations. The most important feeding migrations take place in early summer, when cod follow the capelin into the fjords to the shore, and later in the summer, when cod follow the launce over the banks in the Davis Strait and in coastal waters. Later on cod have been observed feeding quite near the shore in coastal areas, where the food consists of small capelin, Arctic squid and euphausiids. Cod may also be concentrated near icebergs in summer and autumn. Finally, when cod have disappeared from the upper water layers because of winter cooling, large numbers can be taken on the prawn grounds, where *Pandalus borealis* is the main food.

COD PURSUING THE CAPELIN INTO THE FJORDS IN THE EARLY SUMMER

In West Greenland large shoals of capelin (*Mallotus villosus*) migrate into many of the fjords for spawning, and in Southwest Greenland they are often pursued by cod. Both when the capelin before spawning swim in shoals over the deeper parts of the fjords and coastal waters and when they gather near shore to spawn, one can follow the cod hunting them right up to the surface (Hansen, 1949, p. 40), and investigations of cod stomachs show that they are full of capelin. During this period it is often difficult to catch cod with jig or long-line, as they pay no attention to the hooks, even when baited with fresh capelin. Therefore, some years ago, gill nets were used in some fjords in Holsteinsborg and Sukkertoppen districts, and now pound nets have replaced them. After some experiments in 1948 and 1949 the pound net fishery became rather important since 1950 in all districts in Southwest Greenland from Holsteinsborg to Nanortalik.

In some threshold fjords with cold bottom water the local stocks of cod are small, but when the spawning capelin arrive they may be followed by great quantities of coastal cod. That is the case in the Ameralik Fjord in Godthåb district, where a successful pound net fishery was undertaken in 1951 from the beginning of June. At this time 221 stomachs were investigated and 187 were full of capelin.

In the threshold fjord, Tasermiut, in Nanortalik district an interesting experiment was undertaken by The Royal Greenland Trading Company in May 1960. Pound nets were used in seven different places, first in the outer part of the fjord after which they were gradually moved to the inner part. In every place where the nets were set many big cod were taken at the beginning, but then they disappeared and were replaced by small cod, and in this way it was possible to follow the migration of the cod into the fjord. In these catches two cod were recaptured, both of which had been tagged 2 years before outside the fjord.

In some years cod may not follow capelin to the shore if the water there is unusually cold. That happened in the Amerdloq and Ikertoq Fjords after the extremely cold winter of 1948-49, and in the above-mentioned Ameralik Fjord in 1954 (Horsted and Smidt, this symposium).

COD FOLLOWING THE LAUNCE OFF THE COAST IN THE SUMMER

The launce (*Ammodytes lancea*) is a very important food of the cod, especially later in the summer and mainly over the banks, where examinations of cod stomachs reveal large quantities of launce (Hansen, 1949, p. 41, later observations). In July and August large shoals of cod are found over the banks, and in some years a northward migration has been observed over Lille Hellefiske Bank. In 1931 Hansen (*loc. cit.*) had the opportunity of observing such a migration when the weather was calm

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and the water like a mirror. The cod were moving northward with the dorsal fins visible. In addition the marking experiments on cod that year indicated a northward migration. Flocks of kittiwakes (*Rissa tridactyla*) followed the shoals and could be seen diving after the launce, and cod taken by the research cutter were full of launce.

COD FEEDING NEAR THE SHORE IN SUMMER AND IN AUTUMN

During many years cod marking experiments have been carried out at different localities in Greenland waters. We have found that some of these localities when visited at certain times of the year always offer a good fishery.

An example is the locality Kap Egede near Nanortalik (60°08'N.45°25'W.) where the cod fishery is extremely good in August and September every year. It is a matter of experience, however, that one has to be very close to the skerries and the rocks to obtain the best catches. If the cutter drifts away from the skerries and the shore, the fishery quickly diminishes and one has to move back to the shore to get a good catch again. Within distances of about 100 m the output is completely different. Due to breakers and the rocky bottom anchoring is impossible, so one has to make many trips of some few hundred meters back to the skerries during a day's fishing. The same phenomenon is reported by Faroese fishermen who, in August and September, have a dory fishery in the fjords and coastal region of Cape Farewell.

In the same coastal region many birds are seen at this time of the year, especially flocks of kittiwakes, fulmar petrels (*Fulmarus glacialis*) and greater shearwaters (*Puffinus gravis*). These birds are often seen to be very active close to the skerries and small islands while at the same time flocks are resting on the water some distance away. This indicates that their food animals, which may be the same as those of the cod, are concentrated near the shore.

In late August 1961, a trip with the research cutter was made to Nanortalik Bank. The farther away from the coast the less birds were observed. On the echo sounder few fishes were noted. The fishery with jig at the Bank was very poor and no fishing vessels were observed offshore. Obviously the cod migrates from the offshore regions to the coastal area in late summer and this migration is a feeding migration. The food animals of the cod are evidently concentrated close to skerries, small islands and points where breakers and currents keep the water agitated. Probably this agitated water contains small organisms which serve as food for bigger animals and these in turn as food for cod.

Examination of stomach contents has shown that euphausiids, small capelin and Arctic squid (*Gonatus fabricii*) are the most common food animals at this locality.

This phenomenon is observed every year in the Cape Farewell-Julianehåb region but is also observed occasionally in other localities in West and East Greenland (Paul Hansen, personal communication).

A similar phenomenon is often observed in connection with big icebergs, especially when an iceberg is stranded (Rodewald, 1955; Joensen, 1962). Cod are often concentrated at the lee side of the icebergs probably because of upwelling water which contains food organisms. This phenomenon is reported from East as well as from West Greenland. Joensen (*loc. cit.*) presumes that amphipods, which are often found at the icebergs, are the main food animals for the cod here. This is in accordance with observations made by Paul Hansen (personal communication). From Jakobshavn district, Smidt (unpublished notes) obtained information about the same phenomenon from Greenland fishermen, who report that prawns are the main food for the cod at the icebergs. But prawns in the fisherman's terminology may include different crustaceans of some size.

COD FEEDING ON PRAWN GROUNDS IN WINTER

During the winter cooling of the upper water layers cod stay in the warmer deep water, and then large numbers can be taken on the prawn grounds (about 250 to 400 m depth) with the prawn trawl. Stomach investigations have shown that prawns (mainly *Pandalus borealis*) are of great importance as food for the cod there.

Annual investigations have been made on a prawn ground in the inner part of the Godthåb Fjord (at Kapisigdlit) and on a ground in the coastal region south of Godthåb. On both grounds the depth is about 250 m. Below are shown the average numbers of cod taken per hour's trawling with the prawn trawl in each month in the years 1953-62. Most of the cod from the ground in the fjord were bigger than 40 cm in length, while most of those from the coastal area were smaller than 40 cm.

AVERAGE NUMBERS OF COD PER HOUR'S TRAWLING ON PRAWN GROUNDS

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Inner Godthåb Fjord	64	115	61	22	13	6	5	8	21	13	40	47
South of Godthåb (coastal area)	479	430	207	41	5	1	0	3	0	33	74	342

It must be remembered that in winter cod stay in the deep water primarily to escape the cold surface water, and also that the great concentration on the prawn ground at Kapisigdlit in the Godthåb Fjord at the beginning of the year is partly the result of a spawning migration, as this fjord branch is the most important spawning place for the cod stock in the Godthåb Fjord and perhaps the Greenland fjords as a whole.

REFERENCES

HANSEN, PAUL M. 1949. Studies on the biology of the cod in Greenland waters. *Rapp. Cons. Explor. Mer.*, 123: 1-82.

HORSTED, Sv.Aa. and ERIK SMIDT. 1964. Influence of cold water on fish and prawn stocks in West Greenland. *This symposium Contribution No. A-3.*

JOENSEN, J.S. 1962. Pollur's fiskeriforsøg ved Østgrønland. *Skr. Danm. Fisk.-og Havunders.* 22: 91-93.

RODEWALD, M. 1955. Klima und Wetter der Fischereigebiete West-und Süsgrönland. *Dtsch. Wetterd. Seewetteramt*, p. 80.

C-2

FOOD AS A FACTOR OR INDICATOR OF VERTICAL MIGRATIONS OF COD IN THE WESTERN GULF OF ST. LAWRENCE[1]

By

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ABSTRACT

Systematic 24-hour samplings and echo-location of cod, their stomach contents and their pelagic food supply on and 6-9 m above bottom with a bipartitioned otter-trawl and gill-nets were repeated bimonthly from May to October 1960-62 at a single 110 m deep station off Baie des Chaleurs. Two types of cod vertical migrations were detected: (1) The classical nocturnal type, bringing cod in midwater at night, occurring from mid-July to fall, and on which data are limited. (2) A residual type, detected from May to mid-July and bringing more or as many cod in midwater during the day than at night. Echo-location, the seasonal proportion of cod taken 6-9 m above bottom, late spring scarcity of cod and abundance of main pelagic prey (capelin, euphausiids), 24-hour correlations between cod catch and proportion of benthic prey eaten, all provide some evidence that pelagic prey swarming in the maximum June daylight act as visual stimuli attracting cod to midwater from the bottom. Pelagic spawning is another possible but as yet less documented cause.

INTRODUCTION

1. General Knowledge on Cod Vertical Migrations

It is well known that cod perform vertical migrations, becoming pelagic during certain periods of time (Rasmussen, 1954, 1957, Ellis, 1956, Trout, 1957, Lacroix, 1960, Templeman and Fleming, 1962, and my own observations). It seems that, depending on the time scale considered, two types of vertical migrations can be distinguished in the literature: (a) the well-known migrations of the classical nocturnal type, carrying the fish to midwater at night and bringing them back on or near the bottom during the day; and (b) a yearly period during which the fish assume a pelagic behaviour which keeps them in midwater for extended periods of time (Trout, 1957, Ellis, 1956, Templeman and Fleming, 1962.). This type of migration would be a side-effect of the more basic depth change of the cod stock, which seems to occur with little reference to the bottom (Trout, 1957). The nocturnal type of migration would be superimposed on the annual type, and might (Trout, 1957) or might not (Templeman and Fleming, 1962) bring the cod in contact with the bottom during the day, depending on circumstances.

The significance of these vertical migrations is not yet well understood. Their ecological function may have to do with annual horizontal migrations (Trout, 1957, Templeman and Fleming, 1962); it may be trophic, (Konstantinov, 1958) enabling the fish to make contact with large schools of pelagic animals concentrated under the thermocline (Rasmussen, 1957) or with shoals of spawning capelin at the surface or inshore (Templeman and Fleming, 1962); it may serve spawning (Brawn, 1961) and hence egg dispersal purposes; or it may simply serve to bring the fish into a water mass with more favourable temperatures, in the case of the annual pelagic behaviour. The possibility that McLaren's (1963) recent theory of the adaptive value of zooplankton vertical migrations might be extended to fish should also not be overlooked. Whatever the function of such migrations, their importance to fisheries and to a better understanding of the biology of cod and of the ecology of the sea cannot be denied.

The direct cause of this migratory behaviour of cod is not known. Photoperiodism has been suggested (Trout, 1957). Appetitive behaviour toward aggregations of prey, the inner spawning urge, (Brawn, 1961), thermopathy (Jean, 1964) are also possibilities which are implied in the literature.

Although a large number of the publications on cod food are descriptive, many of them based on qualitative observations, the attention of researchers had been focused early on the relation between

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cod migrations, both vertical and horizontal, and preys found in the stomachs. The pelagic or benthic habits of these food organisms were reasonably assumed to play some role in the pelagic or benthic behaviour of cod, and hence on the fishing yield.

That this role is one of direct causation or has a trophic function, however— capelin, herring or euphausiids attracting cod in midwater— is implicit, and sometimes explicit, in several works. While such causation is certainly not unlikely, the evidence for it is usually not given. When some hints are offered, the evidence is generally circumstantial: the schools of cod and those of their prey occur together in space and time, as determined by observations which are often qualitative, heterogeneous, or otherwise difficult to compare. Direct visual witnessing of cod chasing prey in shallow inshore waters has been reported (Templeman, 1948), but this evidence is still mostly circumstantial. Drobysheva (1957) claims that this causal relation has been demonstrated by Russian authors for the Barents Sea cod. However, Konstantinov (1958), referring to this previous Russian work and using new data, still ascribes only secondary importance to food organisms as stimuli which may modify the basic pattern of light-dependent nocturnal vertical migrations. In all the works that I have examined up to date, the data have been collected or are presented in such a way that it is not possible to isolate prey as the most probable explanation of the migrations: it can only be said that pelagic cod have eaten the prey most readily available where they had migrated (Lacroix 1960). Exceptions to this, showing that cod may have actively pursued capelin to the Newfoundland shore too fast to allow another explanation, are mentioned by Templeman (1948, p. 134) and Templeman and Fleming (1962, p. 465-466).

The main difficulty with the study of pelagic and benthic feeding of cod is that of determining accurately enough the level at which the prey are swallowed by the fish. This problem is twofold:

(a) While the typical pelagic habit of such prey as herring, capelin and euphausiids does not need demonstration, the widespread occurrence of nocturnal or other types of vertical migrations in these species makes it necessary to demonstrate that they have been preyed upon at a given level, for a given sample. The extent to which herring, capelin, euphausiids and other pelagic forms can approach and stay close to the bottom is not well known. Euphausiids are definitely known to do so (my own observations), and since they are preyed upon by herring and capelin, the latter two fish could conceivably migrate down to the bottom for feeding on them, especially in shallow water. Conversely, the extent to which such swimming but typically benthic forms as shrimp, amphipods, mysids, can leave the bottom is not well known either. Whereas such forms, in their breeding season, have been shown to migrate at night into the plankton from the infralittoral benthos (Fage, 1933), almost nothing definite seems to be known of such behaviour in deeper water, besides the fact that it can occur. To obviate these difficulties, it is necessary to sample or otherwise measure, directly and simultaneously with the fishing process, the distribution and abundance of the species preyed upon, in addition to examining them in the stomachs of the fish.

(b) The digestion time of different types of prey may vary from 5-6 days in the case of a fish meal to 3-3½ days in the case of a *Gammarus* meal (Karpevitch and Bokova, 1937). This means that, for a sufficiently fine discrimination of the relation between the distribution or abundance of cod and the composition of its food, much less importance must be given to highly digested fish, eaten too far back in time at an undeterminable level, than to highly digested small crustacea, for instance, and less to the latter than to undigested crustacea. Assuming that weight in the stomach is roughly inversely proportional to digestion time, a useful *ad hoc* quantitative index of stomach contents must therefore emphasize weight (or volume) of each category of prey. Frequency (occurrence) and number of individuals, alone or together, are unsuitable measurements for such purposes.

2. Previous Local Work

Tremblay (1948) first examined in 1946-47 the seasonal changes of cod feeding on Miscou Bank and near Grande-Riviere, in the mouth of Baie des Chaleurs, in the western Gulf of St. Lawrence. A similar survey of the feeding of cod on the same fishing grounds was made in 1951-54 by Corbeil (1953, 1956), assisted by the writer, who further analyzed the data later (Brunel, 1960). This work showed the possible importance of euphausiids in affecting the fishing yield of cod. It was therefore followed by studies which demonstrated the local occurrence of well-defined nocturnal vertical migrations of the larger euphausiids (Lacroix, 1960, 1961) and cod (Lacroix, 1960), occurring in July and August (later months not studied) in the presence of a sharp thermocline. Powles (1958) also studied cod feeding in the area in 1955-56, and made limited inferences on pelagic feeding of very young cod.

3. Objectives

The present work was then undertaken (Brunel, 1961, 1962, 1963) to investigate the cause of these migrations, with special reference to the water layer close to the bottom. An attempt was made to overcome some of the limitations of other works by (a) a thorough daily, seasonal and yearly study of a single environment selected so as to eliminate as many variables as possible, and (b) a systematic comparison between the natural quantitative distribution of the species preyed upon, their quantitative importance in the cod stomachs, and the distribution of cod itself.

Cod populations appear to behave differently in the Canadian than in the European Atlantic. Not only are their migrations and distribution more extensive on the European side (Templeman, 1962, Martin and Jean, 1964), but their feeding behaviour seems to differ in two important aspects: (a) whereas feeding stops during the spawning period (Zatsepin and Petrova, 1939, summarized in Zenkevitch, 1963) in the Arcto-Norwegian cod stock, these two processes can apparently occur together and on the same summer grounds in the western Gulf of St. Lawrence (Lacroix and Marcotte, 1961, Jean this symposium; (b) as a probable result of its extensive migrations, the Arcto-Norwegian cod stock undergoes a varied feeding cycle both in time and space, according to which immature fish feed mainly on capelin and herring in February-April, on euphausiids in July-August, and on herring and other fish in October-December (Zatsepin and Petrova, 1939, Petrova-Grinkevitch, 1957). In the Gulf of St. Lawrence, this cycle seems to be compressed, capelin and euphausiids being preyed upon together in June-July (present work). Furthermore, the cod populations becoming pelagic in spring and summer on the American side of the Atlantic can apparently be split in two parts by the negative temperatures of the cold intermediate layer distributed off eastern Newfoundland (Templeman and Fleming, 1956) and in the Gulf of St. Lawrence (Boulanger, 1958). This situation is not reported from the European Atlantic to my knowledge. There is thus a probability that the process of vertical migration may be different in the two regions, and whatever the results obtained with European cod, therefore, the present work was indicated.

Since a full report on this research is in preparation, only a preliminary summary of the results obtained so far is given below. Although the data on the simultaneous samples of prey and those relating food with fish size have not yet been sufficiently analyzed, some interesting information is already available. In the present contribution, "diurnal" refers only to daytime, rather than to the whole 24 hour period, and "nocturnal" only to night-time.

MATERIAL AND METHODS

Information was sought from May to October 1960-62 on the pattern and causes of cod vertical migrations by systematic day and night sampling and echo-location of (a) cod, (b) its stomach contents, and (c) supply of swimming prey, on the bottom and at 6-9 m above, with a horizontally bipartitioned otter-trawl and pair of gill-nets fishing simultaneously at a single locality with uniformly cold (-0.5 to 1°C) water and muddy bottom, at a depth of 110 m (60 fathoms). The advantages of this atypical cod habitat outweighed the disadvantages. From 5,859 cod taken, 2,791 stomachs were examined for food weights and numbers.

RESULTS

Slightly larger fish were caught above than on the bottom (Table 1), at night and in the day and irrespective of seasons. Larger fish were caught in 1960 than in 1961-62, in part because of larger trawl mesh size.

Cod abundance (3 to 175 fish per 1-hour tow; average: 47) was sometimes low enough to handicap sampling somewhat, but apparently without greatly affecting the results. A period of decreased catches centered on June, followed by an increase in July-August,occurred in the 3 years. Lowest June catches occurred in 1962, highest in 1960 (Fig. 1).

First inspection of echograms reveals, in June, more cod in midwater in the day, and, in July-August, more pelagic cod at night. Trawling generally caught more cod in day tows than in night tows from mid-July to October, but mostly more or as many in night tows from May to mid-July, indicating more nocturnal vertical migrations in summer than in late spring. (Fig. 2). The bipartitioned trawl and gill-net pair caught fewer cod above than on bottom at night and in the day, this difference being more pronounced from mid-July to September than earlier (Fig. 3). The trawl and gill-nets segregated cod above and on bottom in a seasonally similar pattern (Fig. 3). Two types of vertical migrations, one nocturnal, the other "residual", are thus distinguished.

TABLE 1

COMPARATIVE SIZE DISTRIBUTION IN 1960-62 OF TOTAL COD CATCH AND OF COD EXAMINED FOR FOOD AT STATION D112N FROM 5 MAY TO 30 AUGUST

Figures are percentages of the total number of cod.

		1960	1961				1962			
			Otter-trawl				Otter-trawl			
	Length classes (cm)	Otter-trawl	Upper half	Lower half	Total	Gill nets	Upper half	Lower half	Total	Gill-nets
Total cod catch	11-30	2.6	4.8	14.6	10.7	0	0	7.2	6.0	0
	31-50	46.6	72.9	68.8	70.4	26.9	64.4	62.8	63.1	13.6
	51-70	44.4	20.2	15.3	17.2	62.3	33.0	28.0	28.9	75.7
	71 +	6.4	2.1	1.4	1.7	10.8	2.5	1.9	2.0	10.7
	Number of individuals	2222	1052	1629	2681	167	118	568	686	103
Cod examined	11-30	1.3	0.8	7.6	4.5	0	0	8.9	6.4	0
	31-50	32.7	66.2	63.6	64.8	26.5	61.8	46.8	50.7	17.5
	51-70	50.0	28.7	25.1	26.7	62.7	35.1	40.3	39.1	71.4
	71 +	16.0	4.3	3.7	4.0	10.8	3.1	4.0	3.8	11.1
	Number of individuals	1058	512	621	1133	166	97	274	371	63

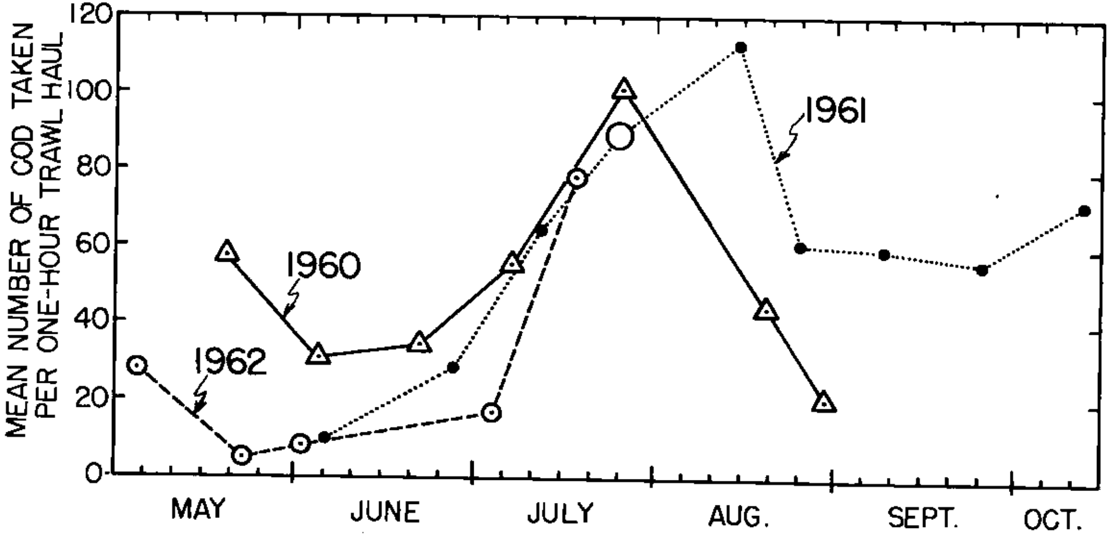

Fig. 1. Seasonal and yearly variations in the cod catch at station D112N in 1960-62. Each symbol represents the average between the mean day catch, based on four (1960) or three (1961-62) tows (one on 1 May 1962, two on 25 September 1961), and the mean night catch, based on two tows (one on 12 October 1961 and one on 1 May 1962). Since no night tows were made on 25 July 1961, the large circle represents an estimate based on a night catch computed as being 60% of the day catch. A 100 mm mesh cotton cod-end was used in 1960, being later covered inside with a 19 mm-mesh cotton (1961) or polythene (1962) liner.

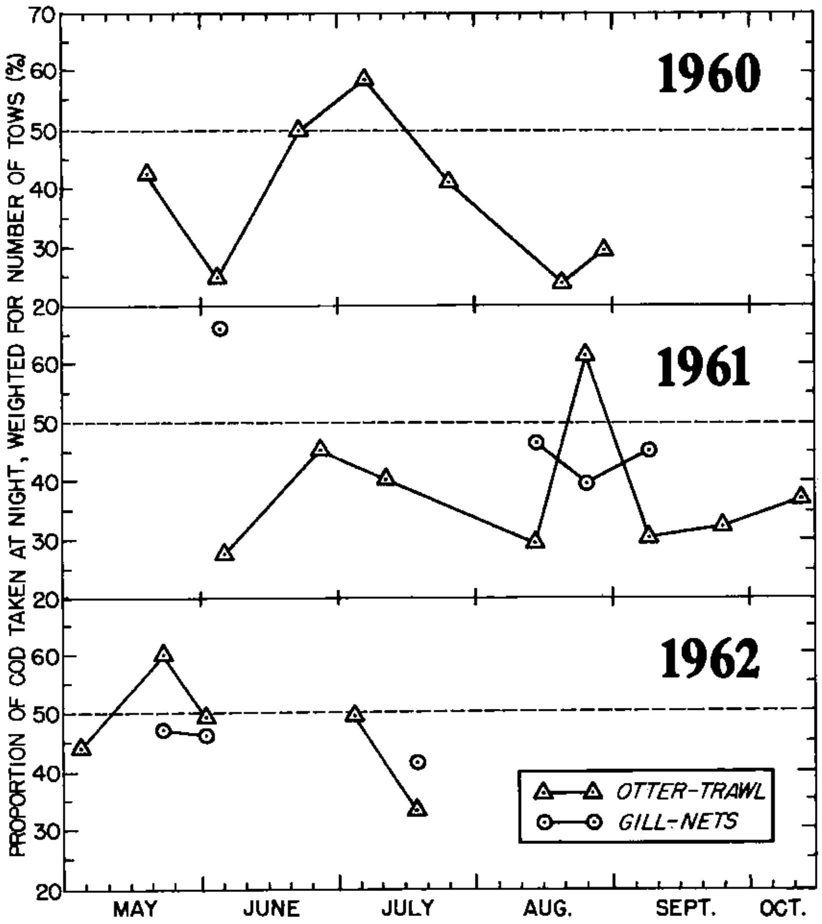

Fig. 2. Seasonal fluctuations in 1960-62 of the extent of the nocturnal vertical migrations of cod in midwater, as indicated by the difference between the mean day catch and the mean night catch at a single locality.

Herring, capelin and euphausiids, in that order, were the most important pelagic prey by weight in the cod stomachs. In 1960-62, seasonal fluctuations of weights of capelin and euphausiids were closely similar, and both showed a period of maximum abundance in June or early July (Fig. 4). *Meganyctiphanes norvegica* replaced *Thysanoessa inermis* as the dominant euphausiid in 1953, 1954 and 1961, and tended to show maximum abundance later (July) than *Thysanoessa*. In the stomachs, herring seasonal abundance was generally inversely related to that of capelin and euphausiids (Fig. 4).

INTERPRETATIONS

Local occurrence of nocturnal vertical migrations of cod from mid-July to fall agrees with other published evidence. The data give little information on their cause but pelagic spawning cannot be excluded.

The residual vertical migrations detected from late spring to mid-July are better documented by the data. The pursuit of pelagic prey is the most probable cause, with five types of evidence: (a) Cod trawled or gill-netted a short distance above bottom were more abundant during the day than at night (Fig. 3), which agrees with its visual feeding habit (Bateson, 1890), and not with its pelagic spawning in darkness (Brawn, 1961). Also in agreement is the seasonal change in the pelagic catches of night trawl tows compared with that of night gill-nets fishing partly in the maximum June daylight but not later (Fig. 3). (b) In the day, cod taken above bottom had eaten more capelin

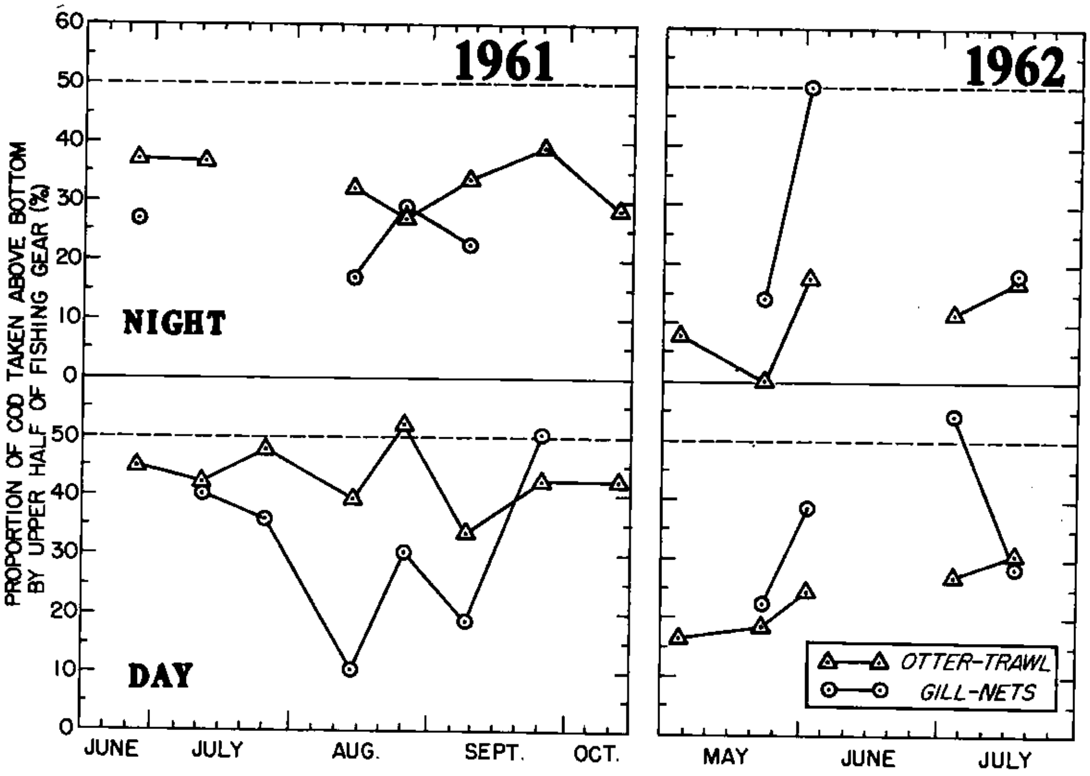

Fig. 3. Seasonal fluctuations in 1961-62 of the extent of the vertical migrations of cod in the vicinity of the bottom (up to 9 m from the bottom), at night and in the day, as indicated by simultaneous fishing at a single locality with a horizontally bipartitioned otter-trawl and with a pair of gill-nets set on and above the bottom.

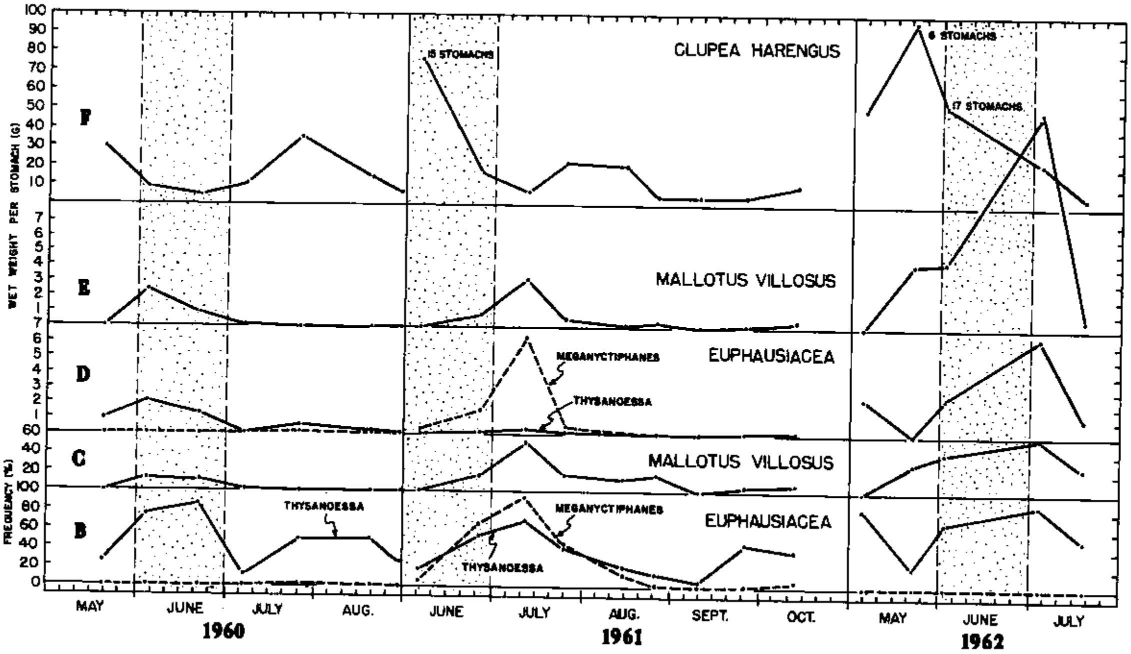

Fig. 4. Seasonal and yearly variations, from 1960 to 1962, of the frequency and wet weight of the three main categories of pelagic prey in the stomachs, euphausiids (B,D), capelin (C,E) and herring (F). Each dot is typically based on 5-6 one-hour trawl hauls, made within 24 hours, and, except as noted, on a sample of at least 50 stomachs (typically about 130) of cod longer than 30 cm (A-E), or 28 stomachs (typically about 50) of cod longer than 50 cm (F). June is stippled for easier comparison between years.

and euphausiids than had bottom cod, but had eaten less at night. (c) Direct echo-location recorded more fish in midwater during the day in June and more pelagic fish at night in July-August. (d) The smallest cod catches in June coincided with maximum abundance of pelagic prey and yearly differences in these two variables coincided also. This indirect evidence is consistent with evidence from commercial and exploratory cod catches showing fish at this time to be pelagic over deep water and relatively concentrated on shallow grounds. (e) The total cod catch of individual tows is positively and imperfectly correlated (Fig. 5), on a 24-hour basis, with the relative proportion of benthic prey by weight in the stomachs (herring and other pelagic prey larger than capelin and euphausiids, being digested more slowly, are excluded,) when capelin and euphausiids are seasonally plentiful and herring are scarce (Fig. 4). This seasonal pattern was less clear in 1961, when *Meganyctiphanes* replaced *Thysanoessa* as the dominant euphausiid. Two hypotheses may account for the latter facts: (1) Cod being visually and gradually attracted upward from the bottom by capelin and euphausiids, they become more strongly attracted to higher levels by the larger herring, and scatter with them, disturbing the basic and measurable pelagic pattern between cod, capelin and euphausiids. (2) Possibly, different pelagic habits of *Meganyctiphanes* obscure the relation in 1961.

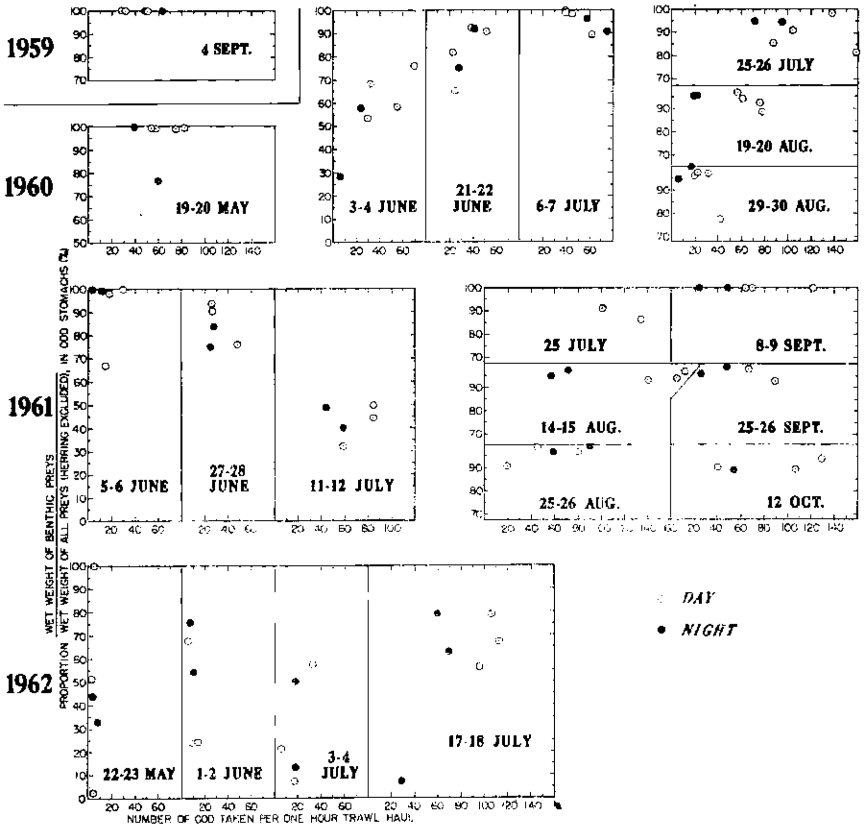

Fig. 5. Relation between the abundance of cod in the vicinity of the bottom and the proportion of benthic prey in their stomachs. The same locality, 10 miles southeast of Grande-Rivière, at a depth of 60 fathoms, was used throughout, except in 1959.

The evidence for spawning as a cause of the residual vertical migrations is both insufficient and weaker than that for food. Cod spawn pelagically in darkness (Brawn, 1961). Possible maximum local spawning in May or June (Powles, 1958) coincides with maximum residual vertical migrations on a seasonal but not nocturnal basis. Larger cod (of spawning size?) were more numerous a short distance above than on bottom, but were only slightly so both at night and in the day and in summer also. Spawning may account better for summer nocturnal vertical migrations, but difficulties remain.

Uniform temperatures and salinities of the sampled water mass and its remoteness from internal tidal waves occurring higher up, practically exclude these factors as causes of the residual vertical migrations.

Whatever the cause for the residual migrations, the data show that food composition can serve as a relatively accurate indicator of cod vertical movements.

Cod are known or thought to exhibit pelagic behaviour in their spring migrations into northern and shallower waters on either side of the Atlantic (Trout, 1957, Templeman and Fleming, 1962). Suspected causes of these annual vertical migrations are photoperiodism (Trout, 1957)and pelagic prey (Templeman and Fleming, 1962). The late spring residual vertical migrations off Baie des Chaleurs may represent the last phase of these annual vertical and horizontal migrations. Visual preying, proportional to the duration of daylight, on pelagic herring, capelin and euphausiids may indeed be an important mechanism in these migrations, at least in this last phase.

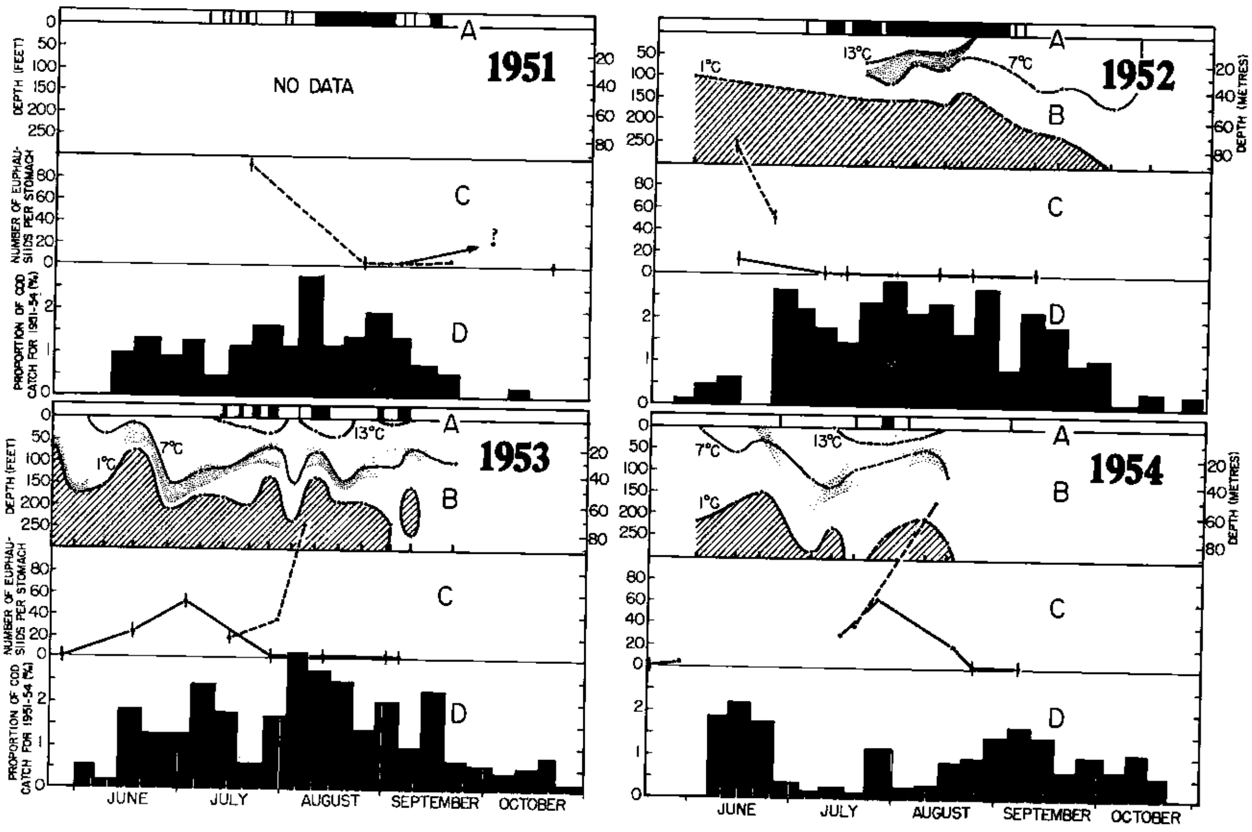

Fig. 6. Seasonal distribution from 1951 to 1954 of (A) days when the surface water temperature at Grande-Rivière wharf was 14°C (average for warmest month of the year from 1938 to 1956) or higher, (B) the depth distribution of three isotherms and the thermocline (stippled areas) at station 112, five miles off Grande-Rivière, (C) the abundance of euphausiids in samples of 25 stomachs of cod taken on or near Miscou Bank (solid line) and Orphan Bank (broken line), and (D) the relative fishing yield of the same eight long-liners from Grande-Rivière fishing on or near Miscou Bank.

In 1951-54 (Fig. 6), poor fishing in 1954 by eight local long-liners coincided on a seasonal and yearly basis with (a) a large weight of euphausiids in stomachs of cod caught on the same grounds, (b) relatively high temperatures in the intermediate cold water layer, (c) relatively cold surface waters above a poorly defined thermocline. Good fishing in 1952 was related to the opposite of these factors, other years being intermediate. These relations may be interpreted as reflecting unavailability to the fishery of cod feeding pelagically on euphausiids, but some difficulties of interpretation subsist. The occurrence of *Meganyctiphanes* in the warmer years 1953 and 1954 may have significance (Drobysheva, 1957). Hopes of better results with more research are justified.

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REFERENCES

BATESON, W. 1890. The sense-organs and perceptions of fishes: with remarks on the supply of bait. *J. Mar. biol. Ass. U.K.*, 1 (3): 225-256.

BOULANGER, J.-M. 1958. Le facteur température et les pêcheries du Bas-Saguenay. *Actualités mar.*, 2(1): 13-18, 28.

BRAWN, V.M. 1961. Reproductive behaviour of the cod (*Gadus callarias* L.). *Behaviour*, 18(3): 177-198.

BRUNEL, P. 1960. Analyse des données sur l'alimentation de la Morue de 1951 à 1954. *Rapp. Sta. Biol. mar. Grande-Rivière*, 1959: 57-62 (mimeo.).

1961. Variations journalières de l'alimentation de la Morue au large de Grande-Rivière en 1960. *Ibid.*, 1960: 86-95 (mimeo.).

1962. Variations journalières et saisonnières de l'alimentation de la Morue au large de Grande-Rivière en 1960-61. *Ibid.*, 1961: 85-104 (mimeo.).

1963. Variations journalières et saisonnières de l'alimentation de la Morue au large de Grande-Rivière, 1960-62. *Ibid.*, 1962: 101-117 (mimeo.).

CORBEIL, H.E. 1953. Analyse du contenu stomacal de la morue *Gadus callarias*. *In* Rapp. ann. Stat. Biol. mar., 1952, *Contr. Dépt. Pêch. Qué.*, (43): 13-18.

1956. Analyse du contenu stomacal de la morue (*Gadus callarias*). *In Ibid.*, 1953, (50): 48-59.

DROBYSHEVA, S.S. 1957. (The effect of some aspects of the biology of Euphausiacea upon the summer feeding conditions for cod in the Barents Sea). *Trudy PINRO*, 10: 106-124. (*Fish Res. Bd. Canada, Transl. Ser.*, No. 224, 1959).

ELLIS, G.H. 1956. Observations on the shoaling behaviour of cod (*Gadus callarias*) in deep water relative to daylight. *J. Mar. biol. Ass. U.K.*, 35 (2): 415-417.

FAGE, L. 1933. Migrations verticales périodiques des animaux benthiques littoraux. *Rapp. Cons. Explor. Mer*, 85: 60-69.

JEAN, Y. 1964. Seasonal distribution of cod (*Gadus morhua* L.) along the Canadian Atlantic coast in relation to water temperature. *This symposium, Contribution No. A-2.*

KARPEVITCH, A.F. and E.N. BOKOVA. 1937. (The rate of digestion in marine fishes, part 2). *Zoologitcheskii Zhurnal*, 16 (1): 28-44.

KONSTANTINOV, K.G. 1958. (Daily vertical migrations of cod and haddock). *Trudy VNIRO*, 36: 62-82. (Translation: Sta. Biol. mar. Grande-Rivière).

LACROIX, G. 1960. Migrations verticales des Euphausides et de la Morue à l'embouchure de la baie des Chaleurs en 1959. *Rapp. Sta. Biol. mar. Grande-Rivière*, 1959: 27-32 (mimeo.).

1961. Les migrations verticales journalières des Euphausides à l'entrée de la baie des Chaleurs. *Nat. Can.*, 88 (11): 257-317.

LACROIX, G. and A. MARCOTTE, 1961. Variations régionales et saisonnières de l'alimentation de la Morue (*Gadus morhua* L.) à l'entrée de la baie des Chaleurs. *Ibid.*, 88 (10): 225-235.

MCLAREN, I.A. 1963. Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration. *J. Fish. Res. Bd. Canada*, 20 (3): 685-727.

MARTIN, W.R. and Y. JEAN. 1964. Winter cod taggings off Cape Breton and on offshore Nova Scotia banks, 1959-62. *J. Fish. Res. Bd. Canada*, 21 (in press).

(PETROVA-) N.S. GRINKEVITCH. 1957. (Year-to-year changes in the food of cod in the Barents Sea). *Trudy PINRO*, 10: 88-105. (*Fish. Res. Bd. Canada, Transl. Ser.*, No. 223, 1959).

POWLES, P.M. 1958. Studies of reproduction and feeding of Atlantic cod (*Gadus callarias* L.) in the southwestern Gulf of St. Lawrence. *J. Fish. Res. Bd. Canada*, 15 (6): 1383-1402.

RASMUSSEN, B. 1954. On the Norwegian pelagic long-line fishery in the Holsteinhorg Deep - 1953. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 4 (3): 40-45.

1957. Norwegian research report, 1956. *Ibid.*, 7 (3): 41-48.

TEMPLEMAN, W. 1948. The life history of the Capelin (*Mallotus villosus* O.F. Müller) in Newfoundland waters. *Nfld. Govt. Lab., Fish Res. Bull.*, 17: 1-151.

1962. Divisions of cod stocks in the Northwest Atlantic. *Int. Comm. Northw. Atlant. Fish. Redbook* 1962, Part II: 79-123.

TEMPLEMAN, W. and A.M. FLEMING. 1956. The Bonavista longlining experiment, 1950-1953. *Bull. Fish. Res. Bd. Canada*, (109): 1-55.

1962. Cod tagging in the Newfoundland area during 1947 and 1948. *J. Fish. Res. Bd. Canada*, 19(3): 445-487.

TREMBLAY, J.-L. 1948. Recherches sur la Morue, année 1947. *Rapp. Stat. biol. St.-Laurent.* 7 (1947): 13-19.

TROUT, G.C. 1957. The Bear Island cod: migrations and movements. *Fish. Invest., Lond.* (2), 21 (6): 1-51.

ZATSEPIN, V.J. and N.S. PETROVA. 1939. Pitanie prom'islov'ikh kosyakov treski v iujnoi tchasti Barentsova Morya ("The feeding of the cod in south part of the Barents Sea"). *Trudy PINRO*, 5: 1-171.

ZENKEVITCH, L.A. 1963. *Biology of the seas of the USSR*. London, G. Allen & Unwin Ltd., 955 p.

C-3

SOME INSTANCES OF COD AND HADDOCK BEHAVIOUR AND CONCENTRATIONS IN THE NEWFOUNDLAND AND LABRADOR AREAS IN RELATION TO FOOD

By

Wilfred Templeman[1]

ABSTRACT

At St. John's from mid-June to early August cod caught in the commercial fishery at 13-38 m ed almost entirely on capelin. From August 19 to 27 November the cod from the commercial fishery, ow at 55-130 m, fed mainly on bottom invertebrates especially crustacea. Spider crabs were over 0% of the crustacean food. Although capelin were not important as food at this time, cod and ome other fishes were, but mainly for the large cod. The onshore migrations of capelin for spawning appear to be the main reason for cod movement in June from their offshore wintering and spawning to their inshore feeding locations on the east and southeast coasts of Newfoundland.

In Ungava Bay small Greenland halibut, capelin, euphausiids and shrimp were important cod food t various depths.

On the offshore part of the Labrador Shelf in late July-early August the largest concentrations f cod were in cold water and associated with heavy feeding on adult capelin, whereas in deeper and armer water other cod schools may have been held together by feeding especially on scaled lancet ish and on lantern fishes. The size of the food was related to the size of the fish, the largest ish feeding mainly on cod and wolffish 35 cm or over in length. The fish prey was evidently obained by pursuit and taken tail first.

The early April cod concentrations on the eastern slope of Hamilton Inlet Bank were mainly on-feeding and were held together by pre-spawning and post-spawning schooling. The early May ainly post-spawning concentrations in the same area were feeding more heavily, almost entirely n portions of cod discarded by trawlers and this may have helped to hold the schools together or t least make them more related to the bottom.

On the northern Grank Bank in late March the food of the main concentrations in cold water as adult and young capelin.

On Flemish Cap in late March cod concentrations were feeding mainly on young cod at the shalower and young redfish at the greater depths.

Haddock on the Southeast Shoal of the Grand Bank in July-August accumulate, often in great umbers, on capelin spawning grounds in sandy areas, to feed on capelin eggs and capelin.

COD

. St. John's

A study was made of the stomach contents of cod, *Gadus morhua* L., from the inshore area at t. John's which is typical of the east coast of Newfoundland. The cod samples were obtained immediately after capture by the inshore fishermen and from the gears and depths normally used by he fishermen at the time (Table 1). Food was measured volumetrically by water displacement.

A sample of cod obtained on 19 May had only 14% capelin, *Mallotus villosus* (Müller), and the emainder mainly bottom food.

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TABLE 1. STOMACH CONTENTS OF RANDOM SAMPLES OF COD FROM COMMERCIAL NEWFOUNDLAND, MAY-NOVEMBER 1947-51. (A LINETRAWL IS

Year	Date	Depth	Method of capture	Total cod in sample	Range of length of cod (snout-midfork)	Total food except bait
		m		*no.*	*cm*	*cc*
1949	19 May	38	Trap	29	41-70	134
1951	14 June	27	Trap	100	31-80	3,315
1949	21-22 June	27	Trap	112	31-80	3,707
1951	26-27 June	20-27	Trap	82	31-100	8,390
1948	30 June-2 July	15-17	Trap	95	31-80	9,606
1947	17-18 July	13-18	Trap	111	41-110	6,422
1948	3-5 Aug.	15-33	Trap	76	31-80	1,771
1947	19-22 Aug.	75	Linetrawl	58	51-110	1,391
1949	31 Aug.	75-110	Linetrawl	55	41-100	313
1949	12 Sept.	75	Handline	50	41-90	1,165
1948	24-27 Sept.	75-110	Linetrawl	86	41-100	981
1947	25 Sept.	80-90	Linetrawl	39	41-90	125
1947	20-21 Oct.	75-90	Linetrawl	80	39-100	866
1948	25 Oct.-1 Nov.	55-130	Linetrawl	105	31-120	3,699
1948	15-18 Nov.	55-130	Linetrawl	109	41-110	4,662
1949	21 Nov.	75-110	Linetrawl	56	31-120	2,330
1949	25 Nov.	75-110	Linetrawl	55	41-150	2,685
1947	25-27 Nov.	110-130	Linetrawl	93	41-140	8,328
% of total food	14 June-5 Aug.	13-33	Trap	476	31-110	33,211
% of total food	19 Aug.-27 Nov.	55-130	Linetrawl and handline	786	41-150	26,545
% of total food	19 May-27 Nov.	13-130	Trap, linetrawl and handline	1,291	31-150	59,890

TABLE 1. (continued)

INSHORE FISHERMEN FISHING MAINLY WITHIN 7 NAUTICAL MILES OF ST. JOHN'S,
A LONGLINE HAULED BY HAND USUALLY FROM A SMALL BOAT.)

Per cent of total food (except bait)													
Coelenterates	Annelids (total)	Crustaceans (total)	Spider crabs (total)	Shrimp	Molluscs (total)	*Cyrtodaria siliqua*	Echinoderms	Other invertebrates and red algae	Fish (total)	Capelin	Cod	Digested animal material	Bait % of total food + bait
%	%	%	%	%	%	%	%	%	%	%	%	%	%
	0.4	37.0	35.7	0.7	47.8	44.8			14.8	14.4			-
0.3	0.1	2.6	1.9	0.2	0.2		0.1	0.03	96.6	96.3			-
		2.6	0.3	1.6	0.1				97.2	97.2		0.08	-
		1.2	1.2						98.8	98.8			-
	0.01	0.6	0.04	0.01					99.4	99.3	0.1		-
	0.007	0.8	0.3	0.01	0.04			0.2	97.2	88.8	8.4	1.8	-
		0.9		0.9				0.5	97.0	94.3	0.7	1.6	-
2.7	0.2	42.0	33.2	6.0	8.2	1.3	1.4	0.1	32.3	14.9	17.3	13.0	41.6
		47.0	45.4	1.6	19.4	18.2			33.6	33.6			61.5
		26.6	24.0	2.4	12.7	12.0			60.7				28.9
0.9	0.3	63.2	48.1	14.9	2.3	0.9	0.6		28.1	6.5	10.7	4.5	61.5
2.6	1.6	68.6	43.6	22.3	1.0		1.7		10.4		8.4	14.0	79.1
	0.3	32.9	26.5	6.0	3.8	2.3	6.6	1.7	52.4	23.1	25.5	2.4	28.9
1.6	0.5	62.1	54.8	6.3	4.2	2.4	0.9		29.2	1.5	25.3	1.6	9.7
0.8	0.7	60.7	53.4	6.8	3.8	3.4	1.2	0.4	32.6	1.7	11.4		27.9
1.0	0.9	83.3	80.0	3.3	6.9	6.4	0.3	0.3	7.5	3.2	1.3		40.4
0.1	0.03	31.0	26.9	3.4	16.6	16.6	0.01		52.3	0.3	39.7		25.9
0.2	2.2	53.6	36.1	17.0	1.4	1.0	2.7	0.02	38.8	0.8	12.9	0.9	3.6
0.03	0.01	1.2	0.6	0.3	0.04		0.01		98.2	96.4	1.7	0.4	
0.7	1.0	54.2	44.3	9.3	5.4	4.4	1.6	0.1	35.5	3.2	15.9	1.5	26.1
0.3	0.5	24.8	20.0	4.3	2.5	2.1	0.7	0.1	70.2	54.9	8.0	0.9	

From 14 June - 5 August (Table 1) the cod fed pelagically on capelin (89-99%). Especially large quantities of capelin were found in the stomachs from 26 June to 2 July. Whereas the trap samples with great quantities of capelin were all taken in shallow water (13-38 m) in which the cod could readily maintain contact with the pelagic capelin, in all samples from 19 August to 27 November at depths of 55-130 m capelin lost their importance as cod food and their place was taken chiefly by bottom invertebrates especially crustacea. Fish other than capelin also assumed considerable importance. Of these the most important in the St. John's area was cod but spiny dogfish, lumpfish, herring and mackerel were also important. Most of the quantities of fish food of this period, however, came from the stomachs of the largest cod which were not present in the shallow trap area. These occasionally had a large cod, dogfish or adult lumpfish in their stomachs and therefore several stomachs in a sample usually provided most of the fish food. There was also a large amount of bait, usually squid, herring or mackerel in the stomachs of these deep-water cod. The cod, eventually hooked by the linetrawls, apparently often managed to take bait from a number of hooks before they were caught. Crustacea and especially spider crabs made up most of the bottom food after 19 August (54% and 44% respectively of total food). In the deeper water feeding of 19 August - 27 November shrimp and molluscs had some importance (shrimp 9.3 and molluscs 5.4% of total food) and the bank clam *Cyrtodaria siliqua* (4.4% of total food) was the most important of the molluscs with whelks supplying half the remaining molluscan food. Polychaetes made up 97% of the 0.5% of annelid food for the whole period. In the 60% of the spider crabs identified by genus or species 48% were *Chionoecetes opilio* and the remainder *Hyas araneus* and *Hyas coarctatus*.

2. Ungava Bay

In Ungava Bay 4-6 September 1959 (Templeman, 1960) cod were found in small amounts, from 10 to 100 kg per tow. (All catches reported in this paper except where otherwise noted are from half-hour tows of a bottom otter trawl of the *A.T. Cameron*. See Templeman and May (this symposium, A-10) for details of ship and trawl, etc. At 365 and 275 m adult capelin predominated in the stomachs and small Greenland halibut, euphausiids and shrimp were also important. The Ungava Bay cod, when feeding on Greenland halibut, ate almost entirely the small 8-12 cm specimens whereas large Greenland halibut feeding on their own species often took individuals of 20 or 25 cm long. At 183 m the most important food was Greenland halibut about 9-12 cm long. Sometimes there would be 20-30 or more of these in a single stomach. At 110 m mysids predominated in the food.

3. Labrador

In sets on the seaward slope of the Labrador Shelf off Port Manvers, about 57°N on 31 July - 1 August 1960 (Templeman, 1961) no capelin were present in cod stomachs and the largest catches of cod at 183, 225, 274, 320 and at 373 m, were respectively: 100 kg at -0.7°C; 125 kg at 0°C; 75 kg at 0.4°C; 135 kg at 3.5°C; and 40 kg at 4.3°C. The most common food in the full stomachs at all these depths from 225 to 373 m was the scaled lancet fish (*Paralepis coregonoides borealis* Reinhardt) about 27-30 cm long. There were sometimes four or more *Paralepis* in one stomach.

In a group of sets on the seaward slope of the Labrador Shelf east of Cape Makkovik at about 55°30'N on 4 August 1960 (Templeman, 1961) the following differences were found in cod food and cod concentrations. At 143 m (30 kg, average weight 0.3 kg, -0.6°C) most of the cod were small, 20-30 cm long, and were feeding almost entirely on amphipods, whereas the larger cod, all below 60 cm long, were feeding entirely on adult capelin. In sets at 181-194 m (450 kg, average weight 1.1 kg, -0.8°C); 230 m (730 kg, average weight 0.9 kg, -0.6°C) and 271-285 m (315 kg, average weight 0.9 kg, 1.4°C) about 95-98% of the food consisted of large adult capelin and the remainder mainly of scaled lancet fish (*Paralepis coregonoides borealis*). These scaled lancet fish were in the larger cod, especially of about 60 cm and over, whereas the capelin were more numerous in the smaller fish. The largest cod in these three sets, however, were feeding on still larger fishes and five between 92 and 136 cm long had five cod 35-48 cm and one striped and one spotted wolffish each 35 cm long in their stomachs.

It was unusual to find a scaled lancet fish in the trawl although the codend liner of 29-mm nylon mesh would have retained them. These scaled lancet fish were all about the same size, 27-30 cm, no small fish being present either in the cod stomachs or in the lined codend. The adult capelin were about 14-21 cm long.

The heads of the scaled lancet fish, cod and wolffish in the cod stomachs pointed forward toward the oesophagus. The heads of the capelin also usually pointed forward, but whereas the heads of the scaled lancet fish were long and hard enough to retain their forward position, the smaller and softer capelin could be turned around or across a large stomach and hence need not be in the stomach in the tail first position in which they were swallowed. Apparently the fish are caught by pursuit, and increasing sizes of fish are able to pursue and capture increasing sizes of food. Also all the fishes swallowed by the cod were whole and not bitten off and the size and depth of the mouth must be important.

In the deeper sets in this area, 324, 368 and 452 m (with catches of only 12, 5 and 4 kg, average weight 0.9 kg and at 1.0 to 3.3°C), the typical stomach contents were scaled lancet fish and lantern fishes.

In this area east of Makkovik the cod were feeding pelagically and the largest quantities of cod were associated with the shallower low temperature region of abundant capelin.

On the seaward slope northeast of Hamilton Inlet Bank, about 54°45'N, 8 August 1960 (Templeman, 1961) in a set at 183 m (830 kg, average weight 1.6 kg, -0.3°C) the cod were feeding well and about 98% of the stomach contents were adult capelin with about 1.5% spider crabs and about 0.5% shrimp and amphipods. At 230 m (1360 kg, average weight 3.1 kg, -0.2°C) the stomachs contained over 95% adult capelin. The remainder consisted mainly of pelagic amphipods with a few small fish feeding almost entirely on amphipods.

At 274 m (250 kg, average weight 1.1 kg, 3.7°C) in the larger cod about 90% of the food consisted of scaled lancet fish (about 27-30 cm long, sometimes four or more in one stomach), about 8% lantern fish, about 1% of pelagic amphipods and less than 1% capelin. The smallest cod were not examined but presumably would have contained more lantern fish and amphipods.

Here again as in the more northerly section off Cape Makkovik the greatest concentration of cod was in the shallower depths with low temperatures where capelin were numerous. Also in the most northerly line at 57°N where there were no capelin and the principal food was scaled lancet fish cod were not plentiful. Apparently the scaled lancet fish were plentiful and an excellent supplementary source of food to the capelin especially in the deeper and warmer water of the seaward slope of the Labrador Shelf but the cod were more attracted in quantity to the presumably more numerous and, for the smaller cod, more easily caught capelin. These inhabit colder and shallower water than the scaled lancet fish.

The main cod feeding in all sections and depths was pelagic. In early April 1963 on the eastern slope of Hamilton Inlet Bank there were large spawning and post-spawning concentrations not brought together by food (Templeman and May, this symposium). On 9 April at 320 m (610 kg, average weight 0.9 kg, 75% of the mature females spent, 2.6°C) in a sample examined 48 cod had empty stomachs, 34 stomachs had an average of less than 1 cc of food, usually amphipods, polychaete worms and small brittle stars and three contained an average of 195 cc of discarded cod viscera, heads, backbones and discarded small cod from trawlers.

In a sample from the greatest catch on 9 April at 274 m (2,450 kg, average weight 0.9 kg, 43% of the mature females spent, 2.6°C) 45 stomachs were empty, 31 had less than 1 cc of natural food, usually amphipods, polychaete worms and small brittle stars, and six had an average of 350 cc of cod viscera, heads, backbones and discarded small cod from trawlers.

From the catches of small fish and invertebrates in the lined net there appeared to be very little natural food in the areas of these large cod concentrations. Very likely much of the local bottom food supply was eaten in the winter period when these cod were probably feeding more heavily, and the small redfish, lantern fishes, eelpouts, grenadiers, etc. inhabiting these depths in summer had apparently gone deeper in winter and early spring.

Later on 2-3 May 1963, in this same area in heavy concentrations of mainly post-spawning cod (2,600 - 4,800 kg per half-hour set and over 85% of the females spent; Templeman and May, this symposium) the cod were feeding more heavily, almost entirely on cod offal being dumped by the very large concentration of trawlers (over 90 visible within a 10-nautical-mile radar range of the *A.T. Cameron*.

4. Northern Grand Bank

On the northern Grand Bank on 28 March 1961 (Templeman, 1962) large quantities of fish, probably cod and capelin, were noted on the echo sounder (Fig. 1). Eight sets were taken between 185 and 666 m. Cod were abundant at 185-190 m (3,610 kg at 1.2°C). These were mainly adult prespawning cod, not expected to spawn for a month or two, and were feeding well, the large and medium cod feeding mainly (about 95%) on adult and young (10-12 cm) capelin. At 230 m, there was a significant but smaller catch of cod (1,340 kg at 2.0°C) and about 90% were feeding chiefly on 10-12 cm capelin with smaller numbers of adult capelin. Evidently in this area the cod and capelin were most plentiful near and shallower than 190-210 m (Fig. 1A) and in deeper water gradually came off

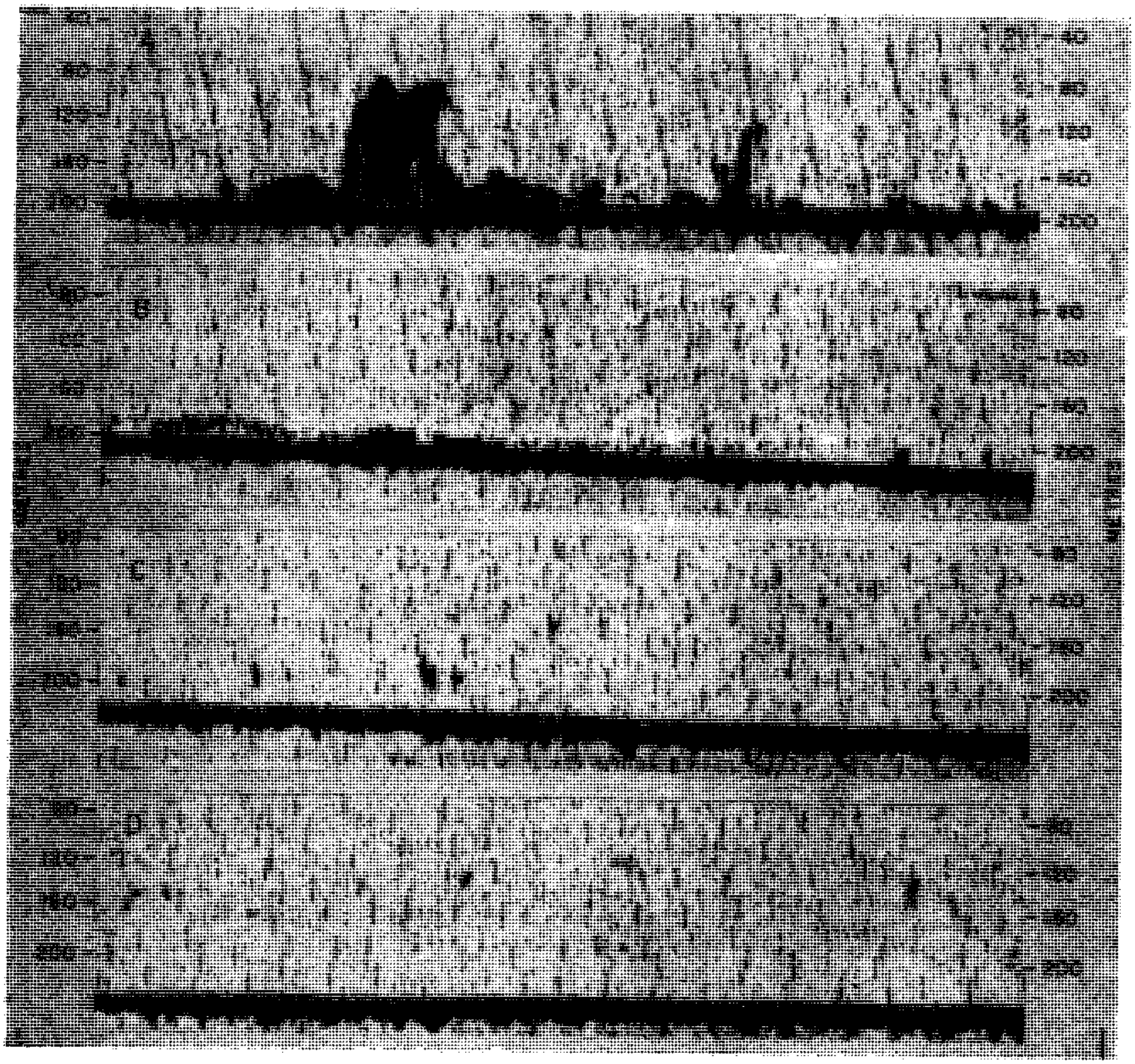

Fig. 1. Echo-sounder records of cod and very likely capelin, northern Grand Bank, 28 March 1961. A, half-hour tow at 185-190 m (3,610 kg cod); D, half-hour tow at 230 m (1,340 kg cod); B and C, ranging from end of A to beginning of D.

bottom so that in the 230-m set (Fig. 1D) no fish concentrations were visible. However, there was still a 1,340 kg catch of cod. This makes it possible that most of the fish visible in Fig. 1A were capelin.

In still deeper water at higher temperatures and progressively lower than the capelin concentrations cod were scarcer, decreasing from 300 kg in a set at 274 m (2.3°C) to 45 kg in a set at 433 m (3.6°C).

5. Flemish Cap

On the southeastern slope of Flemish Cap, 23 March 1961 (Templeman, 1962) the cod, almost all post-spawning, were feeding well and were evenly distributed (450, 370 and 390 kg per set) at 183, 234 and 282 m with a greater concentration (860 kg) at 395 (356-433) m. Temperatures ranged from 3.4 to 4.1°C. In this moderately high temperature area the capelin, usually associated with large concentrations of feeding cod in the Newfoundland area, were absent. Small cod and small redfish were abundant but the young redfish were deeper than the young cod. In the 183 and 234 m depths the small cod formed 80-85% of the food of the medium and larger cod. The stomachs of the smaller cod mainly contained 10-15 cm cod and the stomachs of larger cod more usually 20-25 cm cod. At 282 m and at 395 (356-433)m cod of 50 cm and over contained 95 to 98% small redfish mainly about 10-12 cm long.

6. Discussion and Conclusions

There are many publications on the food of cod and of other commercial groundfishes but relatively little has been written on the effect of food in determining cod concentrations. Great concentrations of pre-spawning and spawning cod may exist, feeding very little and brought together presumably by the schooling instincts existing at this time. The food seeking activities of the hungry post-spawning fish will, however, inevitably scatter these schools unless brought together by the process of feeding on great stores of food. The most favourable of these for cod concentration are the abundant small fish such as capelin which themselves occur in large schools.

In eastern Newfoundland and in Labrador the success of the great inshore fishery appears to depend greatly on the actions of the cod in relation to the schools of capelin. Almost all the cod are spent and are feeding on capelin before the capelin move shoreward pelagically to spawn in late June.

Cod tagged on the western slope of the Grand Bank in 68-93 m on 4-5 June 1948, were spawning or spent and were feeding heavily on capelin. Several weeks later when capelin came inshore to spawn, four of these tagged fish were recovered between 26 June and 12 July on the western part of the Avalon Peninsula during the capelin spawning season. These cod approached shore so quickly that they probably followed the pelagic capelin from the Grand Bank to the shore of the Avalon Peninsula (Templeman and Fleming, 1962). Since the cod of the east coast of Newfoundland and Labrador spend the winter and spring in deep water often far from the coast and do not feed heavily in the pre-spawning period the success of the inshore shallow-water fishery in summer is likely to depend largely on the quantities of hungry spent cod which make contact with the pelagic capelin and follow them to shore.

In Newfoundland capelin advance shoreward in June to spawn. On the east coast this spawning in quantity usually begins in the last third of June, occurs at first on the fine gravel of the beaches and beach spawning continues into early July. After the beach water becomes too warm the capelin spawn progressively deeper in July and August to at least 40 m (Templeman, 1948).

Some cod may approach the coast before the arrival of the great masses of spawning capelin. On parts of the coast this is called the herring run because herring are available on the coast in May and early June before the capelin arrive in shallow water to spawn.

The main bodies of cod on the east coast of Newfoundland also pass shoreward in June from the deeper offshore wintering and spawning areas. These hungry, mainly spent and immature cod follow the capelin inshore, apparently pelagically in the warming surface layer over the cold, below 0°C, water of the intermediate layer (Templeman and Fleming, 1956; Templeman and May, this symposium). At this time many of the cod come so close to shore that often, especially at night or on dull days, they may be caught from the beach.

During the period when capelin are most abundant cod feed almost entirely pelagically on capelin. At this time especially during the mass offshore movement of weakened spent capelin in July, several weeks after the beginning of spawning, the cod, so full of capelin that they can eat no more, lie lazily on or near the bottom ("logy" in the fishermen's expression) and are not readily available to baited hooks or jiggers. In shallow water cod schools have been observed to make a circle around the jigger and to avoid jigger and baited hooks. With cod in this replete condition traps, and in recent years nylon gillnets may still obtain large catches, but sometimes the cod move so little that trap catches also decline greatly. Fishermen agree that during this period a breeze of wind or a strong tide is needed to stir the fish up and make them throw up their food. After the storm line fishing improves. Mr A.M. Fleming, at Bonavista on 26 July 1949, noted a great improvement in the hook and line cod fishery at 35 m and deeper following a storm of northwest wind lasting several days. The cod also had very little food in their stomachs although large amounts of capelin had been present in cod stomachs sampled before the storm. Wave motion may cause the fish in shallow water to empty their stomachs through sea-sickness (McKenzie, 1935), and Newfoundland fishermen say that they have seen cod in shallow water empty their stomachs of capelin after a storm.

The spent capelin evidently move offshore in July and August or being pelagic become separated from the cod which are at this time moving deeper with the gradual warming, in depth, of the inshore waters.

Cod still pelagic and in association with the capelin at this time are likely to move offshore with them and eventually settle into deeper water. These are mainly lost for that year to the inshore mainly shallow-water fishery by small boats.

The success of the largely line and bottom gillnet fishery after July depends to a large degree on what percentage of the cod become separated in depth from the pelagic capelin and become established in bottom feeding on the shallow inshore grounds before the pelagic capelin and associated pelagic cod move off. The habit of the cod with full stomachs settling near the bottom periodically to digest their food is certain to be a factor in this establishment of bottom feeding. As the distance from the pelagic capelin schools to the increasingly deeper bottom areas with suitable temperatures increases with the season it presumably becomes more difficult for the cod, because of airbladder difficulties, to maintain rapid daily contact with them.

Judging by the data for St. John's it is likely that cod prefer fish food when this is available and, apart from the largest cod, prefer fish of small or moderate size. When concentrations of fish food occur cod may also gather in large numbers in the same area to feed on them. On the other hand cod in certain depths and situations will accept whatever fish or invertebrate, especially crustacean, food is available and thus remain in a situation from which in the absence of suitable food they might have to disperse to other localities.

Presumably (apart from the spawning season and temperature traps) the primary necessity for a cod concentration is a food concentration, especially such massed schools as are provided by capelin and other small fishes when they are abundant. When feeding pelagically the cod probably fill up with pelagic food and sink near the bottom to digest it. If the food school maintains the same general position the cod will readily find food again when it rises after digesting its previous meal. Meanwhile new cod come in contact with the food school and are also retained. If the food school is continually moving in one direction, as when the capelin approach the beaches, the cod to maintain contact must have a tendency at this time to move shoreward also. Many cod may reach the warmer surface layer in the offshore area where the intermediate layer of very cold water does not exist or is very thin. When over very cold water cod may sink only to its upper border. We have noted near Seal Islands, Labrador a large school of cod on the echo-sounder at 25 m lying in water of 5.5°C just above the cold layer with a temperature of -1.1°C at a bottom depth of 50 m. The cod were readily caught by jigging (Templeman and May, this symposium). In either case if cod rise to pursue capelin they will find many schools moving shoreward in early summer and pursuit will move the cod toward shore.

There is a very noticeable preference among larger cod for larger food and this also may allow certain sizes to remain where food of the size they prefer is abundant while other sizes may move and concentrate on a more appropriate size of food. Sometimes, as in the accumulations during spawning season, food is so scarce both in the stomachs and in the area, as judged by catches in the lined codend, that food cannot be a major factor in the concentrations.

In the cod concentrations encountered on the southeast slope of Hamilton Inlet Bank in April-May, 1963, the spawning and recently spent cod in the early April concentrations could not have been held together by food. Only 5% were feeding significantly and hence the concentrations were still spawning concentrations. By 2-3 May, however, when most of the cod were spent, the great amounts of discarded cod offal from the salt-fish trawlers may have helped to concentrate some of the cod on bottom in the area pending the movement of some toward Hamilton Inlet Bank and others probably pelagically toward shore.

HADDOCK

1. Introduction

In the North Sea (Bowman, 1923) haddock in the vicinity of a herring spawning area concentrate on the herring spawning ground and feed on herring eggs but Bowman considers that this is only a local and transitory source of food.

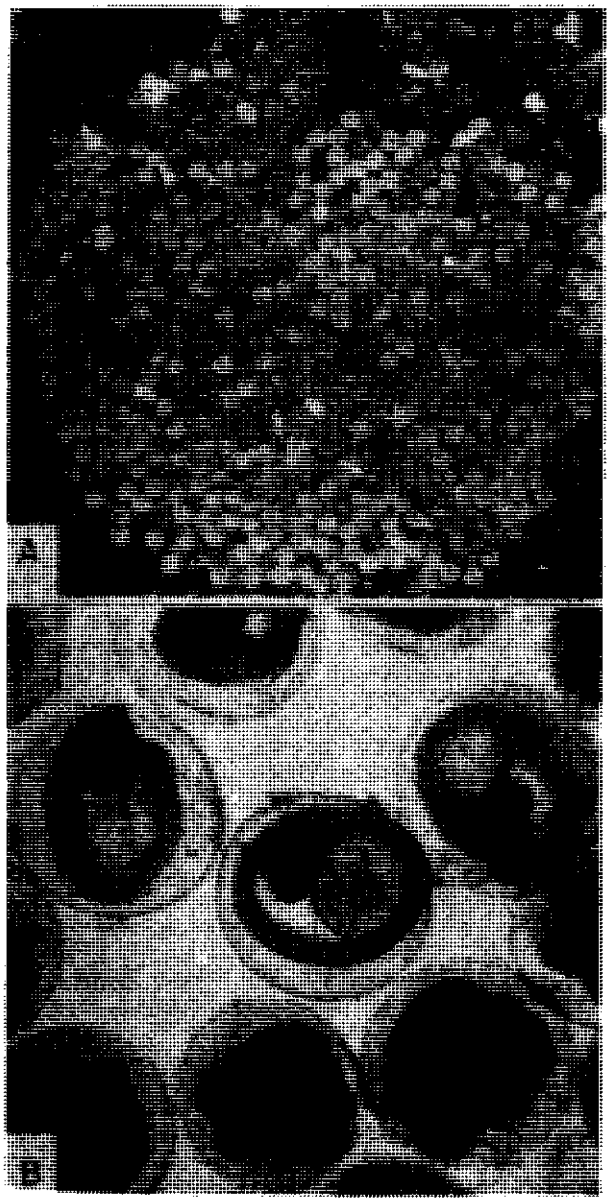

Fig. 2. A, sand and capelin eggs and B, developing capelin eggs from stomachs of haddock from the Southeast Shoal of the Grand Bank. A, August 1950 and B, 15 July 1951. From Pitt (1958).

Rass (1933) found capelin eggs mixed with sand and finely ground shells in the stomachs of haddock from the Barents Sea during capelin spawning which took place usually at bottom depths of 50-100 m and at temperatures of about 2°C.

2. Haddock Concentrations and Capelin Spawning on the Grand Bank

During July and up to the middle of August 1950 there was a very successful Newfoundland and European trawler fishery for haddock, *Melanogrammus aeglefinus* (L.), and cod, concentrated on the Southeast Shoal of the Grand Bank in a capelin spawning area. The Newfoundland otter trawler *Blue Spray* (40 m in length) fishing on the Southeast Shoal of the Grand Bank at about 44°08'N, 50°00'W in 46 m at 2.5 to 2.8°C on 9-12 August 1950, caught haddock and cod for 33, 30- to 45-min, sets at the rate of 7,750 kg of haddock and 2,040 kg of cod per hour's dragging on bottom. At that time about half of these fish were discarded as being too small. At the present time, however, most of these would be retained. There were often large numbers of capelin in the codend.

The haddock were feeding heavily on capelin eggs attached to sand grains (Fig. 2A) and to a lesser degree on capelin while the cod were feeding on the adult spawning capelin. (Capelin spawn usually in contact with the bottom and their demersal eggs of about 1 mm diameter immediately become attached to small gravel or large sand grains. The sand grains found in capelin stomachs on the Southeast Shoal were smaller than the small gravel on which they usually spawn on the beaches (Templeman, 1948).) The concentrations of haddock in the capelin spawning areas and the haddock feeding on capelin eggs, sand and capelin were first noted on 19 July 1950, when haddock from 44°25'N, 50°00'W on the Southeast Shoal were found with both stomachs and intestines containing a large amount of sand mixed with capelin eggs. Many eggs were still attached to the sand grains.

In July 1951 capelin eggs attached to sand grains and in various developmental stages, some with advanced larvae (Fig. 2B), were again found in haddock stomachs from the Southeast Shoal, but fishing was not as successful as in the previous year. Bottom temperatures were higher, 4.2°C on 10 August, 1951.

The numerous small haddock between 23 and 33 cm were feeding relatively more heavily on capelin eggs than the largest fish between 40 and 62 cm which had relatively more capelin (Templeman and Pitt, MS, 1951; FRBC, 1952; Pitt, 1958).

Capelin schools are noted for returning every year to spawn on the same beaches and even the same parts of a beach where the gravel is of a suitable size (Templeman, 1948) and it appears that they also return yearly to the same and probably limited offshore bank areas of sand and gravel.

On a number of occasions between 1952 and 1958 Newfoundland trawlers in July and August went to positions on the Southeast Shoal given to them by the Biological Station as capelin spawning grounds and invariably obtained good catches. The Newfoundland fishery in this area however did not develop greatly due to difficulties in preservation of the fish because of the warm air and water of this period.

From 31 July to 4 August 1959 and from 8 July to 21 July 1960, very large catches of haddock (averaging over 8,500 kg per hour's towing when using a 70-mm-mesh codend) were obtained by the *A.T. Cameron* during alternate-haul mesh-selection cruises to the Southeast Shoal about 44°10'N, 49°44'W and 44°11'N, 49°42'W respectively and with bottom temperatures averaging 2.8 and 3.8°C respectively (Templeman and Hodder, this symposium). These haddock were again concentrated in capelin spawning areas and were feeding on capelin eggs and capelin. Numerous capelin were sometimes caught among the haddock but usually with the large-mesh codends mainly in use in these selection cruises most of the capelin escaped.

The quantities of capelin and haddock available are evident in the echo-sounder records (Fig.3). Small numbers of cod were also present but only negligible numbers of other fishes. The mid-water trace in Fig. 3D is typical of pelagic capelin, and it will be also evident from the discussion of Fig. 4 that large masses of fish on bottom as in Fig. 3B and 3D may be predominantly capelin spawning on restricted patches of sand.

In a relatively few survey sets on the Southeast Shoal with a net lined with 29-mm mesh nylon in July 1961 (Fig. 4) haddock and cod were very scarce in bottom drags during the daytime. There were evidently some of these fish off bottom but the off-bottom traces were much thinner than in the 1959 cruise (Fig. 3). In two sets with heavy bottom traces (Fig. 4A-4D) totals of only 58 and 110 kg of haddock and cod per hour and half-hour tow respectively were taken but, 1,400 and 1,700 kg of spawning capelin were obtained. In another set with heavy bottom traces in which no haddock or cod were taken (Fig. 4E) 1,500 kg of capelin were caught per half-hour's towing. Quantities of other fish were negligible and thus the heavy bottom traces of Fig. 4 must be spawning capelin concentrated as is usual for capelin on small patches of spawning gravel (in this area apparently sand).

Only nine searching sets were made on the Southeast Shoal in July 1961 preliminary to and after a redfish cruise. These were evidently too few or too early for the area surveyed as Soviet trawlers had a successful haddock fishery on the western part of the Southeast Shoal from July to November 1961 (Noskov, MS, 1962). More haddock might have been obtained by our vessel if the dragging had been continued during the night. The large sets of Fig. 3, however, were also in the daytime. The lack of haddock to feed on capelin spawn in recent years since 1961 is very likely to have a significant effect in increasing the capelin population of the eastern and southern Grand Bank and it is easy to imagine that this in turn will significantly increase the consumption of eggs and fry of cod and haddock by capelin.

Noskov (MS, 1962) also found the haddock of the Southeast Shoal of the Grand Bank in July-August, 1961 feeding heavily on capelin eggs and capelin. In early July an average of 5 tons of capelin per haul were taken incidentally to the Soviet haddock fishery in this area.

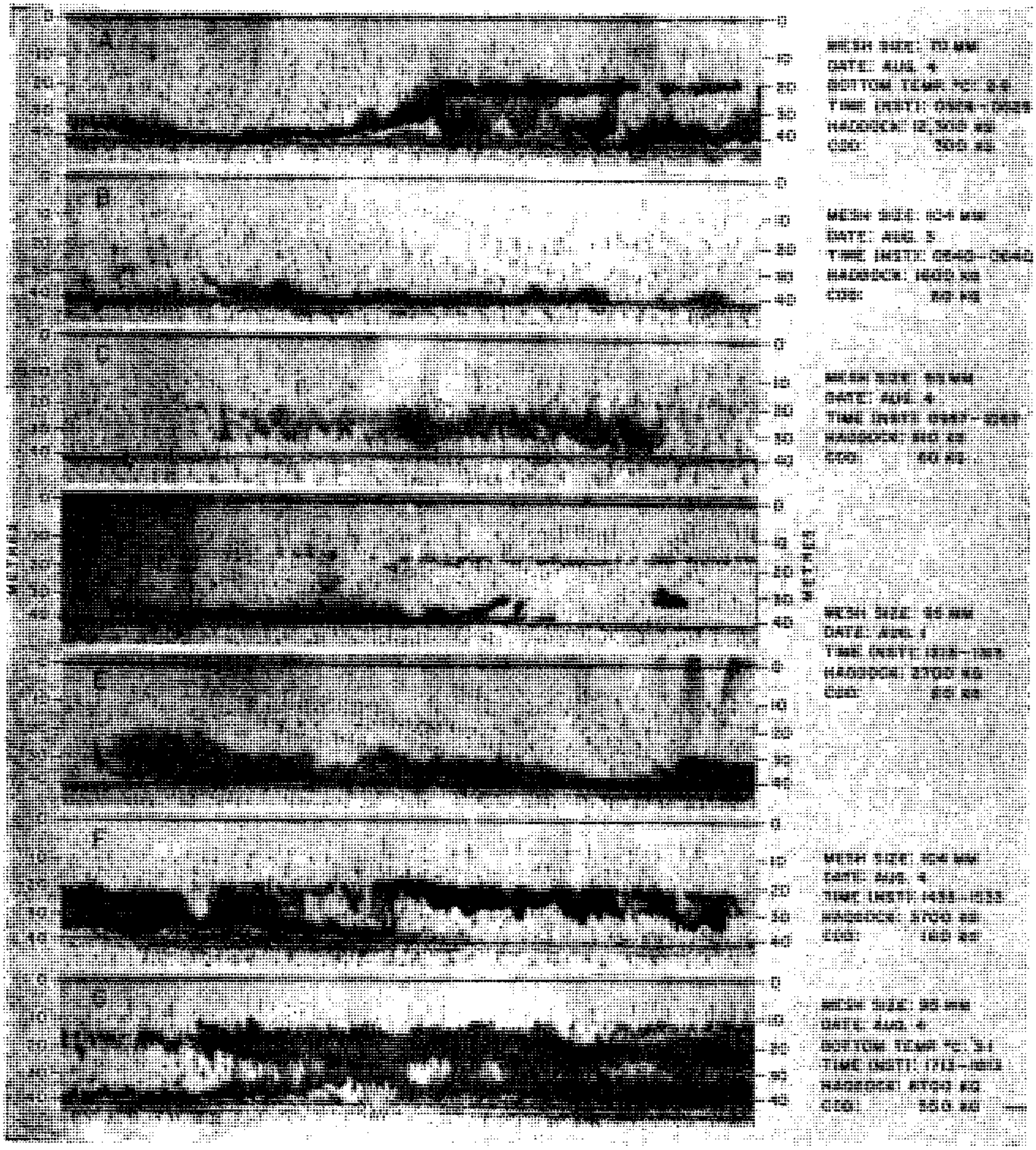

Fig. 3. Surface to bottom echo-sounder records of capelin, haddock and cod and catches of haddock and cod in 60-min bottom otter-trawl tows of the *A.T. Cameron* in 40-46 m, 1-4 August 1959, on the Southeast Shoal of the Grand Bank at 44°09'-44°11'N, 49°42'-49°46'W. (Sections A-G show the most significant 15-min portions of the echo-sounder records of different sets, except that D and E are from the same set. NST = Newfoundland standard time. On the basis of average catches during the cruise, catches should be raised by the conversion factor 2.2 for trawls with 95-mm and 2.5 for those with 104-mm meshes in the codend to render their catches equivalent to those with a codend of 70-mm mesh.)

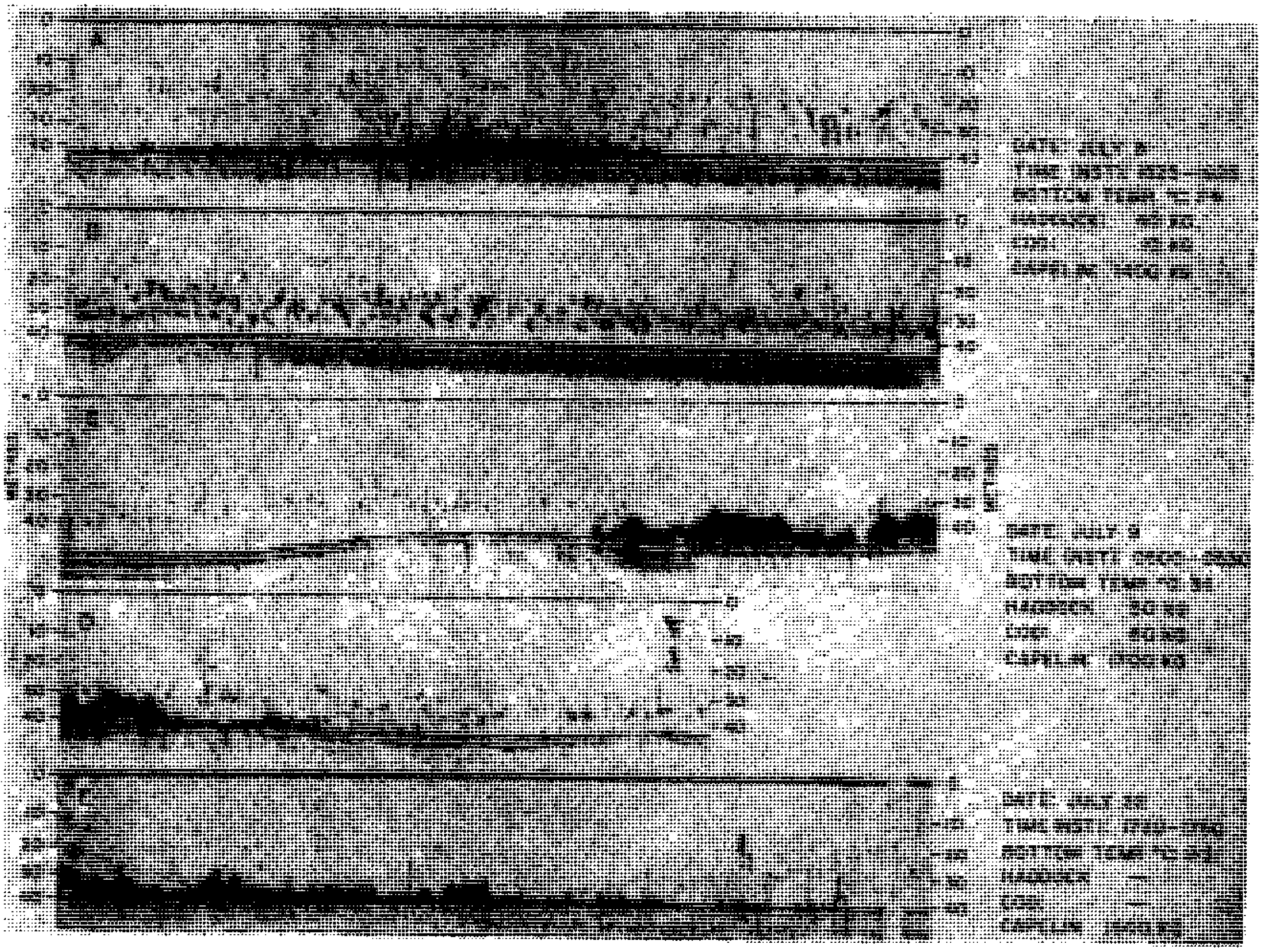

Fig. 4. Surface to bottom echo-sounder records of capelin, haddock and cod in half-hour to 1-hour otter-trawl tows of the *A.T. Cameron* on the Southeast Shoal of the Grand Bank in 38-51 m, 8-22 July, 1961 at 44°03'-44°12'N, 49°40'-49°45'W. (The portions A, B; C, D; E show the most significant portions of three different sets. A + B = 55%, C + D = 100% and E approximately 50% of the record for the set. NST = Newfoundland standard time.)

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REFERENCES

BOWMAN, ALEXANDER, 1923. The occurrence of "spawning" haddock and the locus and extent of herring spawning grounds. *Fish. Bd. Scot. Sci. Inv.*, 1922 No. 4: 1-15.

F.R.B.C. 1952. Report of the Newfoundland Fisheries Research Station. *Ann. Rep. Fish. Res. Bd. Canada for 1951:* 43-65.

MCKENZIE, R.A. 1935. Codfish in captivity. *Fish. Res. Bd. Canada, Prog. Rep. Atl.*, No. 16: 7 - 10.

NOSKOV, A.S., MS, 1962. Haddock observations in the south of the Great Newfoundland Bank. *Annu. Meet. int. Comm. Northw. Atlant. Fish.*, Doc. No. 68, Serial No. 1011: 1-6. (mimeographed).

PITT, T.K. 1958. Distribution, spawning and racial studies of the capelin, *Mallotus villosus* (Müller), in the offshore Newfoundland area. *J. Fish. Res. Bd. Canada*, 15: 275-293.

RASS, THEODOR S. 1933. (The spawning of capelin (*Mallotus villosus* Müll.) in the Barents Sea). *Trudy Okeanogr. Inst.*, 4(1): 3-33.

TEMPLEMAN, WILFRED. 1948. The life history of the capelin (*Mallotus villosus* O.F. Müller) in Newfoundland waters. *Res. Bull. Nfld. Govt. Lab.*, 17: 1-151.

1960. Canadian research report, 1959. A. Subareas 2 and 3. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 10: 19-25.

1961. Canadian research report, 1960. A. Subareas 2 and 3. *Ibid.*, 11: 23-31.

1962. Canadian research report, 1961. A. Subareas 2 and 3. *Int. Comm. Northw. Atlant. Fish. Redbook 1962*, Part II: 3-20.

TEMPLEMAN, WILFRED and A.M. FLEMING. 1956. The Bonavista long-lining experiment, 1950-1953. *Bull. Fish. Res. Bd. Canada*, 109: 1-55.

1962. Cod tagging in the Newfoundland area during 1947 and 1948. *J. Fish. Res. Bd. Canada*, 19: 445-487.

TEMPLEMAN, WILFRED and V.M. HODDER. 1964. Distribution of haddock on the Grand Bank in relation to season, depth and temperature. *This symposium, Contribution No. A-6.*

TEMPLEMAN, WILFRED and A.W. MAY. 1964. Research vessel catches of cod in the Hamilton Inlet Bank area in relation to depth and temperature. *This symposium, Contribution No. A-10.*

TEMPLEMAN, W. and T.K. PITT, MS, 1951. Haddock and cod concentrations due to capelin spawning on the Grand Bank. *Ann. Rep. (mimeo.) Fish. Res. Bd. Canada., Biol. Sta., St. John's, Nfld. for 1951*, App. No. 6, p. 12.

C-4

SOME PROBLEMS IN THE STUDY OF MARINE RESOURCES

By

J.H. Steele,[1]

ABSTRACT

An attempt is made to estimate the production and ecological efficiency of some of the major parts of the food chains in the North Sea.

Some possible relations of food supply to fisheries yield are discussed.

INTRODUCTION

"A system is considered to be scientific only if it makes assertions which may clash with observations; and a system is, in fact, tested by attempts to produce such clashes, that is to say, by attempts to refute it ...Some theories expose themselves to possible refutations more boldly than others. A theory which is more precise and more easily refutable than another will also be the more interesting one. ...there will be well-testable theories, hardly-testable theories and non-testable theories. Those which are non-testable are of no interest to empirical scientists. They may be described as metaphysical."

K. R. Popper, ("Conjectures and Refutations," p. 256).

I was asked to try and write fairly generally about the problem of studying the environment of marine fisheries and the introductory quotation seemed almost too relevant to the forms of argument in which I propose to indulge. Many of us hope that we have passed the stage where observations are collected, tabulated and used as a basis for a verbal generalisation which is still too qualitative to be tested critically. On the other hand, although exact theoretical models can be set up, predictions based on them may not be really testable by present techniques. We (or at least I) accept too readily vague correspondences of excessively simple theories with inadequate and highly variable sets of data.

This problem of metaphysics today - science tomorrow - is certainly the main difficulty and one which will require the development of more sophisticated forms of sampling and also an increase in the role of laboratory experiments directed to ecological problems. Thus the following attempt to set up a very simplified picture of a mainly unknown reality is classifiable as metaphysics. Its only excuse is as a personal attempt to decide which problems may be of most immediate interest; and this may not be a very good excuse.

As an overgeneralisation, the problem can be described as the attempt to discover how much of the sun's energy ends up as commercially exploitable resources, and how this varies seasonally and geographically. As a first step towards reality this can be stated in terms of the rates at which net primary production by plants is converted into present-day fish yields for any roughly self-contained area. This in turn can be stated as the problem of the dynamics of the various trophic levels through which energy passes (Lindeman, 1942). In this field the work of Slobodkin, based on experiments with a herbivore *Daphnia* (Slobodkin, 1959), and more recently a carnivore *Hydra* (reported to the British Ecological Society Jubilee Meeting, March, 1963) together with analyses of field results, supports the classic concept of a fixed "ecological efficiency".

"The ecological efficiency of trophic level x which is fed upon by trophic level $x + 1$ is the food consumption of trophic level $x + 1$ divided by the food consumption of trophic level x.

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"...for all practical purposes ecological efficiency can be considered as a constant. It may be expected that future field estimates will tend to converge on some relatively narrow range of values around 10%".
Slobodkin - "Growth and regulation of animal populations" (1962)

The possible importance of this generalisation in marine ecological studies is obvious and I will make a critical analysis of its application to the North Sea which I will assume is approximately a self-contained unit. This analysis will be very tentative, relying on the combination of inadequate data and excessive guess-work but I hope it may be sufficient to discriminate between two different "pictures of reality" and so between two possible research approaches.

TROPHIC LEVELS IN THE NORTH SEA

The net production of organic carbon by plants, estimated from nutrient and C^{14} uptake, available to higher trophic levels in the northern North Sea is in the range 50-150 g C/m^2/year. I will take an average value of 100 g and assume that 80 g is utilised by pelagic herbivores and 20 g goes to the bottom as detritus, mainly via the superfluous feeding of zooplankton (Beklemishev, 1957).

At the other end of the food chain, details of the commercial yield of fish in the North Sea are obtainable from the ICES Bulletin Statistique (Fig. 1). The pelagic yield excludes Norwegian herring landings during January, February and March which are based on a stock feeding outside the North Sea. The demersal yield excludes the recent German and Danish "industrial" fisheries since they are based mainly on young herring, sand eels and *Gadus esmarkii* which are pelagic feeders. These landings are shown as an addition to the pelagic yield. The demersal values do not show any general trend and have an average value of 0.43 x 10^6 tons/year. The pelagic fisheries show a general increase especially when the industrial landings are included. A value of 1.0 x 10^6 tons/year will be used for the yield based on the most recent landings. Taking the carbon content of fish to be 10% of the wet weight and the area of the North Sea to be 3.3 x 10^5 km^2, these yields are 0.13 and 0.30 g C/m^2/year for demersal and pelagic respectively.

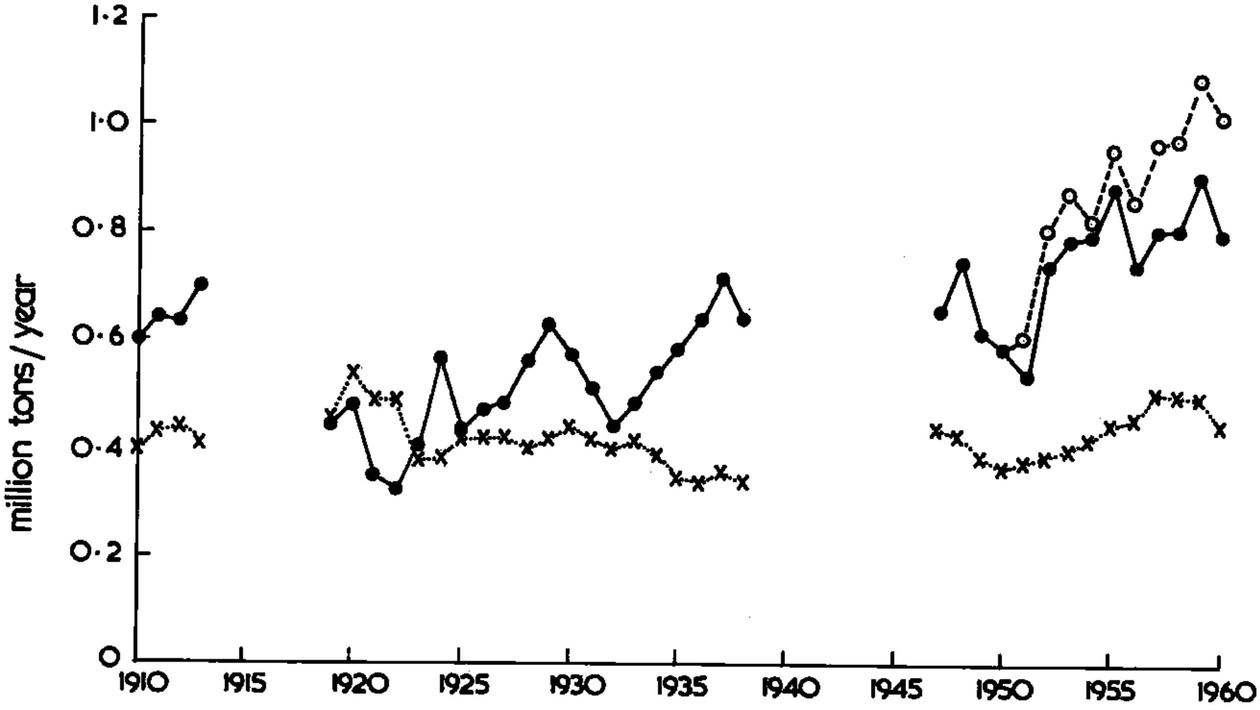

Fig. 1. Fish yields from the North Sea: ...x... demersal; —●— pelagic; - - o - - pelagic plus industrial fisheries.

In addition to the fishing mortality there will be other "natural" causes of death which must be included to give total yield. For haddock, recent estimates (Jones, personal communication) give the fishing mortality as three-quarters of the total mortality. The value used for whiting (Jones, personal communication) appears to be about the same and so this value of three-quarters will be applied to the demersal fisheries to give a total yield of 0.17 g C/m^2/year. For herring which dominate the pelagic fisheries, the estimates of natural mortality are less certain. For the "Bank" stock in the northern North Sea a value of 0.3 has been calculated for the ratio of fishing to total mortality (Parrish and Saville, 1962). For the "Downs" stock in the southern North Sea, the calculated value is 0.7 (Cushing, 1961*a*). A very tentative value of 0.5 is used here to make the total yield 0.6 g C/m^2/year.

If we now assume (a) that herbivores and detrital-feeders yield 1/10 of the original food supply and (b) the food required by pelagic and demersal stocks is 10 times the yield then we obtain the two parts of the food chain shown in Fig. 2.

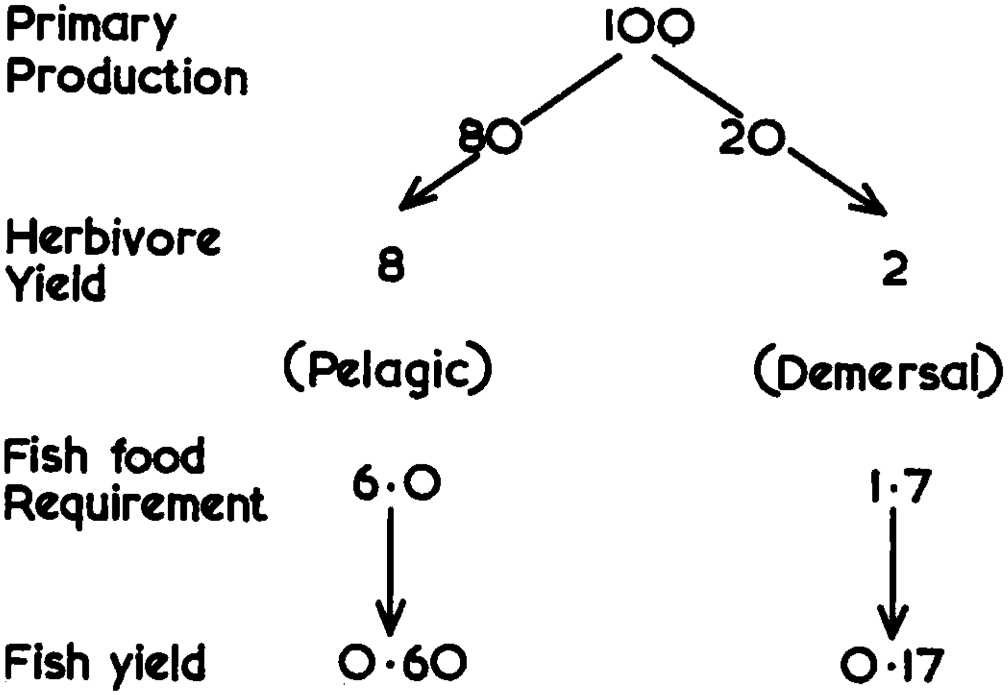

Fig. 2. The herbivore yield deduced from primary production compared with fish food requirement deduced from fish yield (g carbon/year).

The implications of this diagram are obvious. Firstly, there would be only one quantitatively important "trophic level" between plant production and fish yield and this level must be herbivorous (including detritus feeders). Secondly, the more general implication would be that there is a direct relation between the quantity of primary production and utilisable fish yield, so that as a hypothetical extension to other areas one might expect estimates of plant production to provide an index of the utilisable carnivore stocks to be found in these areas. The "picture of reality" consequent on these implications would make estimates of primary production of fundamental importance and would also justify general studies of biomass at different trophic levels in place of more detailed studies of species composition.

The question, for the North Sea, is whether the more detailed knowledge that we have of planktonic and benthic populations would fit into such a simple picture.

1. Zooplankton Herbivores

At present no estimates are available of production by herbivorous zooplankton. The only information is on the dry weight of total zooplankton filtered with nets having 60 meshes per inch. *Calanus* which is dominant in the biomass in the northern North Sea (Adams and Steele, unpublished) has three generations in the six months of the productive seasons and these generations reach stage V about May, July and September. At these times the dry weights are 3-10, circa 3 and 3-10 g/m^2 respectively (Adams, 1963, Adams and Baird, in press). If we take an average value of 6.5 for the spring and autumn and also take the carbon:dry weight ratio as 0.4, then in terms of carbon the population sizes achieved are 2.6, 1.2 and 2.6 g C/m^2. Assuming three generations generally in the zooplankton, then these values would provide a very minimal estimate of the yields during each season. One could reasonably expect the real yield to be two or three times greater than their sum of 6.4 g C/m^2 when grazing is taken into account.

2. Zooplankton Carnivores

The grazing by herring on zooplankton takes place predominantly during spring and early summer and so the earlier estimated food requirement of 6 g C/m^2 is about double the minimal yield for this period deduced from population size in the last paragraph. In the autumn another predator on copepods, *Sagitta* reaches very large numbers when 2,000/m^2 is common over large areas of the northern North Sea (Adams, unpublished). The dry weight of *Sagitta* is about 1 mg and assuming 40% carbon content, the population is equivalent to 0.8 g carbon/m^2.

Again this may be thought of as a very minimal yield, but if this population required 10 times its weight as food then a further 8 g C/m^2 would be needed as herbivore yield.

There are many other predators on the herbivores such as euphausiids, ctenophores, *Gadus esmarkii* and *Ammodytes*. Thus it is apparent that within the three trophic levels, plants - herbivores - pelagic carnivores, there must be efficiencies considerably greater than 10%.

3. Detritus Feeders

Bottom fauna can be divided into three groups dependent on sampling technique (McIntyre, 1956, 1958, 1961): (1) meiobenthos which pass through a 0.5 mm sieve and consist mainly of nematodes and small crustacea, (2) macrobenthos caught by a 0.1 m^2 grab and by the 0.5 mm sieve, (3) epifauna which escape from the grab because of size or mobility and which are the least known group quantitatively.

Studies of meiobenthos in Fladen, Loch Nevis (McIntyre, 1961) and off Cape Cod (McIntyre, unpublished) have shown that this can be a significant fraction of the total not only numerically but even as biomass. The values for Fladen and Loch Nevis are of the order of 0.2 g C/m^2. The macrobenthos in the poorest area (Fladen) is about 0.6 g C/m^2 and in more inshore areas (excluding bottom areas within the euphotic zone) about 1.6 g C/m^2 ; giving a rough average of 1 g C/m^2.

For the macrobenthos in Long Island Sound, Saunders (1956) estimated that the smaller animals produced five times their standing stock in a year and the larger animals twice their standing stock. For a *Mactra* patch in the southern North Sea, Birkett (1959) obtained a factor of 2.5. Thus for the macrobenthos a value of production equal to three times the standing stock is used here to give 3 g C/m^2/year. The much smaller meiobenthos can be expected to have a significantly higher production: standing stock ratio than the macrobenthos. A ratio of 10 would make the calculated meiobenthos production 2 g C/m^2/year.

Ignoring the bacterial populations (which should not be done) the ratio of benthic production to the value of 20 g C/m^2 originally chosen for the detritus implies an efficiency of 25%. Any increase in quantity of detritus available for the bottom fauna will merely decrease the food available for the pelagic stocks. Thus at this trophic level in the demersal communities the data would suggest that a 10% value for efficiency is, again, too low.

4. Carnivorous Benthos

The larger and motile benthos which are poorly sampled are also most important in the food of demersal fish. Data from Jones (1954) gives the food of haddock and whiting by weight as percentages. For example

	Fish	Crustacea	Annelids	Molluscs	Echinoderms
Haddock (31-35 cm)	12	42	12	12	28
Whiting (21-25 cm) Central N. Sea	32	43	16	8	-

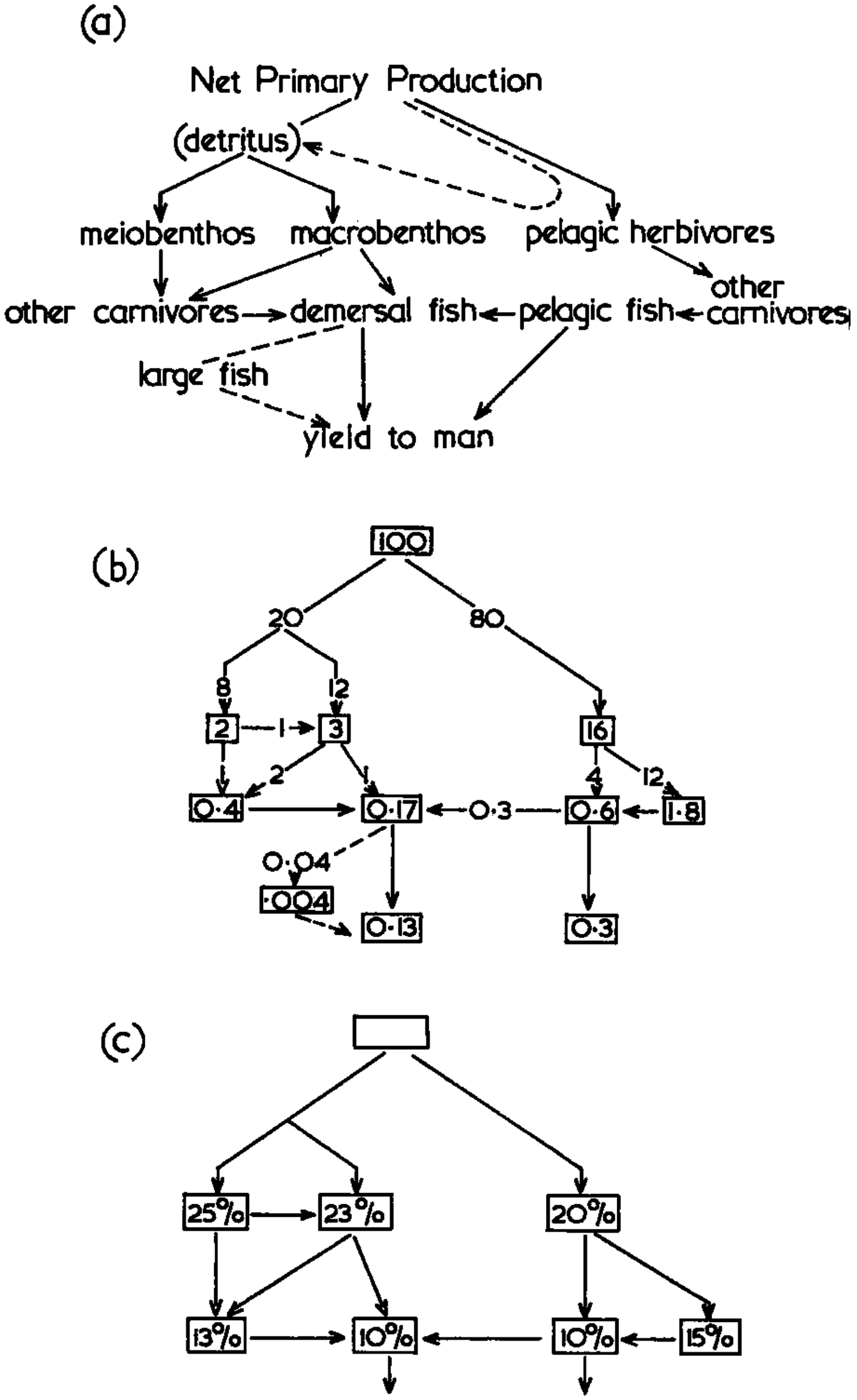

Fig.3. Schematic representation of; (a) simplified food web, (b) production by each group, (c) ecological efficiency of each group.

The fish were *Ammodytes, Gadus esmarkii* and herring, the principal crustacean was *Crangon allmanni*. The fish are both pelagic and bottom feeders while *Crangon* is classed as an omnivore (McIntyre, personal communication). Thus, although it is difficult to assess quantitatively, a large part of the diet of "commercial demersal yield" are not detritus or plant eaters but from the next higher trophic level. This obviously requires that some of the intermediate efficiencies be higher.

POSSIBLE FOOD CHAINS AND EFFICIENCIES

The previous discussion has merely recapitulated a few of the well-known complexities of prey-predator relations. This has been done to show that the available data suggest the need for efficiencies greater than 10%. The diagrams in Fig. 3 are intended to summarise this argument and the final "efficiencies" have little quantitative justification beyond the fact that there is apparently a need for some value to be significantly greater than 10%. It may be that part of this can be resolved by alteration in the values of production at different levels. In particular the primary production might be higher but it seems very unlikely it could be double the value used here.

Food webs of this type tend to make the concept of general trophic levels rather useless practically. However, it is possible to return to a more regular pattern if it is assumed, as holds in Fig. 3, that no species or "group" feeds on more than two adjacent trophic levels. Then the group can be assigned to the higher of the two levels. This definition may appear circular but it permits diagrams having the general form of Fig. 4 to be constructed.

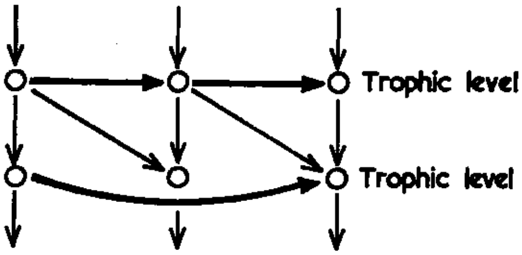

Fig. 4. Part of a generalised food web.

In such diagrams the vertical or diagonal lines indicate the transmission of food (or energy) to higher trophic levels whereas the thicker horizontal lines indicate predation within a trophic level. The latter may be thought of as ecological "cannibalism" and an increase in such cannibalism will decrease the proportion of energy transmitted to higher trophic levels. MacArthur (1955) has shown that in general the number of links in a food web is related to the stability of the ecosystem and also, inversely, to its efficiency as a means of transmitting energy to higher trophic levels. The present argument is a special case. This tendency to have an inverse relation between stability and trophic level efficiency will be discussed more fully later.

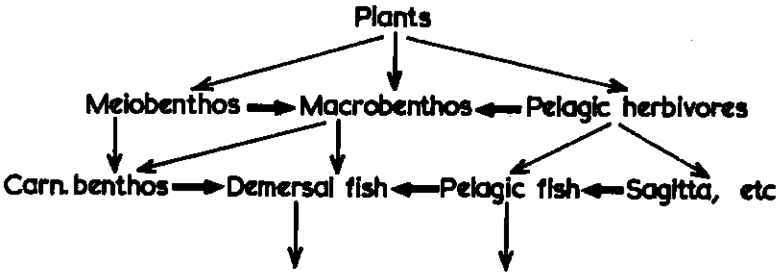

Fig. 5. The general pattern of Fig. 3 expressed as a food web of the type shown in Fig. 4.

Finally, in Fig. 5 the web in Fig. 3*a* has been put in the form of Fig. 4 and in this way it now resembles the original simplified picture of Fig. 2. However, the picture of reality is now quite different since for any "group" the efficiency appears to be much higher and the loss by cannibalism is a main factor to be estimated. This picture is, of course, very much oversimplified, but any further complexities will increase the links in the web, including the horizontal ones, and so would tend to increase the efficiencies required at any point.

Generally Fig. 5 implies a much more flexible system. In particular it is apparent that commercial fish stocks are in competition with other predators and their success or failure may be dominant in determining "commercial yield". Thus measurements of primary production become much less important and the calculation of "efficiencies" and of "cannibalism" become essential features of study.

THE EFFICIENCY OF STEADY-STATE SYSTEMS

The implications of the preceding analysis have one major fault. They appear to contradict Slobodkin's results that in laboratory experiments where population structure is maintained in a steady state, maximum achievable efficiency is about 12%. In such experiments which are run over very large numbers of generations, a stable age structure of a reproducing population is achieved and is maintained by supplying food at a steady rate and by harvesting adults at frequent intervals. In the experiments maximum efficiency defined as

$$\frac{\text{yield of adults}}{\text{food assimilated}}$$

was achieved by harvesting 90% of adults (Slobodkin, 1959).

Slobodkin has pointed out that this kind of situation is very different from that in which a group of young animals are grown till near maturity and then all are harvested. In this latter case efficiencies of 25-50% can be achieved but Slobodkin maintains that this cannot be considered a natural situation since food requirements for reproduction are neglected. However, in temperate and arctic waters the cyclical factors in the physical environment impose a regime which in many ways is not dissimilar to the latter case. In spring a large supply of plant food permits a small stock of overwintering adult herbivores to produce a large juvenile stock and support the growth to near maturity of a large population which is very heavily grazed by carnivores to leave small numbers, either for a similar but less marked autumn outburst or for the next spring. Thus in the northern North Sea the two major zooplankton peaks can be associated with such cyclical situations and in the Arctic the single peak would be of this type (Colebrook and Robinson, 1961). The ratio of maximum spring populations of herbivores to the minimum in winter is about 100 and the production of juveniles per adult in the spring must be several times higher but still within the range, 100-1,000, observed in individual *Calanus* (Marshall and Orr, 1955). In Slobodkin's experiments with *Daphnia* the rate of reproduction was very much lower.

As an illustration of the possible effects on efficiency of different forms of harvesting I have devised the following very hypothetical *Calanus*. The food requirements for different functions expressed as per cent of body weight are taken as

Growth	(20%/day	from 0 to 20 days (egg to Stage V)
	(zero	from 20 to 60 days (Stages V + VI)
Respiration	(30%/day	from 0 to 20 days
	(10%/day	from 20 to 60 days
Reproduction	(20%/day	from 20 to 60 days

The last value is based on the assumption that from Stage V onwards the food assimilated over maintenance requirements is used for reproductive functions rather than for growth.

Two possible reproductive rates, of 10 and 100 viable eggs per animal will be considered and for simplicity egg laying is supposed to occur at the end of 60 days. Thus to maintain a continuing population 90% and 99% respectively of the animals can be harvested at any time (T) during their life cycle and the remaining fraction of 10% and 1% taken at 60 days. By calculating the yield of animals (Y), the total respiratory requirement (R), and the food required to produce the next generation (B), the ecological efficiency,

$$\frac{Y}{Y + R + B}$$

can be calculated as of function of harvesting at variable time T, Fig. 6.

It is apparent that harvesting at the end of the growth phase will give an efficiency several times higher than harvesting adults or eggs (the two methods used by Slobodkin). The peak values are also much higher than can be achieved by regular daily harvesting of a fixed proportion of the population which gives efficiencies of 12% and 20% respectively for the low and high reproductive rates. Recent experiments with *Artemia* (Reeve, 1963) have given efficiency curves with a very

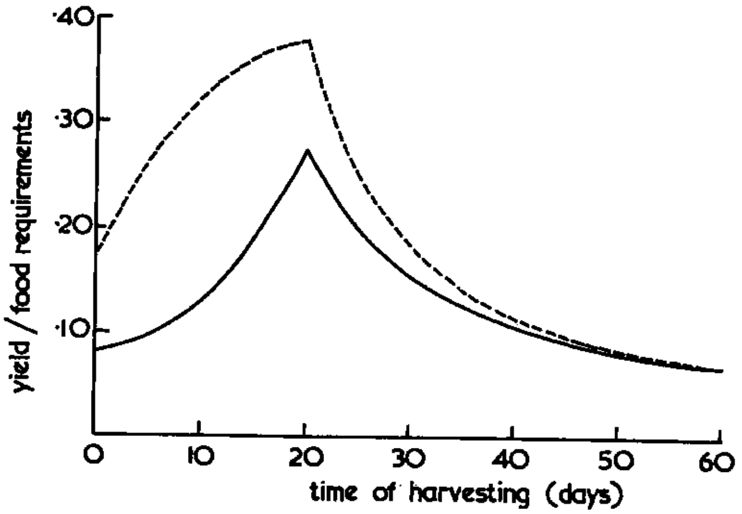

Fig. 6. The calculated efficiencies for a hypothetical *Calanus* with reproductive ratios of 100 (- - -) and 10 (——).

similar general shape to these of Fig.6, although the peak efficiencies, 40-80% depending on experimental conditions, seem rather high.

These points are, of course, merely a restatement of the common practice in most forms of agricultural stock rearing. Their relevance here is to suggest that in cyclical and therefore synchronous populations of herbivores with (a) a potentially high reproductive rate, (b) a periodically rich and suitably varying food supply, and (c) a high rate of grazing on the herbivores near the end of their growth phase, then ecological efficiencies considerably greater than 10% may be achieved. Further it seems probable that these conditions may be found in natural environments in higher latitudes.

LATITUDINAL VARIATIONS

As a result of the large number of measurements of primary production made in the last ten years it has become apparent that there may not be such large yearly differences as might be expected between the typically barren tropical oceans and the rich northern seas. The Sargasso Sea off Bermuda (Menzel and Ryther, 1960), although it has low daily rates, maintains these throughout the year to give net production rates of 50-75 g C/m^2. In the North Sea and higher latitudes the higher daily production in a short season of say 4-6 months may only double the more southerly value, 100-150 g C/m^2. If yield at trophic levels associated with commercial fisheries were assumed proportional to primary production then large areas of the tropics, and not merely special regions of upwelling or equatorial divergence, might be expected to contain moderate stocks. However, both the factors discussed here tend to operate together to nullify the concept of a proportionate yield.

MacArthur (1955) has pointed out that the environmentally forced instability of northern regions will tend to produce simpler food chains with the associated effect of a more efficient transfer of energy to higher levels because of a decrease in "cannibalism". Further, the possibly greater efficiency of a cyclical system to a steady-state one would also provide a more efficient transfer. It is often suggested that tropical plant herbivore systems are very "efficient" in their ability to recycle nutrients. This very different use of the term means that transfer of nutrients to carnivores is a small fraction of that assimilated at any time, which in turn implies "inefficiency" in our present sense. It is not possible to define the results of these additive effects but it is not unlikely that it could result in yields which at the same carnivore trophic level were 20 - 50 times less in the open waters of the tropics than in the Arctic.

Further, the fluctuating environment in northern latitudes is important in concentrating fish in certain areas and at certain times thus making the yield more economic.

It is the upwelling areas in the tropics which are often considered to be the most productive regions of the sea (Steeman *et al.* 1957). Upwelling, however, is seasonal in character in the Benguela current (Hart and Currie, 1960) and in the Peru Current (Guillen, unpublished) so that cyclical productivity, not dissimilar to temperate waters, may occur. But more important, the very large fishery yields in Peru are obviously the result of the herbivorous feeding of the anchovy. Thus the fish meal industry harvested 3.5 million tons in 1960 from an area 800 miles long and 30 miles wide. The estimated food requirement for the guano production is 4.3 million tons (Wooster and Reid, 1963). Adding these and assuming that 10% of the wet weight is carbon, the total yield is 11 g C/m^2. At a trophic level efficiency of 10% this would require a plant production of 110 g C/m^2, but at 20% the required part of the production would be only 55 g C/m^2. Thus the present fish yield or considerably higher yields might not require exceptionally great productivity. Any attempt to estimate the possible yield would depend not only on more knowledge of the yearly plant production but also on the dimensions and resultant effects of its cyclical character.

One aspect of this problem that has general importance concerns the reasons why herbivorous fish with life spans of several years are to be found only in tropical and subtropical regions, whereas in higher latitudes the dominant herbivores are crustacea having life spans that are fractions of a year. Is this difference in length of life a necessary consequence of the great amplitude of yearly production cycles in the higher latitudes?

NORTH SEA FISHERIES

Returning to the North Sea, the problem of economic interest is the manner in which relations between commercial fish stocks and the food available for them may affect the yield of fish. Although the problems of efficient utilization in the trophic levels fish - man have been very fully considered (Beverton and Holt, 1957) comparatively little is known about the effects of variations in fish stocks and their food supply.

The most interesting feature of the demersal yield in the North Sea is its comparative constancy. There are no obvious trends during the 50 years of observations although during this period the effort has probably at least doubled and many of the more heavily fished stocks have shown marked decreases in their average ages. Lundbeck (1953) considers this constancy to be due mainly to economic factors, but it is not unreasonable to suppose that the demersal yield is to some extent determined by the available food as well as by fishing effort, and thus it may be of interest to consider possible relations, similar to those used for *Calanus*, between food supply and the age structure of a fish population.

I have taken recent length-age data for haddock from a fast growing area of the North Sea (Jones, 1962) and combined this with weight-length relations (Raitt, 1933) and respiration-weight formula (Winberg, 1956). For reproductive requirements for fish of three years and older the ovary weight (Raitt, 1933) has been taken and the efficiency of its production assumed to be 50% (Winberg, 1956; Slobodkin, 1962). The testes weight is much smaller and has been neglected. From these data, Table 1, one can calculate the total yield of fish per unit of food from harvesting at different ages (Fig. 7). Also by applying an annual mortality of 10% one can give an estimate of fishing yield where the decrease in efficiency is intensified. It is apparent that an increase in the average age by harvesting implies a decrease in the efficiency of utilisation of the food supply. There are, of course, several objections to the strict application of this argument; the food supply may not be limiting on a heavily fished stock; older fish of any species tend to feed differently from the younger fish, although this is usually only a change in the proportions of different prey. Yet the principles of this approach apply to the total demersal stocks and might provide a compensatory mechanism to the effects of increased fishing effort and also to the effects of changes in mesh size.

TABLE 1. CALCULATIONS TO SHOW THE EFFICIENCY OF HADDOCK GROWTH IN TERMS OF FOOD REQUIREMENT PER YEAR OF LIFE.

Age (years)	0		0.75		1.75		2.75		3.75		4.75		5.75
Weight	0		41		138		297		482		681		875
Yield (Y)				97		162		182		199		194	
Respiratory (R) Requirement				261		566		914		1262		1580	
Reproductive (B) Requirement				-		-		56		108		164	
$Y/Y + R + B$		[.27]		.27		.22		.16		.13		.10	

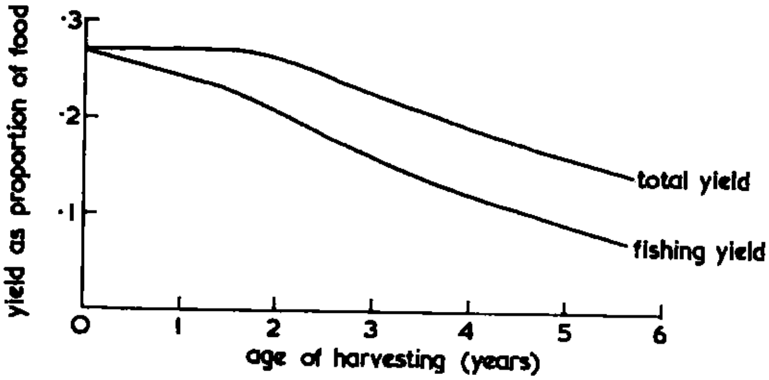

Fig. 7. The yields of haddock per unit of food requirement.

Thus, whether the causes of the comparative constancy in demersal yield are economic or biological it would seem imperative to have a greater understanding of this feature. As Lundbeck points out it may affect our interpretation of questions of overfishing. Further it is relevant to any attempt to increase yield by larval rearing or transplantation.

For the pelagic fisheries (predominantly herring) there is a general increasing trend in yield, particularly marked after 1951. There were other changes associated with the increased herring yield after 1951— an increase in the growth rate, somewhat earlier maturation, and a very marked decrease in the average age of fish in the catches (Parrish and Craig, 1961; Cushing 1961*a*). Using data on weight-length relations (Wood, unpublished) combined with length data before 1951 and from 1954-60 (Parrish, unpublished), curves for the growth rates in the two periods are obtained, Fig.8. Data on fecundity (Baxter, 1959) were used to obtain the relation of gonad weight to length which is similar for both sexes (Wynne Edwards, 1929). Again, a 50% efficiency is assumed, to permit calculation of food requirements. The results in Table 2 show, as one would expect, that the efficiency of yield was lower before 1951 than after. The inclusion of gonad production raises "efficiency" to a much higher level and any increase after 1951 in gonad production at 3 years of age would merely increase the difference between the two periods. For the juveniles of 0-3 years an efficiency of 20% is used in the further calculations.

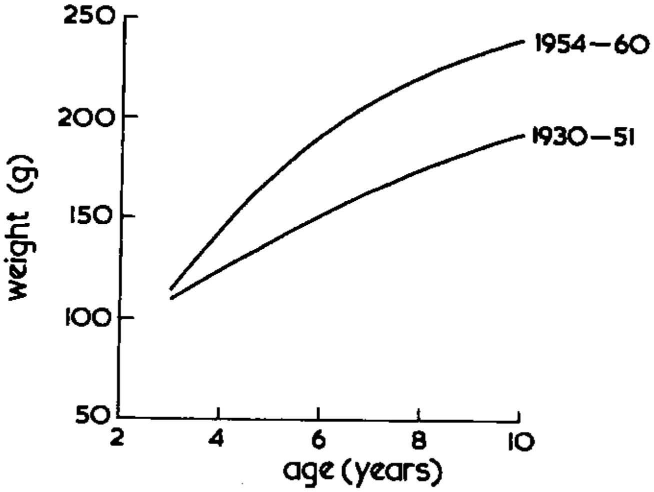

Fig. 8. The age-weight relations for herring used in the calculations (see text).

From data on age composition of the yield in the northern North Sea (Parrish and Craig, 1961), three periods with differing structures are found, Fig. 9. From the data in Table 2 it is possible to estimate the overall efficiency for each period and thus the food requirement of the total yield obtained from the data given in Fig. 1. These show, Table 3, that there is a marked increase in the overall efficiency during 1954-60 due partly to increased growth but also to the decreasing age structure. The period after the war shows the highest food requirement and this would be associated with the unsteady state resulting from the previous lack of fishing effort. It indicates again the relative inefficiency of harvesting a stock of older fish. However, the most interesting feature is the apparent equality of food requirements during 1930-39 and 1954-60 when the yield in the latter period is nearly 50% greater than in the former.

TABLE 2. CALCULATIONS TO SHOW THE EFFICIENCY OF HERRING GROWTH IN TERMS OF FOOD REQUIREMENTS PER YEAR OF LIFE. ALSO THE EFFICIENCY WHEN GONAD WEIGHT (1/2 B) IS INCLUDED IN THE YIELD.

1930-51											
Age (years)	0	3		4		5		6		7	
Weight (g)		110		125		138		152		164	
Yield (Y)			15		13		14		12		
Resp. Requ. (R)			322		352		382		410		
Repr. Requ. (B)			60		72		82		90		
$\frac{Y}{Y+R+B}$	[.20]		.038		.030		.029		.024		[.025]
$\frac{Y+1/2B}{Y+R+B}$			.113		.112		.115		.111		
1954-60											
Age (years)	0	3		4		5		6		7	
Weight (g)		115		142		172		191		208	
Yield (Y)			27		30		19		17		
Resp. Requ. (R)			346		406		456		492		
Repr. Requ. (B)			70		92		112		124		
$\frac{Y}{Y+R+B}$	[.20]		.061		.057		.032		.027		[.025]
$\frac{Y+1/2B}{Y+R+B}$			.140		.144		.128		.125		

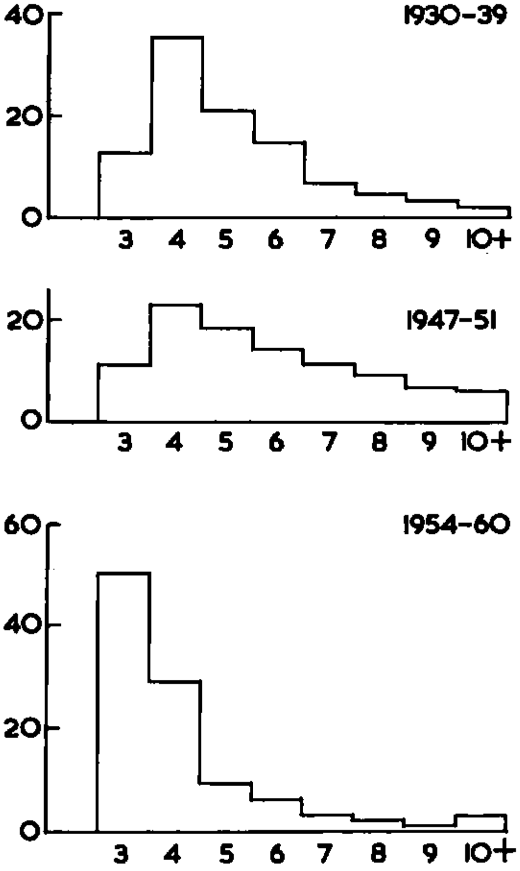

Fig. 9. Percentage are composition of herring in the Northern North Sea.

TABLE 3. PELAGIC YIELD, EFFICIENCY AND FOOD REQUIREMENTS (10^6 TONS) FOR THE NORTH SEA.

	1930-39	1947-51	1954-60
Yield/year	0.57	0.62	0.82
Efficiency	.101	.087	.141
Food required	5.7	7.1	5.8

Between 1947 and 1958 there were major changes in the plankton communities of the northern North Sea, with *Calanus* of greater importance from 1953-1958 than in earlier years and a decline in *Temora* and *Pseudo* and *Para-calanus* (Glover, 1957; Williamson,1961). A similar increase in *Calanus* in the southern North Sea has been linked with increasing growth rate of herring (Cushing and Burd, 1957). Thus is seems reasonable to suppose that the dominance of the larger copepod *Calanus* over the smaller species such as *Temora* could permit more efficient feeding by herring and so higher growth rates and larger juvenile populations. The results in Table 3 suggest, therefore, that there is no necessity to presuppose either an increased total yield of herbivores or, conversely, an unsteady state due to increased fishing effort such as occurs after a war. The environmental changes together with the increased effort could produce a new and higher steady state yield from the same quantity of herbivore food.

Preliminary calculations such as these require much more evidence to substantiate them and in particular the absolute values for the various efficiencies. They are intended merely to indicate the need to consider quantitatively the interrelation of fish with their food supply and in particular the need for more insight than can be obtained from studying the fluctuations in fisheries purely through possible statistical correlations with the environment.

DISCUSSION

The main thesis put forward here is, I am afraid, a very obvious one; that unfortunately it is not possible to solve our problems of estimating potential fisheries yield by measuring primary production and dividing by an appropriate power of ten. We need more detailed knowledge of the effects of phytoplankton cycles on herbivore yield. Beyond this it seems necessary to accept the fact that for many regions such as the North Sea, fluctuations in the yearly production at the plant or herbivore level are too small to explain fluctuations in the yield of particular fisheries. A good example of this has been shown by Cushing's (1961*b*) and Southward's (1963) reconsideration of the disappearance of herring in the English Channel. Although it was suggested originally that decreases in basic productivity were responsible, these changes were at most only fractional. The total disappearance of herring and their replacement by pilchards is more likely to be the consequence of changes in the community structure of their food. Thus the important effect was probably not the quantity of basic production but the differing paths this energy followed through the food web. All the same, our understanding of these paths has to be based on detailed knowledge of the basic production cycles.

A major problem, however, concerns the practical relations of such studies with fisheries management and these will be studied further in a later paper. It may not be unreasonable at the present moment to ignore completely the relation of fish stocks to their food supply, when making assessments of changes in mesh sizes (International Fisheries Convention of 1946, 1957; ICES Cooperative Research Report 1, 1962). However, as opportunities develop for more rational management, the importance of the food supply as a controlling factor is likely to emerge and in particular, the decreasing efficiency of harvesting larger and larger fish could become the dominating factor. Also, in any attempts to stock selected areas with young demersal fish, the need to consider the effects on the benthos would seem paramount.

ACKNOWLEDGEMENTS

It will be apparent from the many references to "personal communications" and "unpublished data" that this paper is very dependent on, and largely the result of, discussions with my colleagues in the Marine Laboratory, Aberdeen. I am extremely grateful to them for their help and advice.

REFERENCES

ADAMS, J.A. 1963. Plankton investigations from Aberdeen during 1960-61; the standing crop of zooplankton. *Ann. biol., Copenhague*, 18: 69.

BAXTER, I.G. 1959. Fecundities of winter-spring and summer-autumn herring spawners. *J. Cons.*, 25: 73-80.

BEKLEMISHEV, R.V. 1957. Superfluous feeding of zooplankton and the problem of sources of food for bottom animals. *Trud. vsesoyuz gidrobiol. obsheh.*, 8: 354-8.

BEVERTON, R.J.H. and S.J. HOLT. 1957. On the dynamics of exploited fish populations. *Fish. Invest., Lond.*, Ser. 2, 19: 533 p.

BIRKETT, L. 1959. Production in benthic populations. *ICES, C.M. 1959*, Near Northern Seas Committee, Paper No. 42.

COLEBROOK, J.M. and G.A. ROBINSON. 1961. The seasonal cycle of the plankton in the North Sea and the north-eastern Atlantic. *J. Cons.*, 26: 156-165.

CUSHING, D.H. 1961*a*. The effect of fishing on the Downs stock of herring in the North Sea. *ICES, C.M. 1961*, Herring Symposium, Paper No. 25.

1961*b*. On the failure of the Plymouth herring fishery. *J. Mar. biol. Ass. U.K.*, 41: 799-816.

CUSHING, D.H. and A.C. BURD. 1957. On the herring of the southern North Sea. Fish. Invest., Lond., 20: 1-31.

GLOVER, R.S. 1957. An ecological survey of the drift-net herring fishery off the north-east coast of Scotland, II: the planktonic environment of the herring. *Bull. Mar. Ecol.*, 5: 195-205.

HART, T.J. and R.I. CURRIE. 1960. The Benguela current. *Discovery Rep.*, 31: 123-298.

I.C.E.S. Co-operative Research Report 1. 1962. Charlottenlund, Denmark. International Council for the Exploration of the Sea.

International Fisheries Convention, 1946. 1957. Report of the *ad hoc* committee established at the fourth meeting of the Permanent Commission, September 1955. *J. Cons.*, 23: 7-37.

JONES, R. 1954. The food of the whiting, and a comparison with that of the haddock. *Mar. Res. Scot.*, 1954, No. 2, 34 p.

1962. Haddock bionomics II. The growth of haddock in the North Sea and at Faroe. *Mar. Res. Scot.*, 1962, No. 2: 19 p.

LINDEMAN, R.L. 1942. The trophic-dynamic aspect of ecology. *Ecology*, 23: 399-418.

LUNDBECK, J. 1953. Zur Frage der Nordseefischerei. *Fischwirtschaft*, 4: 95-96.

MACARTHUR, R. 1955. Fluctuations of animal populations, and a measure of community stability. *Ecology*, 36: 533-536.

MCINTYRE, A.D. 1956. The use of trawl, grab and camera in estimating marine benthos. *J. Mar. biol. Ass. U.K.*, 35: 419-429.

1958. The ecology of Scottish inshore fishing grounds. I. The bottom fauna of the east coast grounds. *Mar. Res. Scot.*, 1958, No. 1, 24 p.

1961. Quantitative differences in the fauna of boreal mud associations. *J. Mar. biol. Ass. U.K.*, 41: 599-616.

MARSHALL, S.M. and A.P. ORR. 1955. *Biology of a marine copepod.* Edinburgh: Oliver and Boyd. 188 p.

MENZEL, D.W. and J.H. RYTHER. 1960. The annual cycle of primary production in the Sargasso Sea off Bermuda. *Deep-Sea Res.*, 6: 351-365.

PARRISH, B.B. and R.E. CRAIG. 1961. The herring of the N.W. North Sea - Post-war changes in the stock fished by Scottish drifters. *ICES, C.M. 1961*, Herring Symposium, Paper No. 23.

PARRISH, B.B. and A. SAVILLE. 1962. The estimation of fishing mortality rate for Bank spawners, from larval abundance data. *ICES, C.M. 1962*, Herring Committee, Paper No. 40.

RAITT, D.S. 1933. The fecundity of the haddock. *Sci. Invest. Fish. Scot.*, 1933, No. 1.

REEVE, M.R. 1963. Growth efficiency in *Artemia* under laboratory conditions. *Biol. Bull. Woods Hole*, 125: 133-145.

SAUNDERS, H.L. 1956. Oceanography of Long Island Sound, 1952-1954. 10. Marine bottom communities. *Bull. Bingham oceanogr. Coll.*, 15: 345-414.

SLOBODKIN, L.B. 1959. Energetics in *Daphnia pulex*. *Ecology*, 40: 232-243.

1962. *Growth and regulation of animal populations*. New York: Holt Rinehart-Winston.

SOUTHWARD, A.J. 1963. The distribution of some plankton animals in the English Channel and approaches. III. Theories about long-term biological changes, including fish. *J. Mar. biol. Ass.U.K.*, 43: 1-30.

STEEMAN-NIELSEN, E. and A. JENSEN. 1957. Primary oceanic production *Galathea Rep.*, 1: 49-136.

WILLIAMSON, M.H. 1961. An ecological survey of a Scottish herring fishery. IV: Changes in the plankton during the period 1949 to 1959. *Bull. Mar. Ecol.*, 5: 207-229.

WINBERG, G.G. 1956. Rate of metabolism and food requirement of fishes. *Nauch. Trud. Belor. Gos. Univ.* 253 p. (Also, 1960. *Fish. Res. Bd. Canada*, Trans. Ser. No. 194).

WOOSTER, W.S. and J.L. REID. 1963. Eastern boundary currents. *In* Hill, M.N., *The Sea,II* New York-London, John Wiley, 253-280.

WYNNE-EDWARDS, V.C. 1929. The reproductive organs of the herring in relation to growth. *J. Mar. biol. Ass. U.K.*, 16: 49-65.

C-5

THE IMPACT OF THE ENVIRONMENTAL FACTORS ON SURVIVAL OF THE FAR EASTERN YOUNG SALMON DURING THE ACCLIMATIZATION OF THE LATTER IN THE NORTHWEST PART OF THE USSR

By

E.L. Bakshtansky[1]

ABSTRACT

The paper deals with some environmental factors that influence the survival of young pink and chum salmon after their release from the hatcheries.

The material is based on the observations carried out on the Kola peninsula during 1959-63.

The main factor responsible for the drastic reduction in the number of the released young salmon was predation which was especially great at the time the young entered the sea.

INTRODUCTION

From the beginning of the work on the acclimatization of pink salmon, *Oncorhynchus gorbuscha* (Walbaum) and chum salmon, *Oncorhynchus keta* (Walbaum) in the north European part of the USSR it became a matter of urgent necessity to establish the reason governing the return of fish that had been released as fry from the hatcheries in their new home waters. In 1959 scientific workers of the Polar Institute (V.V. Azbelev and E.L. Bakshtansky) observed masses of young pink and chum salmon safely migrating down the river and entering the sea. The same year observations were initiated on the young fish in the inlets and bays. Varied returns of pink salmon in 1960-63 also made it necessary to study the sea life of these salmon. The total survival of fish is often determined by the survival in the initial stages of development. Therefore, we may expect that the number of returning adults in the Barents and White Seas will be directly influenced by the rate of survival of the young pink and chum salmon during the first weeks of their life.

Our five year observations on the young pink and chum salmon at sea and in the laboratory enable us to formulate a judgement on the effect of main environmental factors on the abundance of the young pink and chum salmon after their descent to the sea.

Salinity and temperature.

Repeated experiments on determination of the effect of salinity of sea water on young pink salmon have revealed that even the immediate change of salinity from that of the fresh water to 35.5 ‰ (at temperatures of 5-10°C) does not prevent almost total survival of the pink migrants. The fry of pink salmon with residual yolk sac also showed good survival in sea water.

Water temperature appears to be an important factor during the downstream migration of young salmon. Thus, during the experiments on transfer of the young pink salmon to the sea water at the temperature above 18-20°C some of the young fish died, evidently because of the penetration of salt into the body of the fry. At low sea water temperatures of 1°C to 3°C the movements of the young pink salmon became extremely slow and at a sea water temperature below 1°C some of the young fish died. During an experiment in 1963 in 35 ‰ sea water, the following numbers of young died out of the total 50 specimens in each case:

at the temperature ca. 1°C - 28
at the temperature ca. 4°C - 3
at the temperature ca. 8°C - 2

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During the descent of the young pink and chum salmon to the Barents and White Seas in the period from 1959 to 1963 no smolts were observed in the sea at water temperatures of 1°C to 3°C. In the periods of descent of the young pink and chum salmon during these years the temperature of sea water was higher - from 5°C to 10°C.

Food

The adverse effect of this factor is eliminated because the descent of the young pink and chum salmon takes place in the period of maximum growth of zoo- and ichthyo-plankton. The following main food items were found in the stomachs of young pink and chum salmon caught in the White and Barents Seas in 1962 and 1963 (according to O.I. Nilova):

Harpacticus uniremis Kroyer,
Tisbe furcata (Baird),
Tachidius discipes Giesbrecht,
Microsetella norvegica (Boeck),
Gammarus oceanicus,
larvae and pupae of Tendipedidae, air insects.

The degree to which the stomachs were filled with food was 3-4 (in a 5 grade system).

Enemies

During the first year of observation on the descent (1959) we assumed that herring can feed on the pink fry. This assumption was confirmed in the summer of 1962 during observations on the descent of young pink and chum salmon released from the Umba hatchery into the White Sea. The location of the hatchery on the Umba River is 4 km from the mouth and a strong current promotes the rapid downstream migration, so that some part of the young reach the river mouth only a few hours after release.

In the river mouth the young kept in small shoals close to the shore where they were preyed upon by sea trout, Atlantic salmon smolts, and sticklebacks. Observations showed that the young pink and chum salmon migrate downstream poorly during the day time but more actively towards the evening, the migration reaching its peak at midnight. In the north it is still light at this time during summer, so it was possible to see how the shoals of pink and chum salmon, each consisting of several hundred or thousand fishes, swam towards the sea keeping close to the shore. Sometimes the fish schools were so large that mingling together they formed a dark strip 0.5-1.0 m wide, near the shore. On the night of 25 June 1962, during the peak of the descent of the young pink and chum salmon, a shoal of herring entered the mouth of the Umba River and even swam 300-400 m up the river. We witnessed the herring actively preying upon the fry in the river mouth.

During the peak of the descent 102 specimens of White Sea herring, *Clupea harengus pallassi* natio *maris-albi* (Berg) were caught in the mouth of the Umba River. These herring were 4 years old and averaged 15.6 cm in length. In their stomachs 304 young pink and chum salmon were found. The largest number of fry found in one stomach (15 cm herring) was 23, and the average number was 3. It is reasonable to assume the existence of an inverse relation between the return of pink salmon and the catches of herring in the year of fry release.

Figure 1 shows the quantities of herring delivered in 1959-62 to the factories situated nearest to the Umba River, and Table 1 the estimated quantities of pink salmon in the White Sea.

TABLE 1. THE ESTIMATED QUANTITY OF PINK SALMON IN THE WHITE SEA IN 1960-63

Year	Pink salmon
1960	68,300
1961	282
1962	7
1963	23

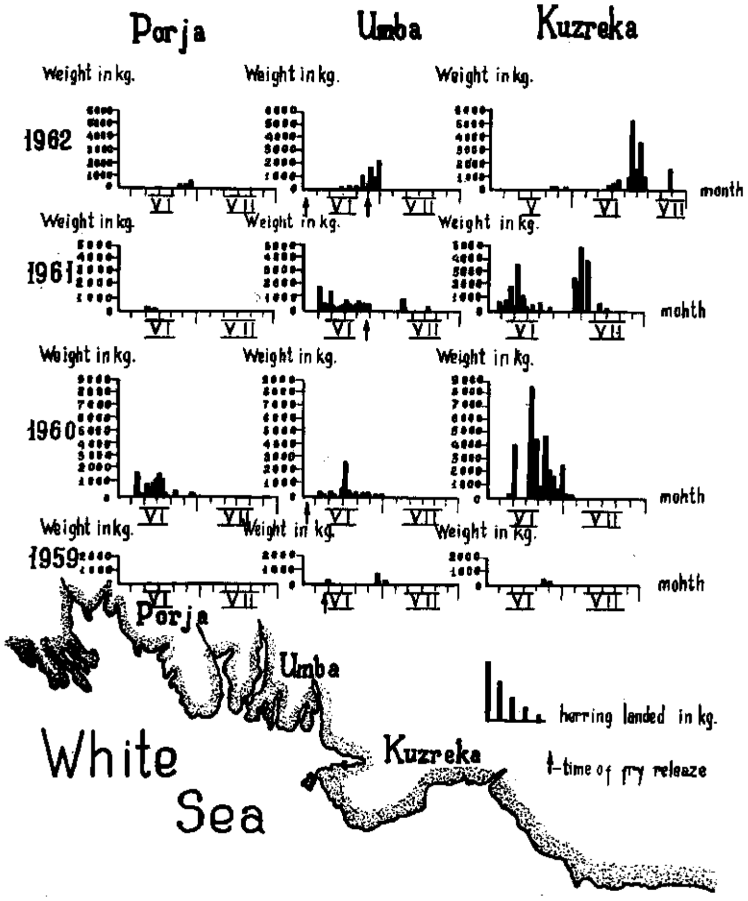

Fig. 1. Quantities of herring delivered in 1959-62 to the factory nearest to the Umba River (the White Sea).

As seen from the figure the least quantity of herring was delivered to the factories of Umba, oria and Kuzreka in 1959. The lack of herring possibly accounted for the good survival of the oung that had been released into the White Sea and for a mass return of the pink salmon in 1960.

The field observations in Uraguba Bay (Barents Sea) in 1960 have shown that a considerable porion of the pink and chum migrants can be destroyed by the young of cod and especially saithe, *Polachius virens* Linné; it is noteworthy that the young chum is destroyed in much greater numbers as result of a longer littoral period of life and lesser mobility in comparison with the young pink almon.

In 1963 a special experiment was carried out in the same Bay aimed at finding the rate of desruction of the young pink and chum salmon by young cod, *Gadus morhua morhua* Linné. The results of his experiment have brought further evidence that the chum salmon are eaten by young cod much more ntensively, so we have a right to assert that it is completely inadvisable to release the young hum in those parts of the littoral area where there are many predators. In the littoral zone of he White Sea the number of predators is smaller, and therefore the young chum is observed for a onsiderably longer time than in the Barents Sea.

CONCLUSION

As a result of field observations and laboratory investigations we have come to the concluion that the main factor governing the numbers of pink and chum salmon returning to the rivers of he north European part of the USSR is the relationship of Far Eastern salmon to the ichthyofauna f the White and Barents Seas.

C-6

THE COPEPOD ECTOPARASITE *SPHYRION LUMPI* (KROYER) IN RELATION TO REDFISH *SEBASTES MARINUS* (L.) IN THE GULF OF MAINE

By

George F. Kelly and Allan M. Barker[1]

ABSTRACT

Redfish is the primary host of *Sphyrion lumpi*, a copepod ectoparasite, in much of the western part of the Gulf of Maine. Sample data from commercial landings during 1942-62 were analyzed for seasonal and annual variations in parasite incidence, depth distribution, sex composition and size composition of parasitized redfish. Parasite incidence increased more than two-fold between 1943-47 and 1957-62. Many aspects of the host-parasite relationship support a hypothesis that small redfish mortality may be caused by *Sphyrion* infestation.

INTRODUCTION

The parasitic copepod *Sphyrion lumpi* is found abundantly on redfish in a large portion of the Gulf of Maine. Since 1942, redfish landings have been sampled routinely at New England fishing ports, the samples including notation of the presence of *Sphyrion*, and degree of infestation of the host. In this paper, we summarize these data to show the relation of the parasite to Gulf of Maine redfish as indicated by *Sphyrion* incidence with respect to sex and size of its host. We examine effects of this parasite on the host, and suggest some factors that may limit the range of *Sphyrion* in this area.

OCCURRENCE OF *Sphyrion*

Kroyer (1845) first described this parasite and named it *Lestes lumpi* from a specimen attached to a lumpfish, *Cyclopterus lumpus*, collected near Iceland. When Wilson (1919) established the new copepod family Sphyriidae, the name of the parasite already had been changed several times, and it had been found to infest several species of fish. In their report of the incidence and distribution of *Sphyrion* on redfish in the Newfoundland area, Templeman and Squires (1960) reviewed taxonomic changes and the many host records for the whole North Atlantic. It is sufficient to cite this reference at the present time and confine our comments to records from the Gulf of Maine.

Wilson (1919) was the first to associate *Sphyrion* with redfish in the Gulf of Maine region, but he did not suggest that redfish was the principal host. The start of the Gulf of Maine redfish fishery in 1935 revealed a high incidence of *Sphyrion* on redfish and, simultaneously, made this parasite economically important when embedded remains of the female parasite's head reduced the value of redfish fillets.

Herrington, Bearse, and Firth (1940) reported on abundance and distribution of *Sphyrion*, and the frequency of occurrence of its embedded remains in redfish fillets from the Gulf of Maine. Nigrelli and Firth (1939) reviewed the taxonomy of *Sphyrion* and corroborated Wilson's earlier classification. They noted that the parasite was found principally on larger redfish, and that distribution of the *Sphyrion* population in this region was confined to the western portion of the Gulf of Maine, with no *Sphyrion* on redfish from western Nova Scotia near Browns Bank. Perlmutter (1951) noted that approximately 92% of the parasites were attached between the base of the dorsal fin and lateral line of Gulf of Maine redfish. He concluded that this pattern of attachment was caused primarily by the fish's ability to scrape off parasites from all but that region of the body.

The frequency of occurrence of *Sphyrion* was used by Sindermann (1961) in studies of several arasites considered as possible parasitological tags for redfish stock identification in the western North Atlantic. Most recently, Williams (1963) reported the incidence of *Sphyrion* on redfish

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to be less than 3% at several locations in the eastern North Atlantic, based on examination of a limited number of *marinus*-type and *mentella*-type *Sebastes* specimens sampled from commercial landings at a fish market in Hull, England, over a 13-month period.

METHODS

All material used in this study was obtained from iced redfish catches on commercial otter trawlers. Samples consisted of 100, occasionally 200, fish. Data recorded include date of sample, location and depth of fishing, sex and length of host fish, number of copepod parasites and stage of parasite infestation. Three stages of infestation were defined:(first) live copepod - live animal still attached to the fish, (second) sore-copepod torn loose, leaving the embedded head and an open wound, and (third) spot - scarred remnant of a healed sore appearing externally as a swollen lump, and internally as an encysted hard tumor in the flesh. Observations of live copepods were confined to those visible to the unaided eye, and, therefore, the data are restricted to fully transformed females.

Since sampling was on commercial trips, samples were concentrated in areas of heavy fishing effort and were not uniformly distributed over the fishing grounds. Table 1 summarizes the number of redfish samples found to contain *Sphyrion* infestation from each statistical subarea in the Gulf of Maine, by year, from 1943-1962 (Fig. 1). It should be understood that sampling was not confined

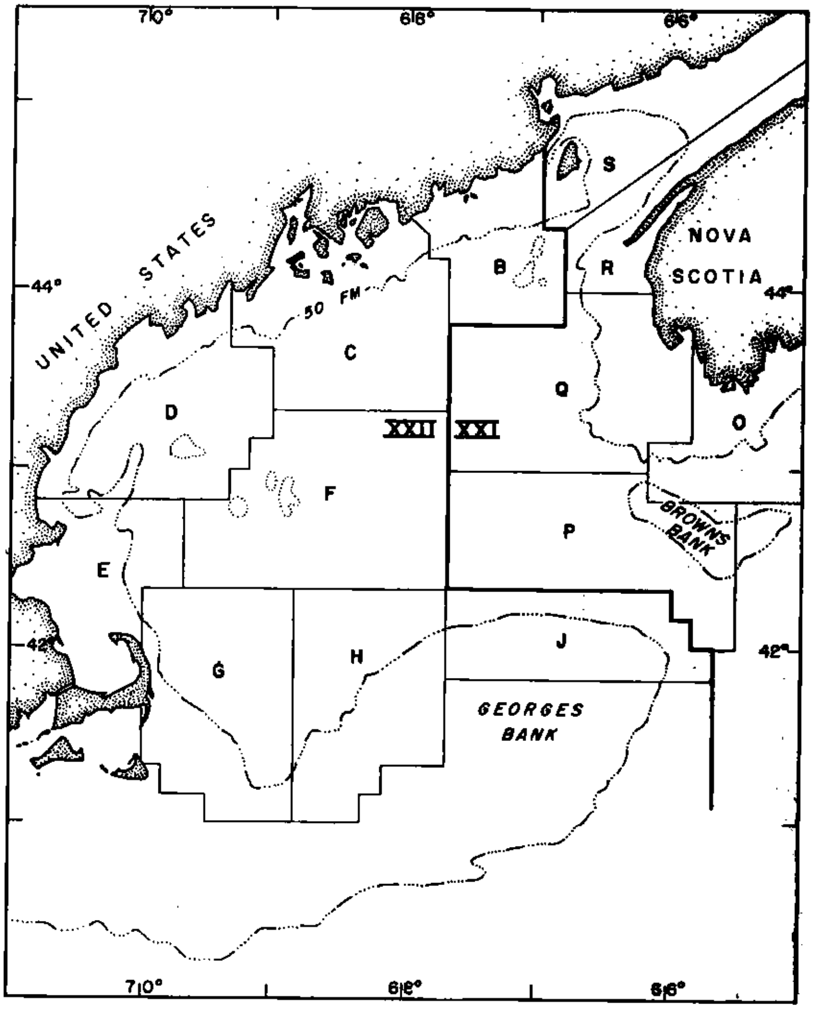

Fig. 1. Statistical subareas of the Gulf of Maine.

TABLE 1. NUMBER OF SAMPLES OF PARASITIZED REDFISH TAKEN IN THE GULF OF MAINE BY STATISTICAL SUBAREA 1943-62

Subarea		'43	'44	'45	'46	'47	'48	'49	'50	'51	'52	'53	'54	'55	'56	'57	'58	'59	'60	'61	'62
XXII	B									-	1	2	1	6	26	38	43	20	10	3	5
		36	26	22	8	4	-	1	2												
	C									-	1	-	-	14	30	52	33	21	6	7	7
	D	28	10	7	9	-	-	-	-	2	1	1	1	8	21	23	29	12	6	22	11
	E	18	17	16	15	6	-	3	-	-	-	-	1	-	6	10	-	6	6	3	12
	F	30	30	32	21	26	12	3	8	19	18	12	12	14	54	80	53	33	23	36	24
	G									16	3	4	1	4	4	8	4	14	3	8	7
		22	23	25	13	16	6	7	-												
	H									1	5	1	1	2	8	4	5	1	2	4	2
XXI																					
P, Q, R, S		-	3	12	11	2	-	-	-	-	2	-	-	-	8	9	2	5	17	18	5
Mixed areas		-	-	-	-	-	-	-	-	7	2	1	3	3	12	-	6	10			3
Total		134	109	114	77	54	18	14	10	45	33	21	20	51	169	224	175	122	73	101	76

to these areas; many thousands of fish were examined from other parts of the Gulf of Maine and eastward, but *Sphyrion* was found on redfish only in these subareas in the vicinity of the Gulf of Maine.

The greatest number of samples was obtained from the area of infestation during 1943-47 and 1955-62. The small number of samples collected from 1948 through 1954 was the result of a general movement of the U.S. redfish fleet from the Gulf of Maine eastward to fishing grounds off Nova Scotia, on the Grand Banks, and in the Gulf of St. Lawrence.

We are indebted to Messrs. C.F. Bocken, P.H. Chase Jr., G.M. Clarke, and R.S. Wolf for their assistance in collecting and analyzing data used in this study.

RESULTS

1. Range, Distribution, and Incidence of the Parasite.

Percentage incidence of live copepods in redfish samples is plotted for 1943-47 and 1957-62, and contour lines are drawn for 5% intervals (Fig. 2 and 3). General distribution of parasitized fish is similar for the 2 periods, and one is impressed with the strictly defined range of this *Sphyrion* population. All records of the parasite are from an area west of a line running from the northern edge of Georges Bank northeast to St. Mary's Bay on the western end of Nova Scotia. Within this area, most of the parasitized redfish are in depths between 90 and 220 m.

The area of occurrence of the parasite appears to be bisected by a region of low infestation extending NW-SE through Cashes Ledge near the center of the Gulf of Maine. *Sphyrion* incidence is higher north and south of this line. Within these smaller regions there are several localities of very high parasite incidence that persist from year to year (Fig. 2 and 3). During 1943-47, the 2 areas of highest infestation were off Cape Cod and near Mt. Desert Island. In 1957-62, these areas of high incidence remained, but there were 4 additional high infestation areas established where only lesser concentrations had existed in the earlier period. Incidence values higher than 15% were confined to comparatively small areas during 1943-47, while those regions during 1957-62 were much more extensive. The increase in size of areas of high parasite incidence indicates that *Sphyrion* has become more abundant in recent years. Despite these considerable changes in percentage incidence of the copepod on redfish, peripheral limits of the group of parasitized redfish have remained virtually unchanged.

2. Stages of Infestation.

The 3 stages of parasite infestation on redfish are similarly distributed in the Gulf of Maine (Fig. 2, 4, and 5). In 1943-47, the second and third stages (sores and spots respectively) were most plentiful off Cape Cod and near Mt. Desert Island, regions of highest copepod incidence. There was an additional concentration of third stage infestation near the tip of Jeffreys Ledge south of Portland, Maine. Second and third stages were less numerous than the first, with the second stage least abundant.

Relative incidence of the 3 stages of infestation is illustrated more clearly with data from smaller areas within the Gulf, in which male and female redfish are treated separately (Fig. 6). In each statistical subarea, percentage of parasite incidence is approximately the same on males and females, and the sore stage is least numerous, usually less than 15% of the infected sample. In all except one subarea, the live copepod stage is the most numerous, usually comprising 45 to 58% of an infected sample. Subarea XXII D is the exception, where third stage infestation (spots) is much higher than the live copepod stage. This was noted above in Fig. 5 as a concentration of third stage infestation near Jeffreys Ledge.

3.

Annual Variation in Parasite Incidence.

Annual changes in percentage incidence of live copepods and total infestation (3 stages) for the entire Gulf of Maine area of parasite occurrence are shown in Fig. 7. The 2 curves are similar and, despite some marked fluctuations, each shows a significant trend toward higher incidence in recent years. Average incidence of live copepods rose from 5.8% in 1943-47 to 14.2% during 1957-62. These measures of incidence are comparable and are representative of the whole parasite population since sampling during both periods contained substantial collections from each

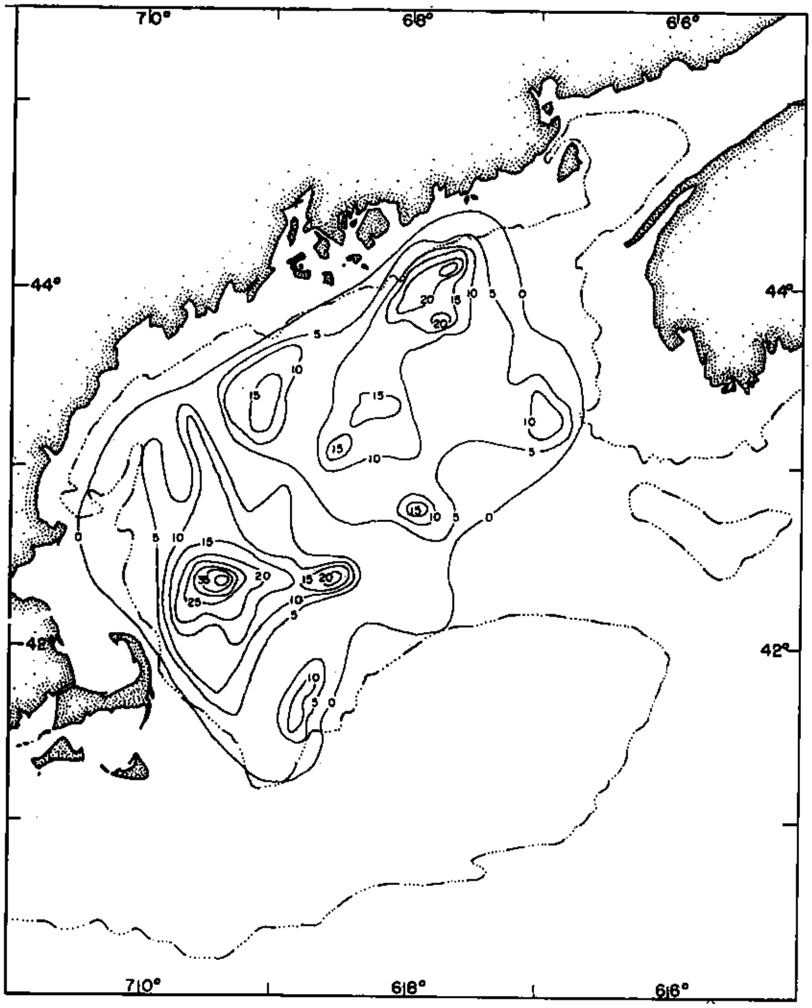

Fig. 2. Distribution of redfish with first stage infestation of *Sphyrion lumpi* in the Gulf of Maine, 1943-47.

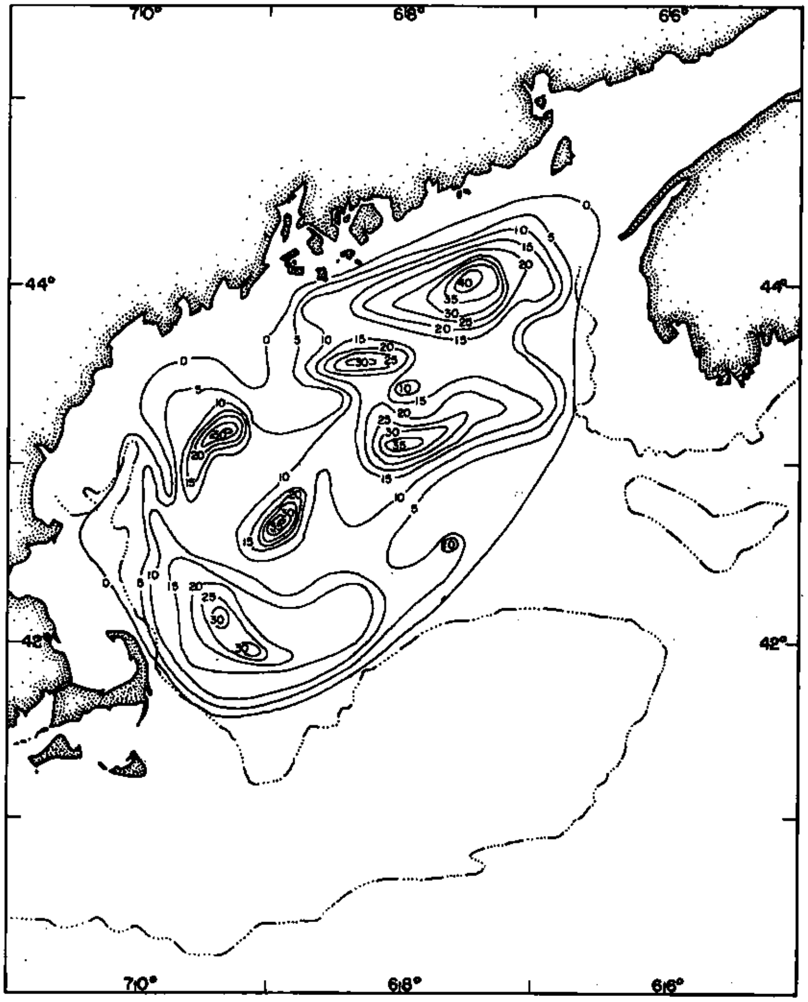

Fig. 3. Distribution of redfish with first stage infestation of *Sphyrion lumpi* in the Gulf of Maine, 1957-62.

subarea. It should be noted that sampling during 1948 through 1954 was relatively light and these samples may not represent average conditions for the whole population. Annual incidence variations are seen in more detail in data for live copepods from a portion of the Gulf of Maine with male and female redfish separated (Fig. 8). Here again a more than two-fold increase in *Sphyrion* incidence is shown. Also, there has been an interesting change in relative levels of incidence on male and female fish; values for females were consistently higher than for males in 1943-47, but lower than male values during most of 1957-62. The significance of this reversal will be discussed later.

4. Seasonal variation in Parasite Incidence.

Incidence of live *Sphyrion* on redfish was highest in winter and spring and lowest during summer and fall (Fig. 9 and Tables 2 and 3). Data for the southern Gulf of Maine during 1943-47 show the highest value in February, a rapid decline until June, and generally low values from June through November. Parasitization of males and females followed a similar pattern, females showing consistently higher levels of incidence than males throughout most of the year.

In 1957-62, a similar winter-summer difference existed, but the magnitude of change was less than during the earlier period. There was a higher level of incidence at all seasons which reflects the recent general increase in parasite incidence mentioned earlier. Furthermore, the relative

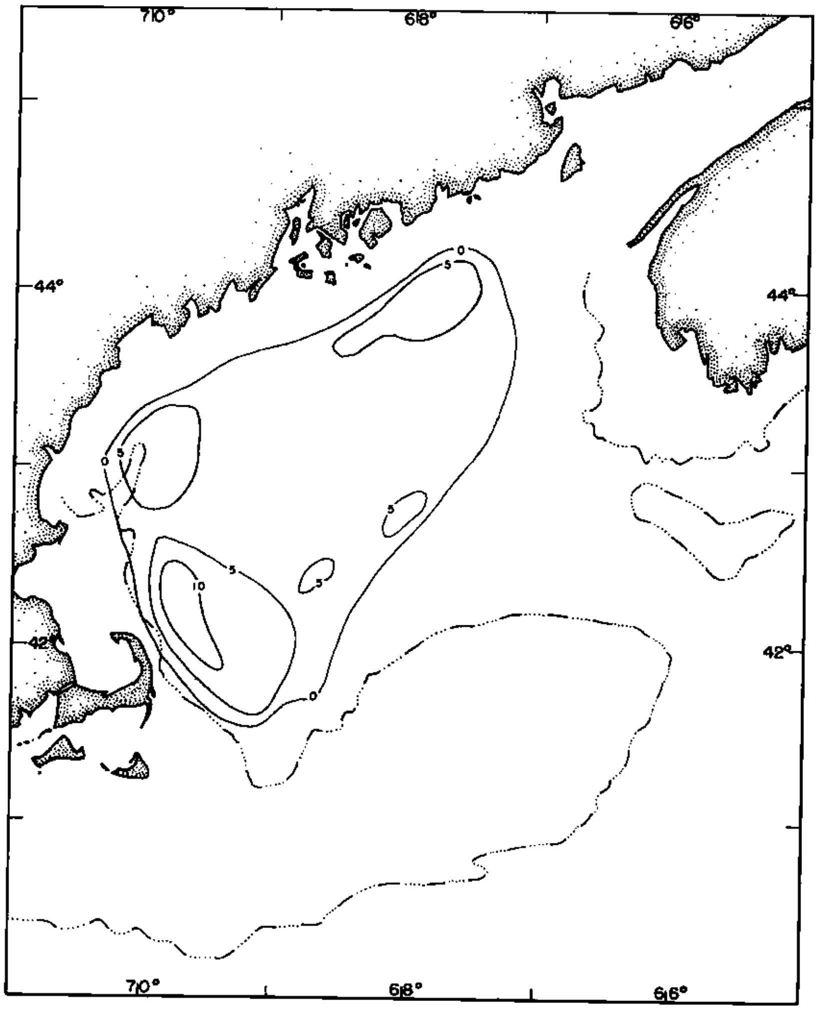

Fig. 4. Distribution of redfish with second stage infestation of *Sphyrion lumpi* in the Gulf of Maine, 1943-47.

level of parasite incidence on males and females had changed from that of the earlier period, a reversal of values similar to that noted earlier in the year-to-year comparison.

The winter-summer cycle of variation suggests that the parasite infests the host in late winter, and the number of parasitized fish decreases during the summer and fall, when the reproductive cycle is again repeated. The decrease may be caused by fish shedding the copepods, or it may be due to mortality of the parasitized fish.

5. Changes in Sex Ratio of Redfish.

The sex composition of Gulf of Maine redfish has changed considerably since 1942 when sexed samples of redfish were first collected (Fig. 10). From 1942 until 1954 the samples contained more than 54% females each year, the average being 55.6%. From 1955 through 1962 the proportion of females was below 53.5% each year, and the average decreased to 51.9%. The downward trend, which could be said to have started as early as 1949, has been most evident since 1955. It was accentuated during the last 4 years by the lowest percentages of female redfish observed since sex composition data were first collected routinely in 1942.

The sex composition of parasitized redfish (live copepod stage) has shown even greater change

TABLE 2. SEASONAL VARIATION IN NUMBER AND PERCENTAGE INCIDENCE OF LIVE *Sphyrion* ON REDFISH IN SOUTHERN GULF OF MAINE, SUBAREAS XXII, E, F, AND G, 1943-47. MALES AND FEMALES SEPARATED.

	1943		1944		1945		1946		1947		TOTAL		
Month	No. fish sam-pled	No. fish para-sit.	No. fish sam-pled	No. fish para-sit.	No. fish sam-pled	No. fish para-sit.	No. fish sam-pled	No. fish para-sit.	No. fish sam-pled	No. fish para-sit.	No. fish sam-pled	No. fish para-sit.	Per-cent para-sitized
MALES													
Jan.	219	22	152	8	159	26	-	-	-	-	530	56	10.6
Feb.	144	9	76	14	39	12	51	2	-	-	310	37	11.9
Mar.	243	27	-	-	295	8	-	-	90	7	628	42	6.7
Apr.	130	7	258	19	73	0	49	2	91	2	601	30	5.0
May	179	13	313	9	693	32	453	31	283	24	1,921	109	5.7
June	281	5	433	10	314	5	159	2	241	9	1,428	31	2.2
July	196	2	583	8	265	4	409	12	360	7	1,813	33	1.8
Aug.	916	7	370	3	422	8	166	18	286	11	2,160	47	2.2
Sept.	136	1	331	1	453	3	232	10	394	2	1,546	17	1.1
Oct.	201	0	356	7	64	3	305	4	230	5	1,156	19	1.6
Nov.	304	9	382	8	138	1	54	0	48	5	926	23	2.5
Dec.	72	0	108	12	-	-	-	-	41	7	221	19	8.6
Total	3,021	102	3,362	99	2,915	102	1,878	81	2,064	79	13,240	463	-
Percent incidence	3.38		2.94		3.50		4.31		3.83			-	3.50
FEMALES													
Jan.	231	15	148	4	141	28	-	-	-	-	520	47	9.0
Feb.	156	16	124	29	61	16	49	4	-	-	390	65	16.7
Mar.	257	41	-	-	255	12	-	-	110	7	622	60	9.6
Apr.	145	3	342	22	127	0	51	2	109	9	774	36	4.7
May	221	17	287	10	807	52	490	78	317	37	2,122	194	9.1
June	369	20	567	22	386	9	241	6	459	16	2,022	73	3.6
July	304	5	817	12	335	6	491	31	440	10	2,387	64	2.7
Aug.	759	8	430	11	678	30	234	30	314	7	2,415	86	3.6
Sept.	189	0	419	4	447	14	368	38	406	12	1,829	68	3.7
Oct.	248	3	444	25	136	10	395	9	370	6	1,593	53	3.3
Nov.	296	1	468	10	162	3	46	1	52	0	1,024	15	1.5
Dec.	98	1	92	16	-	-	-	-	59	8	249	25	10.0
Total	3,273	130	4,138	165	3,535	180	2,365	199	2,636	112	15,947	786	-
Percent incidence	3.97		3.99		5.09		8.41		4.25			-	4.93

TABLE 3. SEASONAL VARIATION IN NUMBER AND PERCENTAGE INCIDENCE OF LIVE *Sphyrion* ON REDFISH IN SOUTHERN GULF OF MAINE, SUBAREAS XXII E, F, AND G, 1957-1962. MALES AND FEMALES SEPARATED.

Month	1957		1958		1959		1960		1961		1962		TOTAL		
	No. fish sampled	No. fish parasit.	No. fish sampled	No. fish parasit.	No. fish sampled	No. fish parasit.	No. fish sampled	No. fish parasit.	No. fish sampled	No. fish parasit.	No. fish sampled	No. fish parasit.	No. fish sampled	No. fish parasit.	Percent parasitized
MALES															
Jan.	148	7	275	39	294	20	158	26	-	-	296	37	1,171	129	11.0
Feb.	874	59	326	78	153	7	102	9	364	122	53	-	1,872	275	14.7
Mar.	800	140	334	57	321	59	326	77	313	70	188	53	2,282	456	20.0
Apr.	588	77	369	48	459	74	150	18	-	-	115	6	1,681	223	13.3
May	466	84	246	60	149	25	212	44	700	152	416	28	2,189	393	18.0
June	315	26	239	7	295	27	-	-	468	97	456	79	1,773	236	13.3
July	326	5	213	18	165	13	117	8	142	24	149	15	1,112	83	7.5
Aug.	251	11	169	7	248	18	241	27	199	18	422	11	1,530	152	9.9
Sept.	277	11	243	36	350	58	-	-	54	19	34	-	958	124	12.9
Oct.	281	21	83	7	-	-	191	13	-	-	-	-	555	41	7.4
Nov.	214	14	128	12	59	12	92	2	-	-	-	-	493	40	8.1
Dec.	90	6	-	-	99	15	-	-	170	28	-	-	359	49	13.6
Total	4,630	461	2,625	369	2,592	328	1,589	224	2,410	530	2,129	289	15,975	2,201	-
Percent incidence		9.96		14.1		12.7		14.1		22.0		13.6		-	13.8
FEMALES															
Jan.	152	4	325	51	206	11	142	19	-	-	304	40	1,129	125	11.1
Feb.	826	54	374	82	147	2	98	7	336	106	47	-	1,828	251	13.7
Mar.	700	106	366	53	381	57	274	48	287	55	210	54	2,218	373	16.8
Apr.	712	114	331	41	441	59	150	10	-	-	85	5	1,719	229	13.3
May	534	87	354	74	151	23	188	29	600	160	384	46	2,211	419	19.0
June	435	56	261	5	305	34	-	-	532	102	465	63	1,998	260	13.0
July	374	12	287	18	135	10	183	9	158	21	151	14	1,288	84	6.5
Aug.	349	15	231	8	252	23	259	25	201	25	478	71	1,770	167	9.4
Sept.	323	7	257	31	550	95	-	-	46	22	66	-	1,242	155	12.5
Oct.	319	41	117	6	-	-	209	29	-	-	-	-	645	76	11.8
Nov.	286	22	172	19	41	2	108	7	-	-	-	-	607	50	8.2
Dec.	110	10	-	-	101	9	-	-	130	20	-	-	341	39	11.4
Total	5,120	528	3,075	388	2,710	325	1,611	183	2,290	511	2,190	293	16,996	2,228	-
Percent incidence		10.3		12.6		12.0		11.4		22.3		13.4		-	13.1

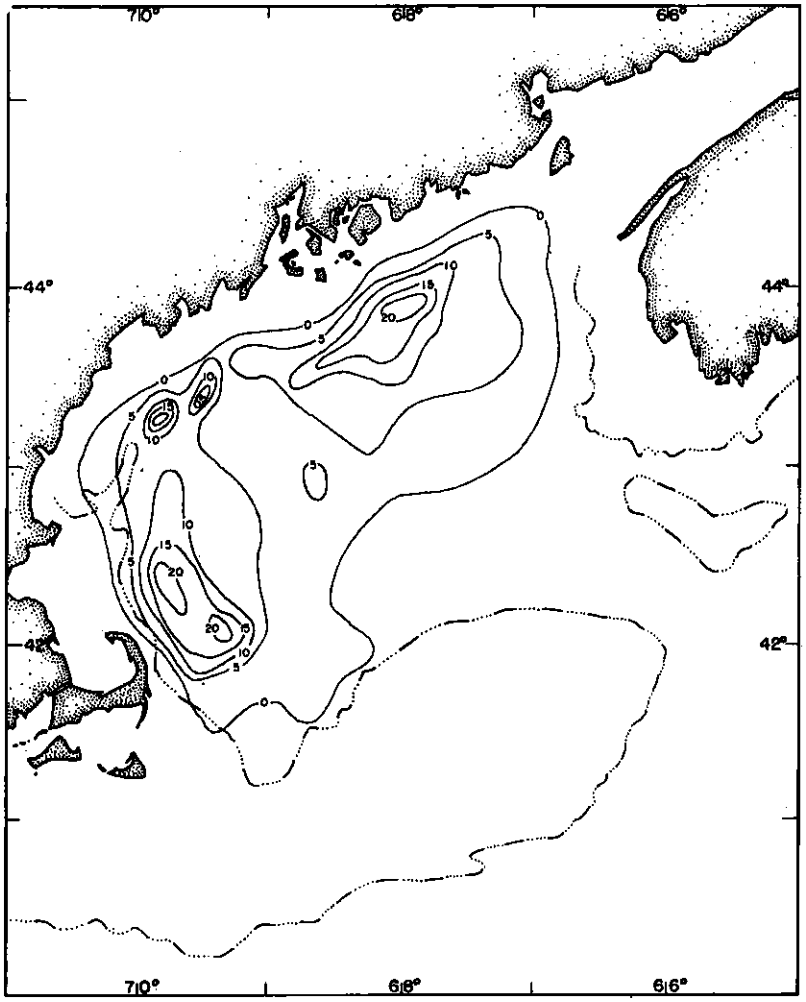

Fig. 5. Distribution of redfish with third stage infestation of *Sphyrion lumpi* in the Gulf of Maine, 1943-47.

than the total Gulf redfish population. From 1943 through 1951 the proportion of females in the samples was greater than 55% each year. From 1952 through 1962 females comprised less than 54% in all except one year, and during 4 successive years the value was as low as 46-49%.

Comparing the 2 curves in Fig. 10, it is evident that sex ratios of both parasitized and non-parasitized redfish changed during the period of study, the change being greater in the parasitized portion of the population than in the whole Gulf of Maine redfish population. This general alteration in sex ratio will be discussed later in relation to the reversal in percentage incidence of *Sphyrion* on male and female redfish that was noted earlier.

6. Depth Distribution of Parasitized Redfish.

Contour charts of *Sphyrion* distribution in the Gulf of Maine (Fig. 2-5) showed areas of highest parasite incidence on redfish in waters deeper than 130 m, depths where redfish generally are most abundant in this region. To examine depth distribution of redfish in more detail, regressions of percentage incidence of *Sphyrion* on depth of capture of host redfish were calculated for several statistical subareas for 2 recent years when sampling of the redfish catch was extensive (Fig. 11).

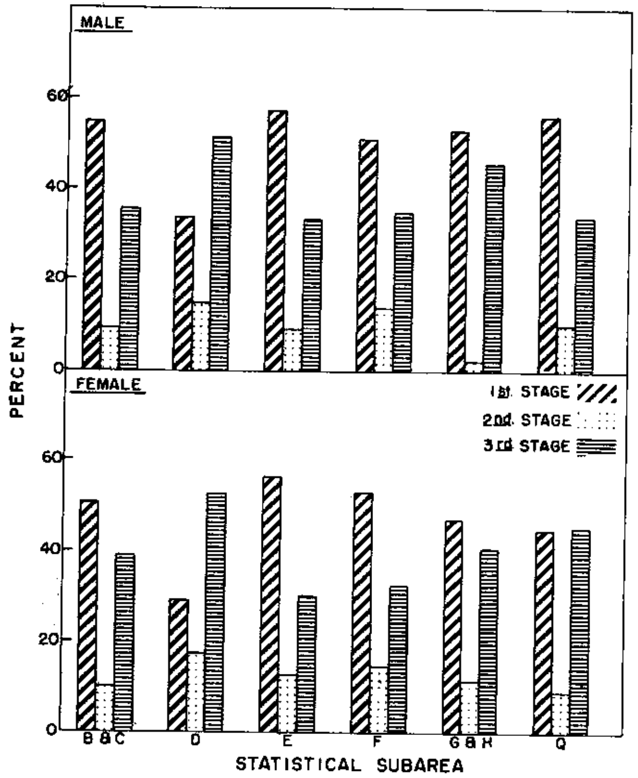

Fig. 6. Percent composition of parasitized redfish having three stages of infestation. Average values for the period 1943-51, by statistical subarea, for males and females separately.

Usually parasite incidence increases with depth, but below 185 m incidence of the parasite diminishes. In all subareas examined, the highest incidence values were distributed through the middle of the depth range, from 120 to 185 m. There is considerable variation in the slopes of the fitted lines, but the mean depth of mean parasite incidence is fairly consistent within the subarea.

Depth distribution of parasitized redfish in the Gulf of Maine is limited by the comparatively shallow depths found there. We confine our interpretation of depth distribution of parasitized fish to this area, realizing that different conditions may prevail on the edge of the continental shelf where redfish occur to much greater depths than in the Gulf of Maine.

7. Variation in Redfish Mean Length and Size Composition.

Mean length of Gulf of Maine redfish, sampled from commercial landings, has shown a gradual downward trend during the last 20 years, and a sharp decrease since 1960 (Fig. 12). Data for males and females show similar annual variations. During most of this period, parasitized redfish have averaged larger than the mean length of the total redfish sample from the Gulf (Fig. 13). Because of differences in size composition of fish in different parts of the Gulf, mean length comparisons

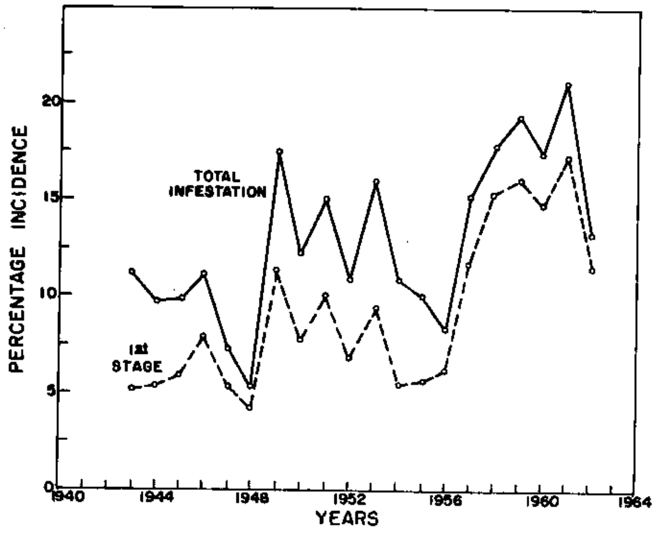

Fig. 7. Variation in annual average percentage incidence of live *Sphyrion* and total parasite infestation on Gulf of Maine redfish, males and females combined, during 1943-62.

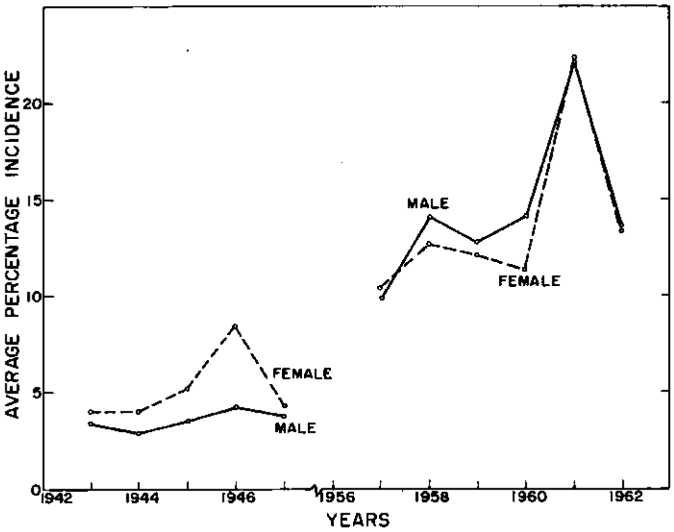

Fig. 8. Variation in annual average percentage incidence of live *Sphyrion* on redfish, males and females separated, in subareas XXII E, F, and G, southern Gulf of Maine, in 1943-47 and 1957-62.

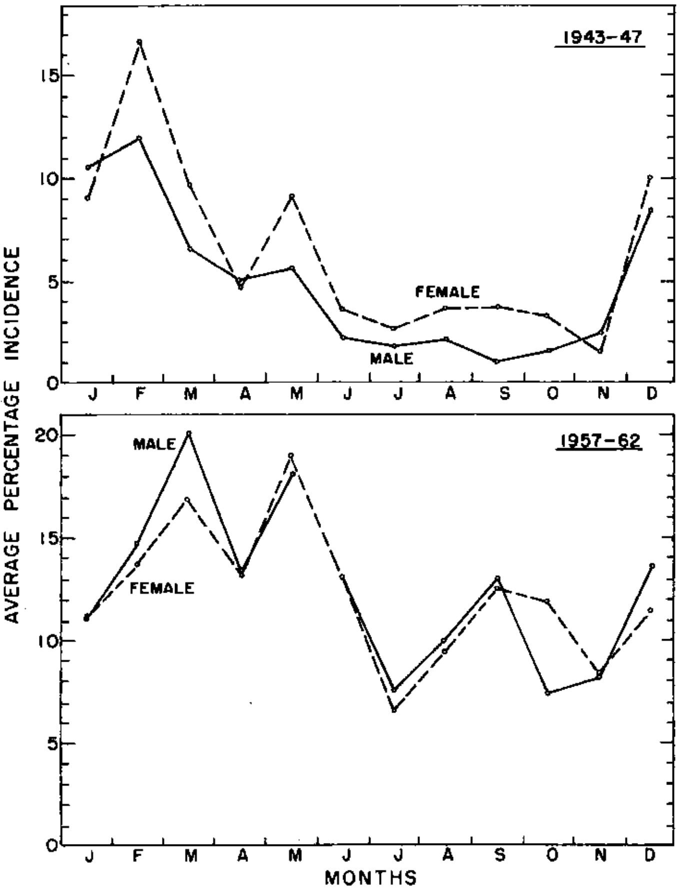

Fig. 9. Seasonal variation in percentage incidence of live *Sphyrion* on redfish in southern Gulf of Maine, subareas XXII E, F, and G. Average monthly values for 1943-47 and 1957-62 are given as percent of each sex parasitized.

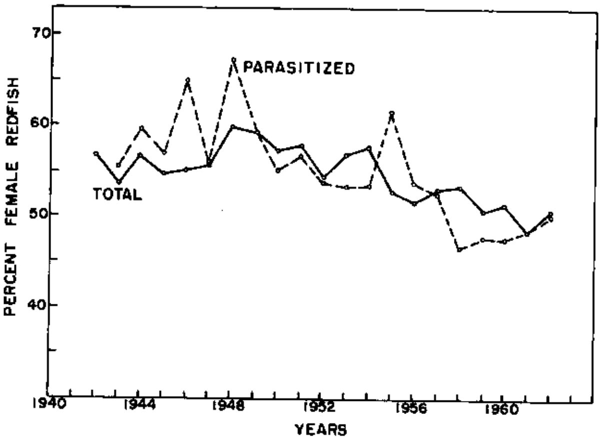

Fig. 10. Annual variations in percentage of female redfish in total Gulf of Maine sample and in samples infested with live *Sphyrion*.

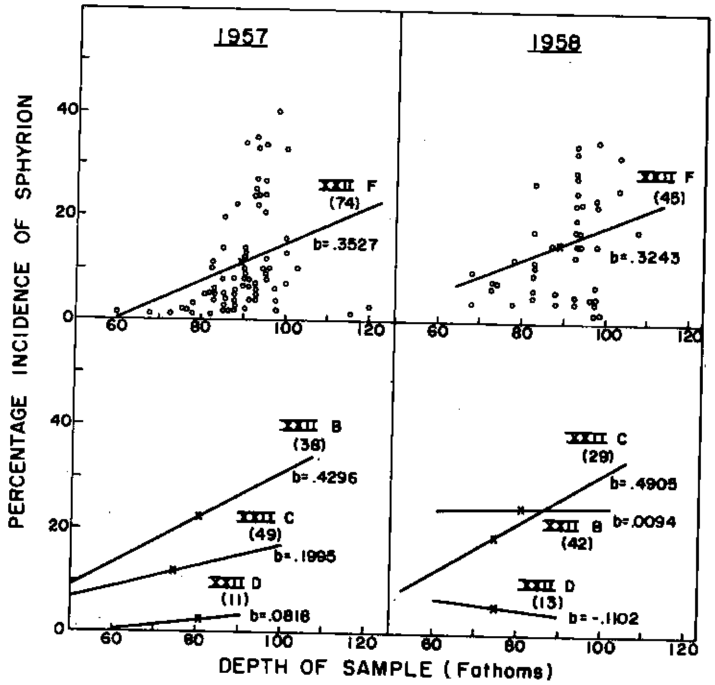

Fig. 11. Regression of percentage incidence of live *Sphyrion* on redfish in relation to depth of capture, by subarea, during 1957 and 1958. Number of samples from each subarea is shown in parentheses.

were made within each statistical subarea, and the results were used to compute weighted mean annual differences for the whole Gulf. Despite differences in length between parasitized fish and the total sample, this relationship has persisted for both male and female fish. Since about 1955, the magnitude of difference has diminished for both males and females. Parasitized females were smaller than the mean length of the total female sample during 1959-61.

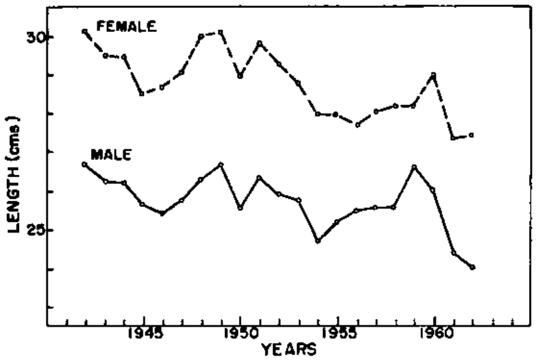

Fig. 12. Variations in mean length of redfish in the Gulf of Maine, 1942-62.

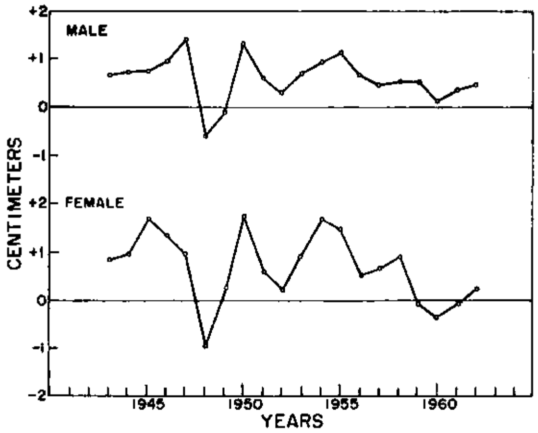

Fig. 13. Difference between annual mean lengths of parasitized redfish and total redfish sample from the Gulf of Maine, 1943-62. Zero lines represent mean lengths of total male and female samples.

Annual variations in mean length of parasitized and nonparasitized redfish are shown best by data from the smaller statistical subareas (Fig. 14). Females are larger than males in all subareas, and local differences in redfish mean length, within the Gulf, are apparent. Recently, a downward trend in mean length in subareas D, E, F, G, and H, was sufficient to offset an upward tendency in subareas B and C, resulting in the overall decrease in mean length in the Gulf shown earlier in Fig. 12.

In all subareas, parasitized redfish were larger than the mean length of total subarea samples during most of the study period. The difference in mean length between the 2 groups has diminished in recent years, especially in subareas B, C, and F, the most heavily fished subareas, where the relationship has been reversed, or nearly so, since 1959. It is noteworthy that, within subareas, the concurrent variations in mean length are similar for males and females.

During the early years of the study, a rather consistent host-size relationship existed among the groups of redfish infested with the 3 stages of parasite infestation (Fig. 15). Average length of parasitized fish was greater than that of the whole sample during most of the years studied. Length relationship of the stages of infested fish was as expected in a time-dependent series of samples where growth of the host was not inhibited by the parasite. Of the infested fish, first stage hosts were smallest, second stage hosts next largest, and third stage hosts were largest. Although Fig. 15 includes data combined for both sexes from all subareas of the Gulf, the resulting relationship suggests that fish infested with each successive stage of infestation averaged about 1 cm larger than those in the preceding group.

A similar host-size relationship is shown in recent average length data from a single subarea (Fig. 16 and Table 4). There is a difference of almost 1 cm between the mean lengths of fish grouped by stage of parasite infestation, males and females separated.

In these data, we have divided first stage infestation fish into groups according to the number of live copepods present on each host in order to compare size compositions of the groups. There is no evidence that size compositions of fish having from 2 to 7 parasites are skewed consistently from the length distribution of fish with only one parasite. There are variations in length-frequencies of multiple infestation groups around the mean of the single infestation group, but it cannot be shown that fish with more than one live copepod parasite are likely to be consistently larger or smaller than those with only a single parasite.

We have rarely seen Gulf of Maine redfish bearing more than 7 parasites. There is an obvious

TABLE 4. LENGTH-FREQUENCY OF NONPARASITIZED FISH AND PARASITIZED FISH, BY STAGE OF INFESTATION, FOR SUBAREA XXII F, 1957-59.

Length cm	Non-parasitized	First Stage Infestation Number of *Sphyrion*							Second Stage Infestation (Sores)	Third Stage Infestation (Spots)	Total Sample
		1	2	3	4	5	6	7			
MALES											
14	1										1
15	-										-
16	4										4
17	23										23
18	55	2							1		58
19	114	6									120
20	211	4									215
21	278	14							2		294
22	427	29	3						1		460
23	583	48	4		1				2	3	641
24	813	84	10	4	1				5	3	920
25	1,015	134	29	9	5	1			14	15	1,222
26	1,066	162	27	13	2				23	17	1,310
27	912	143	30	6	2	1			31	43	1,168
28	641	85	10	4	1				16	32	789
29	335	33	8		1	1		1	11	17	407
30	124	14	2	1					2	12	155
31	35	7							5	4	51
32	20	2								2	24
33	6	4	1							1	12
34	6										6
35	1										1
Total	6,670	771	124	37	13	3		1	113	149	7,881
Average length cm	25.5	26.3	26.6	26.5	26.3	27.5		29.5	27.2	27.9	25.7
				26.4 cm							
FEMALES											
14	1										1
15	1										1
16	1										1
17	8										8
18	33	1									34
19	87	1			1						89
20	150	3	1								154
21	279	16	3								298
22	312	24	5	1							342
23	382	32	2						1		417
24	411	42	5	1					9	4	472
25	524	65	8	3	1				8	8	617
26	627	71	10	4	2	1	1		5	4	725
27	693	108	16	3	1				9	11	841
28	710	107	15	1	1				14	14	862
29	695	101	15						20	21	852
30	614	85	11	1	1				19	17	738
31	550	80	11	4					21	34	700
32	428	59	5	2					21	22	537
33	409	49	4	3					18	25	508
34	277	38	4	1					19	22	361
35	166	23		2					9	26	226
36	69	9							5	6	89
37	17	5							1	4	27
38	7	2								1	10
39	3										3
Total	7,454	911	115	26	7	1	1		179	219	8,913
Average length cm	28.2	29.0	28.4	29.5	26.4	26.5	26.5		30.9	31.8	28.4
				28.9 cm							

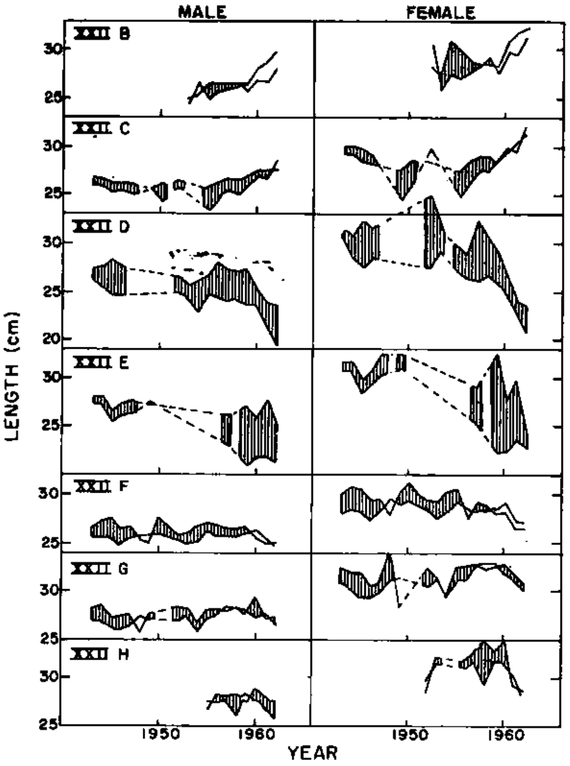

Fig. 14. Variation in mean lengths of parasitized redfish and total redfish sample, by statistical subarea, in the Gulf of Maine, 1943-62. Shaded area represents years when parasitized redfish were larger than the mean length of the whole redfish sample from that subarea.

inverse relationship between number of parasites per host and number of hosts, but we do not know if this represents a level of maximum parasitization that has any biological significance. The number of parasites carried by a host may depend on influences such as physiological factors limiting the density of parasite crowding on the host, mathematical limits governing the parasite's change of finding a host, or the possibility of host mortality caused by parasitization beyond a maximum level. We can only speculate on the relative importance of these factors at this time.

To compare the degree of difference in length-frequencies of parasitized and nonparasitized fish, data from Table 4 are summarized as percent size composition, sexes separated (Fig. 17). The upper portions of the two curves are similar, and the major difference is the comparative lack of small parasitized fish. For both males and females, 96% of the parasitized fish are larger than 22 cm, whereas approximately

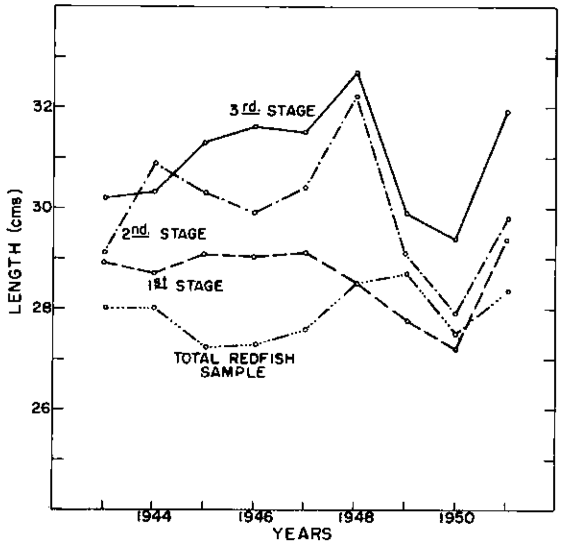

Fig. 15. Comparative annual mean lengths of redfish with first, second, and third stage infestations of *Sphyrion* and that of the total redfish sample from the Gulf of Maine, 1943-51.

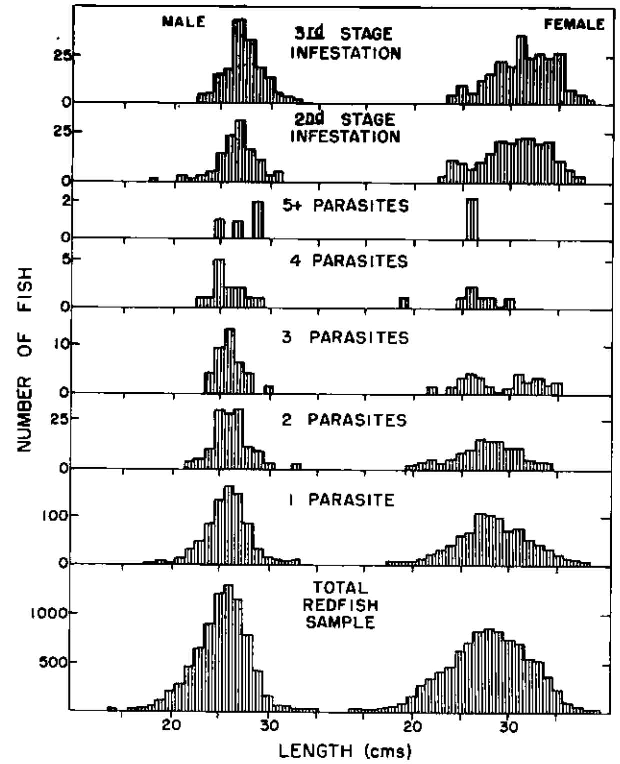

Fig. 16. Comparative size compositions of redfish, grouped as follows: nonparasitized; first stage infestation with 1, 2, 3, 4 and 5 or more live copepods; second stage infestation; and third stage infestation. Data are from statistical subarea XXII F, 1957-59, males and females separated.

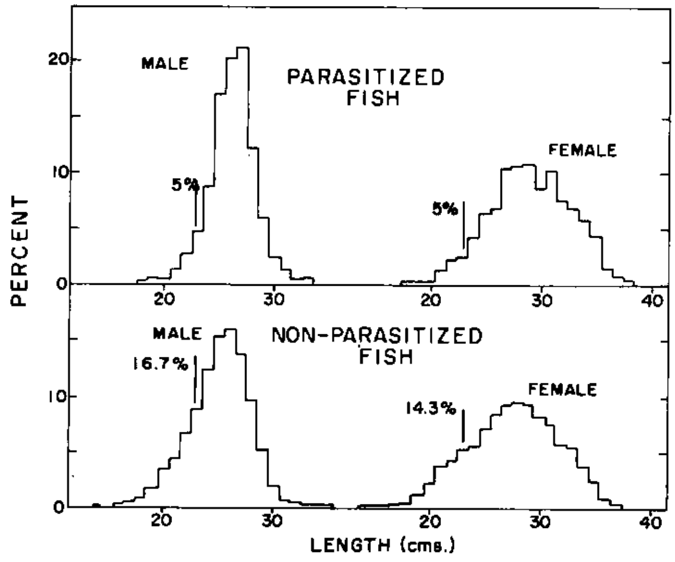

Fig. 17. Percent size composition of parasitized and nonparasitized redfish, sexes separated, in subarea XXII F, 1957-59.

85% of the nonparasitized fish exceed that length. If this difference is attributable to presence of the parasite, the absence of small parasitized fish can be interpreted in two ways: (1) as evidence of specificity of host size for the parasite, of (2) as evidence of small fish mortality caused by copepod parasitization. Whatever the cause, approximately 10% of the fish represented in samples of nonparasitized fish are not present in the size compositon of parasitized redfish.

DISCUSSION

1. Factors Influencing *Sphyrion* Distribution.

A discussion of the effect of *Sphyrion* infestation on redfish is inevitably clouded by our relative ignorance about early life history of the parasite. When *Sphyrion* spawns, how long its larvae are pelagic, whether it infests an intermediate host, how fast it grows, and how long it lives as an adult, are questions we cannot answer. Until direct evidence from the study of *Sphyrion* life history is available, a degree of speculation about effect of the parasite on its host must be permitted.

The relatively restricted range and stable limits of the Gulf of Maine *Sphyrion* population suggest that it is strongly influenced by hydrographic or ecological factors peculiar to the region. Within this area, the great variability of parasite incidence on redfish indicates optimal conditions for parasite survival in some localities, with very poor or intolerable conditions nearby. There is no evidence that the range of *Sphyrion* is limited by range of redfish, the primary host in this region. Redfish are distributed continuously from the Gulf eastward along the Nova Scotia banks, but the range of the parasite terminates abruptly in the midst of the host stocks.

We agree with Templeman and Squires (1960) that it is difficult to explain the high incidence of *Sphyrion* on redfish in the widely separated areas of the Gulf of Maine and Hamilton Inlet Bank off the Labrador Coast, with a vast area between where the parasite has never been recorded. There is no published evidence that range of the parasite might depend on the existence of an intermediate host, but this must be held as a possibility that could afford a simple explanation for its discontinuous distribution. While it seems unlikely that two species of *Sphyrion* are involved, taxonomic study of the two parasite populations is necessary before the matter is settled.

Some aspects of Gulf of Maine hydrography suggest that the strictly limited range of *Sphyrion* may be controlled primarily by hydrographic factors. The eastern limit of *Sphyrion* occurrence in the Gulf, shown in Fig. 2 and 3, closely parallels a line where temperature and salinity reach maximum values, and dominant nontidal currents flowing into the Gulf contribute to a counterclockwise gyral called the "Gulf of Maine eddy" by Bigelow (1927). According to Bigelow, the 8°C temperature and 35.00 $^{o}/oo$ salinity boundaries lie along the eastern edge of the eddy approximately as shown in Fig. 18, representing the maximum northward penetration of slope water into the Gulf. Northwest of these lines, temperature and salinity of bottom water does not exceed those values anytime during the year, except on a few shoal areas close to shore. Waters southeast of the lines are generally warmer and more saline than these limits during much of the year. Aside from river inflow, the primary source of water entering the Gulf is from the southeast throughout the year, mainly through the Eastern Channel.

It is not suggested that 8°C and the $35.00^{o}/oo$ represent the maximum temperature and salinity in which *Sphyrion* can survive. However, proximity of these maximum lines to the observed boundary of the parasite's distribution suggests these values as likely starting points for seeking limiting environmental factors for the parasite or a possible intermediate host. Since we know so little about the early life history of the parasite, perhaps there is only a short period during the pelagic stage when it is vulnerable to mortality from hydrographic factors, and this period may coincide

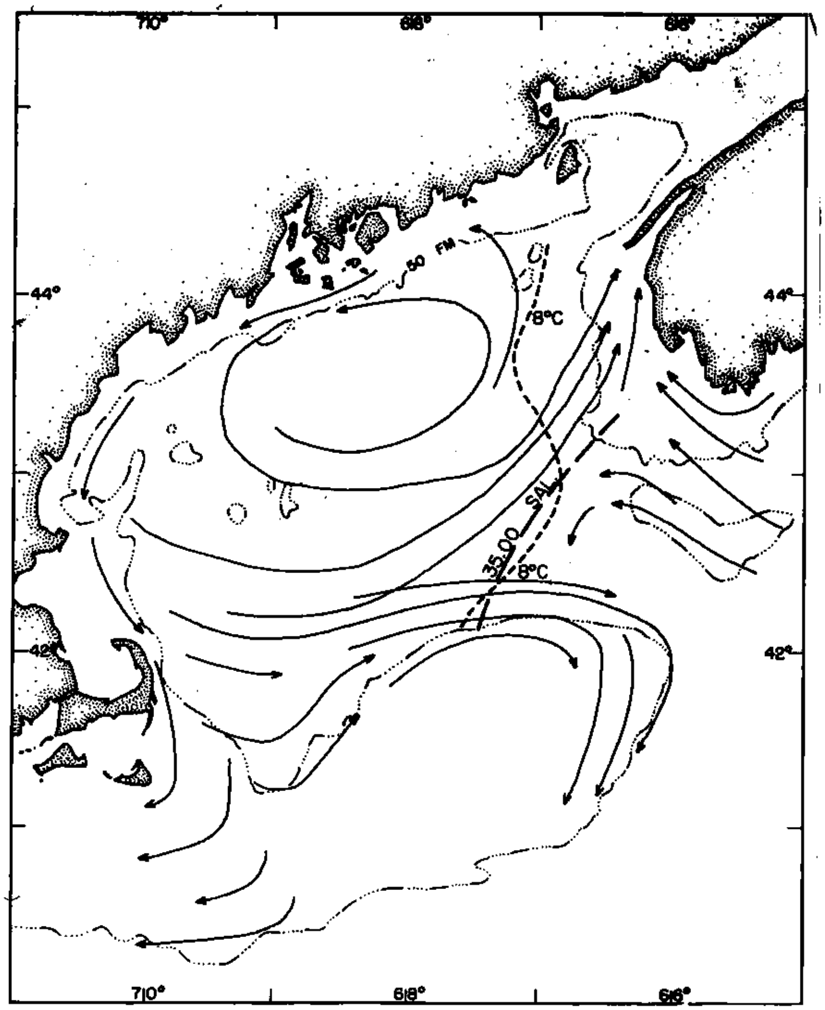

Fig. 18. Approximate location of 8°C bottom temperature and 35 o/oo salinity boundaries representing maximum penetration of ocean water into the Gulf of Maine (Data from Bigelow, 1927).

with a season of rigid hydrographic stability. We cannot discount the effect of inflowing currents around western Nova Scotia which may be sufficient to confine the larvae within the Gulf during this pelagic stage. Any outflow of water from the Gulf is southward around the eastern tip of Georges Bank, or through the South Channel near Cape Cod. *Sphyrion* larvae carried south in this fashion would enter waters where redfish are scarce, and there would be little possibility of finding a host of this species.

2. Changes in Host and Parasite Populations.

Evidence presented above suggests that concurrent changes in the host and parasite populations resulted in a major change in the host-parasite relationship between 1943-47 and 1957-62. The two-fold increase in *Sphyrion* incidence on redfish gives an approximate measure of the parasite population increase. United States landings statistics show that the Gulf of Maine redfish fishery differed greatly during the two periods of intensive study. The 1943-47 period was characterized by heavy fishing effort and high redfish landings; average annual effort of 8,500 vessel-days fished and 97 million pounds of redfish landed. Fishing effort decreased to 3,300 vessel-days per year and landings reduced to 31 million pounds annually during 1957-62. We will not attempt, in this paper, to analyze the complex effects of these changes in rate of exploitation on the redfish stock.

It is sufficient to note that the accumulated redfish stock was comparatively large during the early period and was smaller in the latter period.

The observed changes in redfish sex ratio and size composition probably can be attributed primarily to the effect of fishing. In a population where females initially average about 2 cm larger than males, and outnumber them, otter trawl fishing effort imposes higher fishing mortality on females. Prolonged intensive fishing effort would tend to equalize the sex ratio and minimize differences in size composition between sexes, resulting in changes such as we observed.

3. Effect of Parasite on Host.

Several aspects of the host-parasite relationship suggest that the parasite harms its host. The relative abundance of the three stages of infestation, differences between size of nonparasitized fish and those having the three stages of infestation, and seasonal variation in parasite incidence all indicate that *Sphyrion* infestation may kill some fish.

Although we do not know the longevity of the parasite, a difference of 1-2 cm in average length between fish groups infested with each stage indicates that each successive group, based on our knowledge of redfish growth, is about 1 year older than the preceding one (Fig. 15). This means that an average female parasite is about one year from the time it is first visible to the unaided eye until it attaches, dies, or is removed from the host. Since many of the parasites are broken off, it is likely that an unmolested parasite lives considerably longer, perhaps two years or more.

The second stage of infestation is least numerous and, therefore, is probably shorter than the other two stages. Since it is, by definition, a transitory stage, perhaps only a few weeks are required from the time a copepod is broken loose until the wound has healed. From what we have observed the third stage has potentially the longest duration. Heads of the parasites are so deeply and firmly embedded that usually they become encysted in the flesh when the wound heals. These cysts apparently persist for years in a healthy host.

Relative numbers of fish parasitized with each stage of infestation, and the approximate duration of each stage, may indicate the probable rate of survival of parasitized fish through the three stages. Assuming that the second stage is shorter, and the third longer, than the first stage then, after several years of parasitization, the third stage should be about as abundant in the population as the first. Since the third stage is less numerous than the first, fish with encysted parasite remains either remove the cysts, or die. It seems unlikely that cysts can be absorbed completely by surrounding tissue, or can be discharged from the tissue as matter from a festering sore, but this is possible. Redfish natural mortality may be sufficiently high to cause this reduction, but *Sphyrion* infestation probably kills many fish.

The great difference in winter and summer parasite incidence is not what would be expected of a long-lived and durable parasite such as *Sphyrion* appears to be. Highest incidence in late winter suggests a single spawning period in early winter with infestation immediately thereafter (Fig. 9). Reduction of about 50% in numbers from winter to summer indicates either a high removal rate of parasites from the host, or, as was mentioned earlier, a high mortality rate of parasitized fish.

Removal of *Sphyrion* could result from at least three causes: (1) natural mortality of the parasite, (2) abrasion by the host, or (3) predation by fish or invertebrates. There is no evidence that redfish are involved in commensal parasite-removal relationships with other animals, but similar relationships have been shown in reef fish communities (Limbaugh, 1961), and may occur here. Perlmutter (1951) proposed abrasion by the host as the major factor controlling position of the parasite on Gulf of Maine redfish. This proposal is debatable since it does not apply to the Hamilton Inlet Bank and Eastern Grand Bank areas where a different pattern of infestation suggests either different environmental conditions,or, perhaps, different genetic characteristics of the parasite stocks (Templeman and Squires, 1960). Natural mortality of *Sphyrion* is not likely to be high enough to account for the entire reduction in parasite incidence. Each of the three factors mentioned may contribute partially to the reduction in numbers of parasitized fish, but mortality of the host due to infestation is a probable cause of seasonal reduction in parasite incidence.

Difference in size between parasitized and non-parasitized redfish is one of the most obvious effects of infestation, but the reasons for this difference are not clear. Aside from variations in growth rate of the host, three factors could change the size composition of one or more of the groups of fish infected with the three stages of infestation. (1) Duration of parasite recruitment year? (2) Minimum length of host that *Sphyrion* will invade, and (3) Whether the parasite kills its host, either directly or indirectly.

We showed earlier that infestation of the host probably occurs in late winter. Assuming that infestation occurs only then growth of parasitized fish will steadily increase the mean length of that group during the remainder of the annual cycle, with no recruitment of smaller sizes of parasitized fish to the group. Nonparasitized fish also will grow during that time, but small fish will join the group, causing the mean length of nonparasitized fish to be less than that of the parasitized fish. The influence of this factor can account only for the difference in size composition between nonparasitized fish and first stage parasitized fish, and does not apply directly to differences between the three stages of infestation. However, since the three stages of infestation proceed in time then fish surviving to the later stages are larger than fish comprising preceding groups assuming that growth of surviving parasitized fish is not inhibited. Continuing this process for several years would result in size differences similar to those observed in the Gulf of Maine redfish population, but this factor alone may not account for the magnitude of difference, or the relative degree of skewness, shown between size compositions of redfish having the three stages of parasite infestation.

If *Sphyrion* infests only fish larger than a specific size, then this factor alone accounts for parasitized fish being larger than nonparasitized fish, and there is no need to speculate about possible mortality of the host due to parasite infestation. However, there is neither experimental evidence that *Sphyrion* requires a certain size host, nor that it is influenced by secondary factors related to size or maturity of its host. If the parasite requires only a supply of blood to survive, then it is probable that all sizes of redfish are attacked, and many infested small fish weaken and die. Since *Sphyrion* can grow to a length of 6 cm, it is conceivable that fish smaller than 20 cm are unable to survive the stress of a growing parasite.

CONCLUSIONS

The hypothesis that redfish mortality may be caused by *Sphyrion* infestation is supported largely by fragmentary evidence. No single aspect of the parasite's incidence proves that it kills its host, but the aggregate effect suggests that it does. Many of the changes in the redfish population might be results of mortality caused by parasitization, but there are equally plausible alternative explanations. If *Sphyrion* attacks redfish smaller than 20 cm long the relative scarcity of parasitized fish in that size group suggests that parasite infestation may kill many small fish.

From evidence shown in these gross studies of *Sphyrion* incidence on redfish, we conclude that the parasite is sufficiently important in the Gulf of Maine fishery to deserve more detailed study of its relationship to redfish. Investigation of *Sphyrion* life history and environmental factors influencing its distribution must be given high priority.

REFERENCES

BIGELOW, H.B., 1927. Physical oceanography of the Gulf of Maine. *U.S. Fish.Bull.*, 40 (2): 511-1027.

BUMPUS, D.F., 1960. Sources of water contributed to the Bay of Fundy by surface circulation. *J. Fish. Res. Bd. Canada*, 17 (2): 181-197.

DAY, C.G., 1958. Surface circulation in the Gulf of Maine as deduced from drift bottles. *Fish Bull. U.S.*, 58 (141): 443-472.

HERRINGTON, W.C., H.M. BEARSE, and F.E. FIRTH. 1940. Observations on the life history occurrence, and distribution of the redfish parasite, *Sphyrion lumpi*. *Spec. Sci. Rept., U.S. Fish Wildl. Serv.*, No. 5, 18 p.

KROYER, H. 1845. Lestes lumpi Kroyer. *Danmarks Fiske.* 2, Copenhagen, p. 517.

LIMBAUGH, C., 1961. Cleaning symbiosis. *Sci. Amer.*, 205 (2): 42-49.

NIGRELLI, R.F., and F.E. FIRTH. 1939. On *Sphyrion lumpi* (Kroyer) a copepod parasite on the redfish, *Sebastes marinus* (Linnaeus), with special reference to the host-parasite relationships. *Zoologica*, 24 (1): 1-10.

PERLMUTTER, A. 1951. The positional pattern of the copepod parasite *Sphyrion lumpi* on the rosefish, *Sebastes marinus*, and its relationship to the behaviour of the fish. *Copeia*, No. 1: 97-98.

SINDERMANN, C.J., 1961. Parasitological tags for redfish of the western North Atlantic. *Spec. Publ. int. Comm. Northw. Atlant. Fish.*, No. 3, p. 111-117.

TEMPLEMAN, W., and H.J. SQUIRES. 1960. Incidence and distribution of infestation by *Sphyrion lumpi* (Kroyer) on the redfish, *Sebastes marinus* (L.), of the western North Atlantic. *J. Fish. Res. Bd. Canada*, 17 (1): 9-31.

WILLIAMS, I.C. 1963. The infestation of the redfish *Sebastes marinus* (L.) and *S. mentella* Travin (Scleroparei: Scorpaenidae) by the copepods *Peniculus clavatus* (Müller), *Sphyrion lumpi* (Krøyer) and *Chondracanthopsis nodosus* (Müller) in the eastern North Atlantic. *Parasitology*, 53: 501-525.

WILSON, C.B., 1919. North American parasitic copepods belonging to the new family Sphyriidae. *U.S. Nat. Mus. Proc.*, 55: 549-604.

C-7

DENSITY-DEPENDENT FOOD RELATIONSHIPS WITH REFERENCE TO NEW ENGLAND GROUNDFISH

By

Roland L. Wigley[1]

ABSTRACT

From the ecological standpoint, food webs and the quantitative aspects of major pathways in food webs are exceedingly important because of the fundamental and comprehensive influence of nutrition on individual organisms. Many of the population attributes fishery biologists are concerned with, such as survival rate, growth rate, length-weight relationship, age composition, sex ratio, fecundity, migration, density distribution, are all profoundly affected by nutrition.

Contagious distributions are characteristic of animal populations; New England groundfish, haddock in particular, provide good examples of this type of distribution. Food is a major element in attracting animals to particular places.

Past research has neglected the quantitative relationships between groundfish stocks and their food supply. Preliminary data presented here indicate that groundfish on the New England Continental Shelf congregate in specific geographical areas. Furthermore, macrobenthic invertebrates — a major source of groundfish food — tend to be aggregated in the same localities. It is suggested that more intensive studies of this subject may provide some of the information necessary to understand the present biological status of, and prognosticate future changes in, groundfish abundance, growth, distribution, size composition, and other population attributes.

INTRODUCTION

In ecological investigations the importance of food and feeding cannot be overemphasized. According to Borradaile (1923) "Relations between an animal and other organisms in its surroundings are almost always based in the long run upon nutrition". Even the reproductive process is reduced or ceases when nourishment falls to substandard levels. Nourishment for each individual must be obtained from its environment, and there is obviously a limit to the quantity of food the environment can produce. It follows, then, that food can be a major influence governing population size and composition.

It is the purpose of this report to call attention to the ecological importance of foods, review some of the density-dependent food relationships, and discuss some preliminary results of food concentrations in relation to the density of New England groundfish.

In this report a food shortage is considered the converse of too many predator animals. It is the absolute shortage of food (or the relative density of consumers versus food) that is relevant to this topic.

POPULATIONS LIMITED BY FOOD SHORTAGES

Good evidence exists to indicate that food shortages are effective in limiting the population size of certain animal species. This phenomenon has been observed in representatives of various animal groups, and undoubtedly numerous unstudied species are similarly restricted. Insects such as sheep blowflies, *Lucilia* and *Chrysomyia*, and flour-beetles, *Tribolium*, have been shown to have their numbers restricted by food shortages (Ullyett,1950; Park, 1948; Park and Frank, 1950). Bird populations are likewise limited by food (Lack, 1954).. Large mammals, for example mule deer and white-tailed deer, *Odocoileus*, elk, *Cervus*, and other large ungulates, have been reported as being limited by food shortages (Leopold, 1943; Doman and Rasmussen, 1944; Raush, 1950; and Krefting, 1951). Food shortage is also one of the principal factors restricting populations of small mammals, such as voles, Cricetidae, squirrels, *Sciurus*, hares, *Lepus*, and foxes, *Alopex*, (Dice, 1952; Elton,

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1942). Even the human population has been strongly influenced by food limitations. Primitive man is believed to have been held in check by food shortages, or his ability to obtain food (Andrewartha, 1961). Famines and food-motivated emigrations by modern man during the early historical period and even in more recent times in Ireland and China (Carr-Saunders, 1922; Lack, 1954) provide further evidence of the vital influence food supplies have on the survival of human beings.

More pertinent to our topic are population limitations of aquatic organisms, particularly fish, resulting from food shortages. In addition to fluctuations in numbers of fish (survival rate) in relation to food supplies, other manifestations of food-related limitations are: (a) growth rate, (b) length-weight ratio, (c) fecundity, and (d) migrations.

The relatively recent entry of the sea lamprey *Petromyzon* into the Great Lakes provides a good example of changes in population abundance (survival rate) resulting from quantitative changes in food supply. Before sea lampreys were present in the upper Great Lakes, the lake trout *Salvelinus* - principal source of lamprey food - were plentiful. Lake trout landings amounted to millions of pounds annually in both Lake Huron and Lake Michigan. Several decades later the lamprey population had increased greatly whereas the trout population had been reduced to virtual extinction. This forced the lampreys to switch to alternate food sources, which consisted of several species of chubs, *Leucichthys* and whitefish, *Coregonus* and *Prosopium*. Subsequently the abundance of these species was severely reduced, some to near extinction. During the latter phase of this cycle a pronounced decline in number of lampreys became evident (Applegate, 1950; Erkkila, *et al.*, 1956; Moffett, 1958). If effective control measures had not been instituted by Federal and State (Provincial) agencies, the establishment of a numerical balance between the lampreys and their host species would have been expected.

Inasmuch as many kinds of fish are capable of surviving rather extended periods with little or no food, the short-term effect of food shortage is not necessarily a high mortality, but rather a retardation in growth. Brown (1957) states "Food supply is probably the most potent factor affecting the growth of fishes..." Thus, growth rate measurements may sometimes be useful in predicting low food supplies and subsequent limitations in fish abundance and fish production. For example, the average weight of individual sockeye salmon, *Oncorhynchus* in Cultus Lake, Canada, was reduced one half when the number of salmon was increased threefold (Foerster and Ricker, 1941). This example illustrates growth retardation resulting wholly or in part from food limitations. Numerous other reports in the literature indicate stunted populations of fishes, notably yellow perch, *Perca*, and bluegill sunfish, *Lepomis*, in situations where severe food competition exists (Carlander, 1950; Clarke, 1954).

Spectacular increases in growth rate of trout, salmon, and other species, after migrating from nursery streams to lakes or the sea results, at least in part, from richer food supplies. Migrations motivated by food requirements will be discussed in a later section.

Low fecundity among animals due to inadequate nourishment may be considered to have general application. According to Brody (1945), "... there is no doubt that egg production is related exponentially to feed consumption..." This is a well established principle heeded by agriculturists and fish culturists, and pertains to both domestic and wild populations. The effect of nourishment on fecundity in animals other than fish, for example birds and mammals (Lack, 1954; Cheatum and Severinghaus, 1950) has been adequately demonstrated.

In regard to fishes, Nikolsky (1963) reported, "The fecundity in a single population may undergo considerable fluctuations in relation to the supply of nourishment." In this same report he cites evidence of this relationship in two species, the humpback salmon, *Oncorhynchus*, and the roach, *Rutulis*. Information from other sources (Brown, 1957; Lagler, *et al.*, 1962) concur that "condition" and "environmental and physiological conditions" influence fecundity in fishes.

AGGREGATIONS OF ANIMALS SEEKING FOOD

An overall view of the planet Earth clearly shows concentrations of life in particular areas, such as the tropic and temperate regions in contrast to relatively barren deserts and portions of the polar regions. A more restricted view, considering the oceanic life from the shore zone to mid-ocean (Fig. 1) also reveals pronounced areal differences in quantity of plant and animal life. On a still smaller scale are the dense concentrations of aquatic life represented by schools of fish, coral reefs, shellfish beds, and similar groupings.

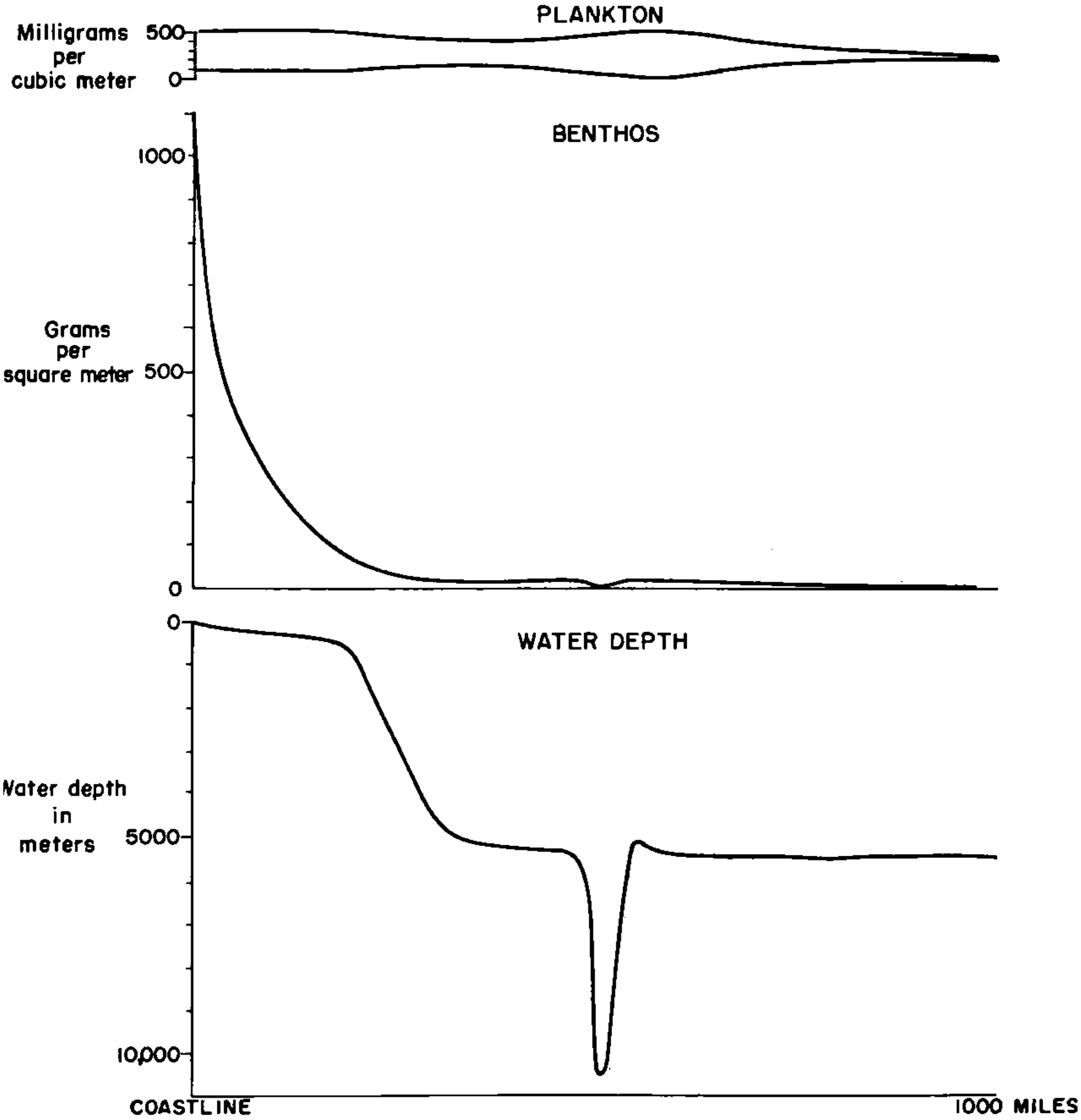

Fig. 1. Quantitative changes in the standing crop of plankton and benthos from shore to 1,000 miles offshore (modified after Zenkevich, 1956).

"Contagious distributions are the rule in nature. Sessile as well as motile animals settle or ollect in favorable localities...." according to Allee *et al.*, (1949). Moreover, third in the ist of aggregations cited by the same authors is "Collections about food". Clarke (1954) states .....sources of food or shelter similarly serve as a focal point at which animals from the surounding areas tend to congregate."

The aggregation of fish and other aquatic organisms about their food is particularly pertinent o the subject of this report. The following few examples have been selected from the literature to xamplify the type of relationship considered here.

Plankton-feeding whales (humpback,*Megaptera*, blue, fin, and sei, *Balaenoptera*) concentrate in areas where planktonic organisms, chiefly euphausiids and copepods, upon which they feed, are most abundant. This relationship has been well documented (Hjort and Ruud, 1929; Hardy and Gunther,1935). Reports of nekton feeding whales, dolphin, *Delphinus*, and the false killer whale, *Pseudorca*, also stress the association with schools of fish and cuttlefish, *Sepia*, (Legendre, 1922, Hinton, 1928).

Herring, *Clupea*, is a good example of pelagic species which aggregate in areas where their foods are present in abundance. Reports by Lucas (1936) and Hardy, *et al.*, (1936) deal with the correlation between the density of *Calanus*, the principal food of North Sea herring, and the quantity of herring caught by commercial fishermen. These reports clearly show that the herring catch was largest where *Calanus* was abundant and the catch was considerably lower where *Calanus* was sparse. Based on this relationship, a special plankton sampler called the plankton indicator was developed by Dr Hardy and his associates for use by commercial herring fishermen to assist them in locating suitable fishing grounds.

Fishing records show that tuna, such as albacore, *Thunnus*; bluefin, *Thunnus*; skipjack, *Katsuwonus*; yellowfin, *Neothunnus*, and related species, concentrate in areas of high biological productivity. Investigations by King and Ikehara (1956) and King and Hida (1957) revealed a general correspondence between zooplankton abundance and large catches of yellowfin tuna. Skipjack, according to Schaefer (1961), tend to be most abundant in highly productive areas where their forage is most plentiful. Yabe *et al.* (1963), in summarizing some of the literature pertaining to tunas and their environment, reported that several studies by other scientists defined the area of largest concentration of albacore in the North Pacific as being closely associated with the highly productive "transition zone", and that upwelling and divergence zones in the mid-Pacific equatorial waters produce very favorable conditions for increased productivity and consequently affect the abundance of yellowfin tuna. Laevastu and Rosa (1963) state "...the best tuna fishing areas coincide with more productive areas in the tropics and medium latitudes. A general relation between tuna abundance and abundance of macro-plankton and small nekton holds true in general". Howard (1963) concluded, "Observations on the nature and occurrence of commercial concentrations of tunas have shown they aggregate in particular localities. Beyond their direct response to surface temperature, and perhaps other factors not yet recognized, the important reference is their food supply".

The sea lamprey, *Petromyzon*, in Cayuga Lake, New York, exhibited marked differences in abundance from one section of the lake to another. The two sections of the lake containing the highest lamprey density were the same areas where lake trout, *Salvelinus*, were most abundant (Wigley,1959).

F.M. Davis at Lowestoft, England, was one of the few biologists who have reported on the density-dependent nature of marine groundfish and their food supply. In 1923 he stated, "...it seems reasonable to suppose the discovery of rich feeding grounds will throw light on the shoaling of food fish. In this connection it is interesting to note that the position of [a dense patch of *Spisula* and *Mactra*] was given to several skippers of Seine Boats working out of Lowestoft and Yarmouth and two of them found young haddock in large quantities — one of them after failing on other grounds — in June 1923. The fish were gorged with shell remains".

Evidence that fish concentrations, and their foods, occur in deep as well as in comparatively shallow water is apparent from the statement by Murray and Hjort (1912): "Even down to 500 fathoms the 'Michael Sars' found just as many fishes as on the bank, viz, about 300 fishes in one haul, and these were not small. <u>At the same time the trawl was also crammed with other animals.</u>" Some of the "other animals" were presumably prey for the fish.

For many fish species, feeding aggregations are closely interrelated with feeding migrations. Thus, a brief consideration of migrations is appropriate before concluding this discussion.

Migrations of fishes stem from two major biological requirements, (1) food and (2) reproduction. We are concerned here only with the former. Nikolsky (1963) described the general sequence of events motivating a feeding migration as follows: "As they consume their food organisms, the fish reduce the concentration of food to a level at which energy expended in obtaining food cannot ensure the necessary rate of accumulation of the energy resources. When they have reduced the concentration of the food organisms below a certain level (which varies from species to species of both food and fish), the fish must move away and seek further concentrations of food organisms."

Feeding migrations may be active or passive, vertical or horizontal, and the periodicity of migration is most commonly diurnal or annual. Of special interest to the theme of this report is the aggregation of juveniles and adults on the feeding grounds resulting from either active or passive migration or a combination of both. It has been well documented that a variety of different fishes (salmon, *Oncorhynchus*, *Salmo*; trout, *Salmo*; herring, *Clupea*; cyprinids, Cyprinidae; sturgeon, *Acipenser*; cod, *Gadus*; pilchard, *Sardinia*; porbeagle, *Lamna*; mackerel, Scombridae; swordfish, *Xiphias*; whitefish, *Coregonus*; bream, *Abramis*; tunny, *Thunnus*; and many others) undertake food-motivated migrations (Norman, 1947; Nikolsky, 1963). These migrations need not be reviewed for the purposes of this report, but two examples pertaining to marine groundfish are relevant to subsequent sections.

Smidts' (1951) studies of the Danish Waddensea fauna revealed a summer migration of 0-group plaice into the wadden at precisely the time the greatest quantities of microfauna, upon which plaice feed, were present. Zenkewich, *et al.*, (1928) report a study in the Barents Sea that illustrates another food-related groundfish migration. The authors state the "...distribution of production in the Barents Sea is evidently connected with the migration of the cod and haddock, and with the distribution of some other fishes of industrial importance. The cod and haddock, in moving eastward, keep for the most part along the edges of shallows, their final goal being the Petchora waters and those near the Kanis peninsula, where food is plentiful."

To briefly summarize, a general application of ecological principles together with specific examples, cited in the foregoing account, signifies that contagious distributions are not only common in nature, but more specifically, may be expected for many marine groundfish species. Furthermore, a concentration of food organisms undoubtedly provides a strong stimulus affecting groundfish aggregations, particularly when food shortages exist.

NEW ENGLAND GROUNDFISH

Bottom-dwelling fishes inhabiting New England offshore waters clearly exhibit a contagious distribution. Commercial landings data (Power, 1962; Ackerman, 1941; and others), although grouped according to rather large geographical areas, reveal sizable differences in quantity of fish caught on the various fishing grounds. This information gives a gross indication of groundfish aggregations. Another indication of groundfish aggregations is the fishing effort by the commercial fleet. Large differences in effort from one area to another are obvious (Schuck, 1952; Colton, 1955). Undoubtedly the prospect of larger catches on particular fishing grounds strongly influences the selection of areas to be fished. More detailed information concerning the distribution of New England groundfish is the work by Colton (1955), in which he describes the spring and summer distribution of haddock on Georges Bank. This species was found to have a pronounced contagious distribution. Some of the principal factors evaluated and found to be associated with haddock distribution were: geographical area, season of year, water depth, and age of haddock.

More recent information showing aggregations of New England groundfish was obtained from two sources: (1) commercial landings statistics, and (2) research vessel catch records.

Commercial landings statistics for United States medium and large trawlers in 1962 are one data source analyzed specifically for this report to calculate groundfish density distribution. Only those trips in which trawler captains were interviewed to determine the geographic area fished, fishing effort (days fished), and related data were used in this analysis. Although information from this source represents only a small portion of the total fishing effort, it provides a reasonably good index of localities fished, and the catch rate in various sections of the New England area.

Groundfish inventories made by the US Bureau of Commercial Fisheries research vessels are the econd source of groundfish distribution data. Autumn inventories by *Albatross III* and *Delaware* during the years 1955 to 1961, were analysed. These vessels used a standard No. 36 otter trawl 24-m groundrope and 18-m headrope) with a fine-mesh liner. Values from this source are based on he number of fish caught per 30-min haul. A total of 588 otter trawl hauls were made in the study area.

Dominant fish species comprising the catch in both the commercial landings data and research vessel catch were: haddock, *Melanogrammus*; cod, *Gadus*; silver hake, *Merluccius*; pollock, *Polachius*; redfish, *Sebastes*; butterfish, *Poronotus*; yellowtail, *Limanda*; winter flounder, *Pseudoleuronectes*; and American dab, *Hippoglossoides*. The spiny dogfish, *Squalus*, was abundant in reearch vessel catches, but was not present in commercial landings.

The haddock, one of the most abundant New England groundfishes, has been selected to illustrate the density-distribution of a single species. The autumn distribution of haddock in New

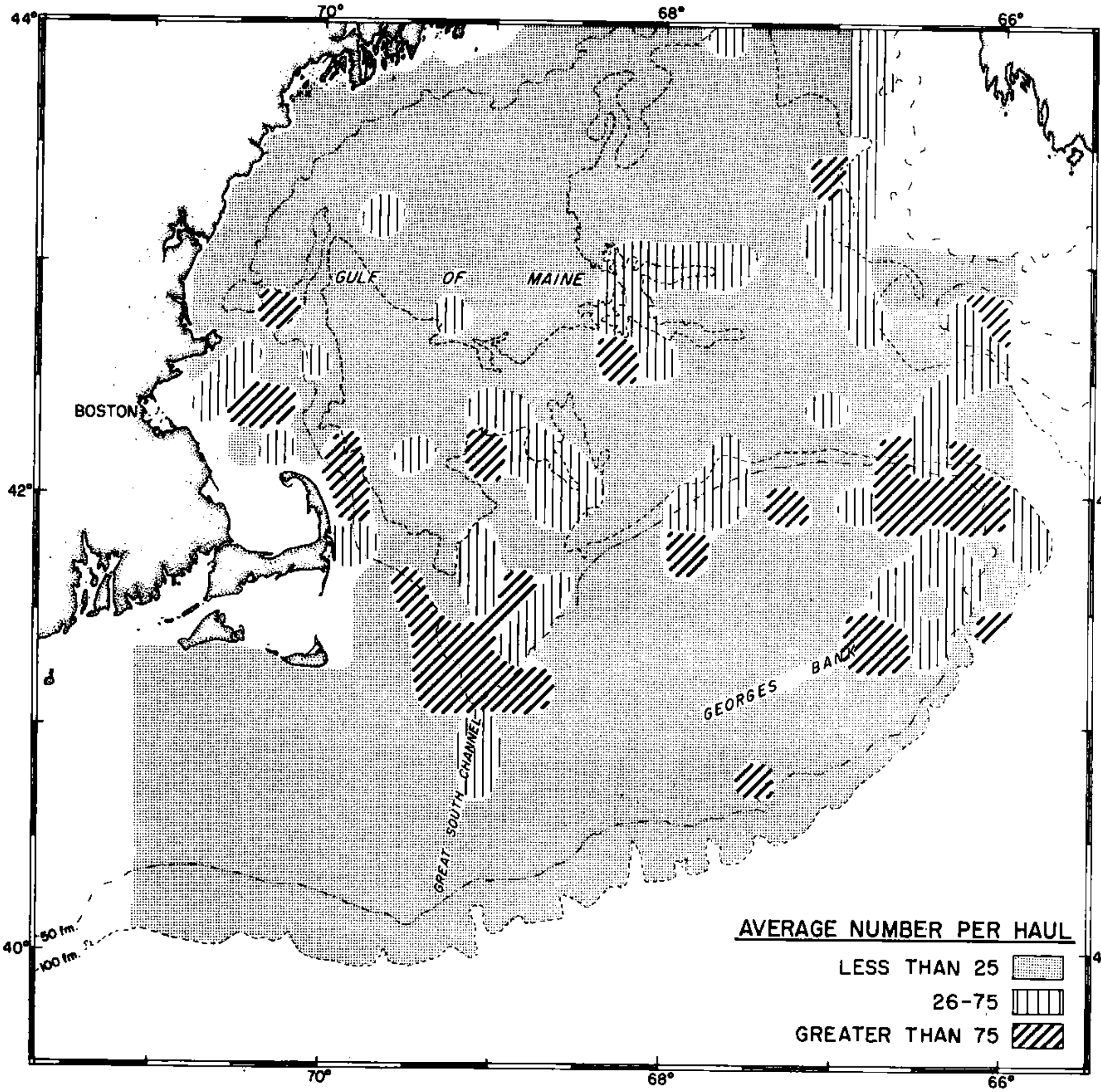

Fig. 2. Autumn density-distribution of haddock based on inventories conducted by research vessels *Albatross III* and *Delaware* from 1955 through 1961. Values are mean numbers of haddock caught per 30-min haul in a No. 36 otter trawl.

England offshore waters is shown in Fig. 2. This distribution chart is based on the mean number of haddock per haul for each 12-min section of latitude and longitude resulting from research vessel trawl catches from 1955 through 1961. It is apparent that haddock are abundant in some areas and sparse in others. Both this information and data presented by Schuck (1952) and Colton (1955) disclose that haddock concentrations occur chiefly in the northern and eastern sections of Georges Bank and in the vicinity of Great South Channel.

Evidence that groundfish — all species combined — are aggregated in a similar manner, and in some of the same localities as haddock, is shown by the following data. Illustrated in Fig. 3 is

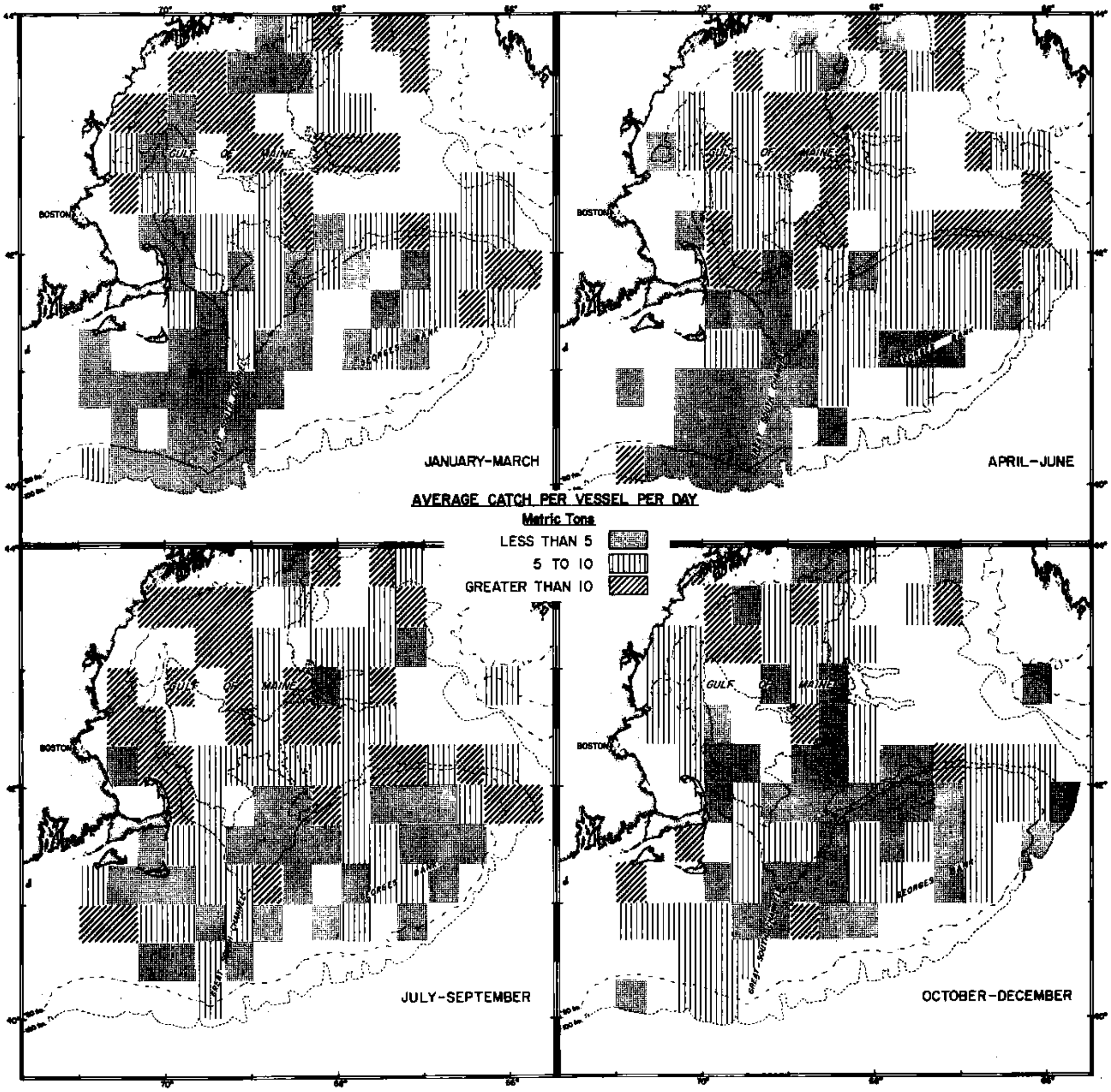

Fig. 3. Seasonal density-distribution of New England groundfish based on commercial landings statistics for 1962. Values are catch per vessel per day in metric tons.

the catch (metric tons) per vessel per day by the commercial fishing fleet for each season of the year. This chart is based on mean value per 20-min section of latitude and longitude. Groundfish concentrations occurred in all seasons, but were least pronounced during the fourth quarter, October-December. Wide fluctuations in the catch rate occurred in coastal areas and south of Cape Cod and the islands of Martha's Vineyard and Nantucket. This is due mainly to large catches of migrant species in April-June and July-September. Relatively high catch rates were maintained throughout the year in large areas in and near Great South Channel (particularly in the northern part), northern and eastern Georges Bank, and several sections in the Gulf of Maine. Catch rates remained relatively low at all seasons in southwestern and east-central Gulf of Maine and southwestern Georges Bank.

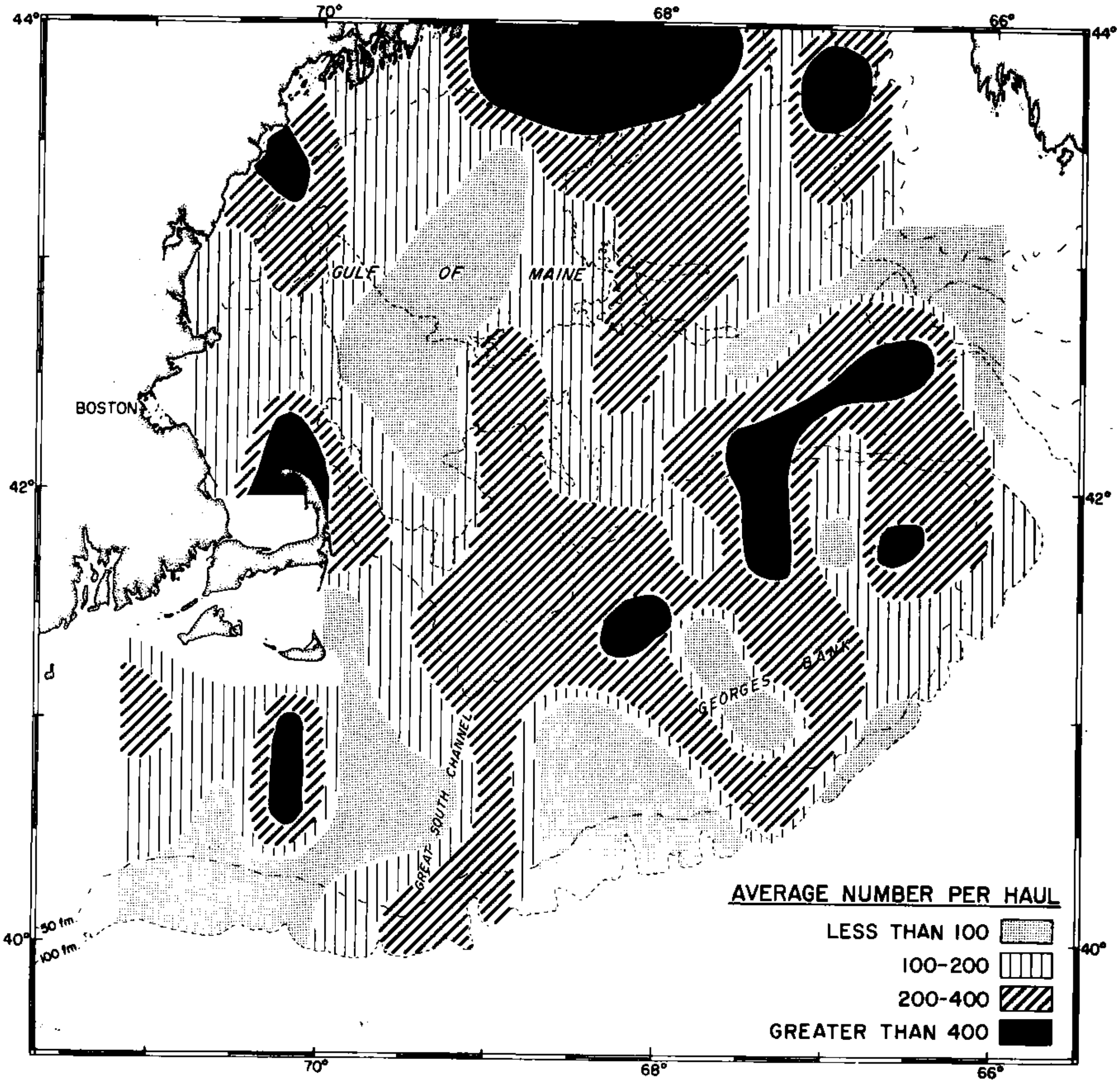

Fig. 4. Autumn density-distribution of New England groundfish based on inventories conducted by research vessels *Albatross III* and *Delaware* from 1955 through 1961. Values are mean number caught per 30-min haul in a No. 36 otter trawl.

Research vessel trawl catches reveal a groundfish density-distribution pattern similar to that described above. The mean number of groundfish per trawl haul in fall census cruises of 1955 through 1961 is shown in Fig. 4. Basis for this chart are mean values for each 24-min section of latitude and longitude. Large catches were prevalent over much of Georges Bank, especially on the northern part; Great South Channel; and the western, northern, and central portions of the Gulf of Maine, plus somewhat localized areas along the coast and south of Cape Cod and the islands of Martha's Vineyard and Nantucket. Low catches were common on southwest Georges Bank, west-central and east-central Gulf of Maine, and portions of the area south of Cape Cod and adjacent islands.

In both the commercial and research vessel catches the occurrence of semi-pelagic groundfish species - which accounts for a significant proportion of the Gulf of Maine catch - should be given general consideration until this subject is investigated and treated quantitatively.

The quantitative comparison between the distribution of groundfish and their food supply is the subject of this section. Principal source of nourishment for New England groundfish appears to be holobenthic and merobenthic invertebrate organisms (Bigelow and Schroeder, 1953; Wigley, 1956). Small fishes, of course, are an important food for many large groundfish but a substantial number of these small prey fishes also depend heavily on benthic organisms for food.

The one available quantitative measure of groundfish food supplies on the New England Continental Shelf is based on samples of macrobenthic invertebrates. This information was rather difficult and time consuming to obtain due to the enormous area involved, strong tidal currents, deep water, and coarse bottom sediments. However, some preliminary estimates of the benthic biomass were obtained during the summer months from 1957 to 1962. A total of 426 quantitative samples collected with a Smith-McIntyre grab sampler have been analysed. The analysis procedure consisted of washing each sample through a 1-mm mesh screen and weighing (wet weight) the retained fauna. Wet weights were converted to dry weights by using conversion factors derived from representative specimens. The results are plotted in Fig. 5. In order to present a more accurate measure of the food supply, polychaete tubes, mollusk shells, and calcareous matter in other organisms are omitted.

Distinct differences in macrobenthos density from one area to another are apparent in Fig. 5. Particularly noticeable is the quantitatively rich benthic fauna south of Cape Cod and the islands of Martha's Vineyard and Nantucket. The Gulf of Maine biomass is rather low, and that in the vicinity of Georges Bank is intermediate. High benthos density is common in the Great South Channel area, northern edge of Georges Bank, and north-central Gulf of Maine, in addition to its prevalence south of the islands. Intermediate density is especially widespread in the Gulf of Maine area. Low density occurs over extensive areas in the Gulf of Maine and Georges Bank.

The density distribution of benthic organisms (Fig. 5) compared geographically with groundfish density (Figs. 3 and 4) shows a general similarity between the two. For example, Great South Channel, northern periphery of Georges Bank, portions of the Gulf of Maine, and a large part of the area south of Cape Cod and the islands of Martha's Vineyard and Nantucket have high densities of both fish and invertebrates. Conversely, low densities of both categories occur in west-central Gulf of Maine, and southwestern and southeastern Georges Bank. A few areas, such as northern Gulf of Maine and some areas south of Cape Cod and the islands, show either an inverse correlation or no correlation.

A more specific comparison of the relationship between density of groundfish and food supply, is that between haddock (Fig. 2) and benthic invertebrates (Fig. 5). A comparison of these two components discloses a reasonably good correlation, except in the southwestern portion of the study area. It should be noted that haddock is a boreal species and would not be expected to occur in large numbers in the temperate waters in the southwestern portion of this region.

Although the long-range objective of obtaining detailed information necessary for density comparisons between each groundfish species and its food supply has not yet been attained, further evaluation of existing data is expected to provide useful results. Two principal aspects now under consideration are: (1) the pelagic feeding excursions of some groundfish species, and (2) the ranking or classifying of benthic organisms according to their energy value and utilization as foods by groundfish.

SUMMARY AND DISCUSSION

Aggregations of natural animal populations, both large and small, commonly result from biological as well as physical-chemical influences. The density or degree of concentration in these populations is sometimes related in a predictable manner to environmental factors. Reports in the literature indicate that a variety of animal groups, such as insects, birds, mammals, and pelagic fishes (1) congregate where foods are plentiful, and (2) that food shortages can limit population size and alter its structure (size, age, sex ratio).

In the past, little research has been devoted to quantitative aspects of groundfish food supplies. Also, little is known about species composition, population structure, and density distribution of groundfish stocks as related to food supplies. Scarcity of quantitative studies of

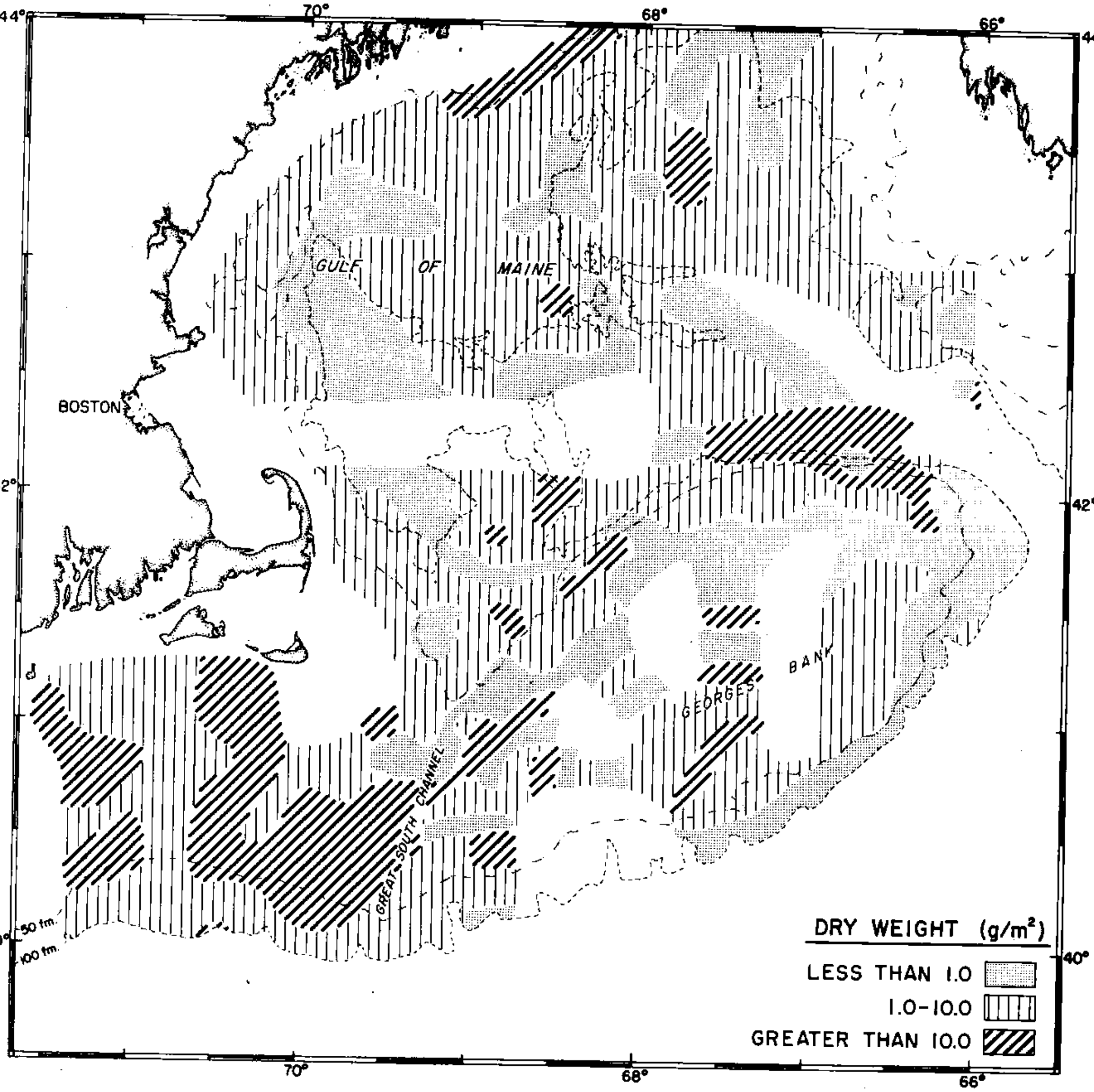

Fig. 5. Biomass of the macrobenthic invertebrate fauna collected with a Smith-McIntyre grab sampler. Values are dry weight (grams) per square meter.

groundfish density and food organisms over sufficiently large areas have impeded studies on this subject. A little information is now available bearing on this aspect of New England offshore groundfish. Research vessel census data and commercial fishery catch records indicate that New England groundfish tend to aggregate in specific, geographic localities. Also, quantitative measures of benthic invertebrates reveal pronounced aggregations of these organisms. Of special interest is the fact that geographically the correlation in density between groundfish and benthic invertebrates is generally good. This correlation warrants further investigation, since it is anticipated that inventories of groundfish and their food, conducted simultaneously or nearly so, would provide an index to the well being of existing populations and yield clues to future changes in abundance, size and age composition, fecundity, and related biological characteristics.

I thank Mr Raymond L. Fritz and personnel in the biostatistical unit at the Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, for providing groundfish inventory data and assistance in processing catch statistics.

REFERENCES

ACKERMAN, E.A. 1941. New England's fishing industry. University of Chicago Press, Chicago. 303 p.

ALLEE, W.C., A.E. EMERSON, O. PARK, T. PARK, and K.P. SCHMIDT. 1949. Principles of animal ecology. W.B. Suanders Co., Philadelphia and London. 837 p.

ANDREWARTHA, H.G. 1961. Introduction to the study of animal populations. Methuen and Co., London. 281 p.

APPLEGATE, V.C. 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. (*Spec. Sci. Rep. U.S. Fish Wildl. Serv.-Fish.*) (55): 1-237.

BIGELOW, H.B. and W.C. SCHROEDER. 1953. Fishes of the Gulf of Maine. *Fish. Bull.*, U.S. 53 (74): 1-577.

BORRADAILE, L.A. 1923. The animal and its environment, a text-book of the natural history of animals. Henry Frowde and Hodder and Stoughton, London. 399 p.

BRODY, S. 1945. Bioenergetics and growth, with special reference to the efficiency complex in domestic animals. Reinhold Publishing Corp., New York. 1,023 p.

BROWN, M.E. (Editor). 1957. The physiology of fishes. Volumn 1, Metabolism. Academic Press, Inc., New York. 477 p.

CARLANDER, K.D. 1950. Handbook of freshwater fishery biology. Wm. C. Brown Co., Dubuque, Iowa. 281 p.

CARR-SAUNDERS, A.M. 1922. The population problem; a study in human evolution. Clarendon Press, Oxford. 57 p.

CHAETUM, E.L. and C.W. SEVERINGHAUS. 1950. Variations in fertility of white-tailed deer related to range conditions. *Trans. N. Amer. Wildl. Conf.*, 15: 170-189.

CLARKE, G.L. 1954. Elements of ecology. John Wiley and Sons, Inc., New York. 534 p.

COLTON, J.B. 1955. Spring and summer distribution of haddock on Georges Bank. *U.S. Fish Wildl. Serv.-Fish.*, (156): 1-65.

DAVIS, F.M. 1923. Quantitative studies on the fauna of the sea bottom. No. 1. Preliminary investigation of the Dogger Bank. *Fish. Invest.*, Lond. (2), Ser. II, 6 (2): 1-54.

DICE, L.R. 1952. Natural Communities. University of Michigan Press, Ann Arbor. 547 p.

DOMAN, E.R. and D. I. RASMUSSEN. 1944. Supplemental winter feeding of mule deer in northern Utah. *J. Wildl. Mgmt.* 8: 317-338.

ELTON, C. 1942. Voles, mice and lemmings. Problems in population dynamics. Clarendon Press, Oxford. 496 p.

ERKKILA, L.F., B.R. SMITH and A.L. McLAIN. 1956. Sea lamprey control on the Great Lakes 1953 and 1954. *U.S. Fish. Wildl. Serv., Spec. Sci. Rep.-Fish.*, (175): 1-27.

FOERSTER, R.E. and W. E. RICKER. 1941. The effect of reduction of predaceous fish on survival of young sockeye salmon at Cultus Lake. *J. Fish. Res. Bd. Canada*, 5: 315-336.

HARDY, A.C., C.E. LUCAS, G.T.D. HENDERSON, and J.H. FRASER. 1936. The ecological relations between the herring and the plankton investigated with the plankton indicator. *J. mar. biol. Ass. U.K.*, 21: 147-291.

HARDY, A.C. and E.R. GUNTHER. 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926-1927. *Discovery Rep.*, 11: 1-456.

HINTON, M.A.C. 1928. Stranded whales at Dornoch Firth. *Nat. Hist. Mag., British Mus., (Nat. Hist.)*, 1 (5): 131-138.

HJORT, J. and J.T. RUUD. 1929. Whaling and fishing in the North Atlantic. *Rapp. Cons. Explor. Mer.*, 56(1): 1-123.

HOWARD, G.V. 1963. The matter of availability and the harvest of tunas. *FAO Fish. Rep.*, 3 (6): 1041-1055.

KING, J.E. and T.S. HIDA. 1957. Zooplankton abundance in the Central Pacific, Part II. *Fish. Bull., U.S.*, 57 (118): 365-395.

KING, J. and I.I. IKEHARA. 1956. Comparative study of food of bigeye and yellowfin tuna in the Central Pacific. *Fish. Bull., U.S.*, 57 (108): 61-85.

KREFTING, L.W. 1951. What is the future of the Isle Royale moose herd? *Trans. N. Amer. Wildl. Conf.*, 16: 461-470.

LACK, D. 1954. The natural regulation of animal numbers. Clarendon Press, Oxford. 343 p.

LAEVASTU, T. and H. ROSA. 1963. Distribution and relative abundance of tunas in relation to their environment. *FAO Fish. Rep.*, 3 (6): 1835-1851.

LAGLER, D.F., J.E. BARDACH, and R.P. MILLER. 1962. Ichthyology. John Wiley and Sons, Inc., New York. 545 p.

LEGENDRE, R. 1922. Notes biologiques sur le dauphin commun (*Delphinus delphis* L.). *Bull. Soc. zool. Fr.*, 47: 370-379.

LEOPOLD, A. 1943. Wisconsin's deer problem. *Wis. Conserv. Bull.*, 8: 1-11.

LUCAS, C.E. 1936. On certain interrelations between phytoplankton and zooplankton under experimental conditions. *J. Cons.*, 11: 343-362.

MOFFETT, J.W. 1958. Attack on the sea lamprey. *Mich. Cons. Mag.*, May-June. 8 p.

MURRAY, J. and J. HJORT. 1912. The depths of the ocean. Macmillan and Co., London. 821 p.

NIKOLSKY, G.V. 1963. The ecology of fishes. Academic Press, New York. 352 p.

NORMAN, J.R. 1947. A history of fishes. A.A. Wyn, Inc., New York. 463 p.

PARK, T. 1948. Experimental studies of interspecies competition. 1. Competition between populations of the flour beetles, *Tribolium confusum* Duval and *Tribolium castaneum* Herbst. *Ecol. Monogr.*, 18: 265-307.

PARK, T., and M.B. FRANK. 1950. The population history of *Tribolium* free of sporozoan infection. *J. Anim. Ecol.*, 19: 95-105.

POWER, E.A. 1962. Fishery statistics of the United States 1961. *Statist. Dig., U.S. Fish. Wildl. Serv.*, (54): 1-460.

RAUSCH, R. 1950. Observations on histopathological changes associated with starvation in Wisconsin deer. *J. Wildlife Mgmt.*, 14: 156-161.

SCHAEFER, M.B. 1961. Tuna oceanography programs in the tropical central and eastern Pacific. *Calif. Coop. Oceanic Fish. Invest., Rep.,* 8: 41-44.

SCHUCK, H.A. 1952. Offshore grounds important to the United States haddock fishery. *Res.Rep., U. S. Fish and Wildl. Serv.,* 32: 1-20.

SMIDT, E.L.B. 1951. Animal production in the Danish Waddensea. *Medd. Danm. Fisk. Havundersøg. Ser. Fisk.,* 11: 1-151.

ULLYETT, G.C. 1950. Competition for food and allied phenomena in sheep blowfly populations. *Phil. Trans. (B),* 234: 77-174.

WIGLEY, R.L. 1956. Food habits of Georges Bank haddock. *Spec. Sci. Rep., U.S. Fish. Wildl. Serv.,-Fish.,* (165): 1-26.

WIGLEY, R.L. 1959. Life history of the sea lamprey of Cayuga Lake, New York. *Fish. Bull., U.S.,* 59 (154): 561-617.

YABE, H., Y. YABUTA, and S. UEYANAGI. 1963. Comparative distribution of eggs, larvae and adults in relation to biotic and abiotic environmental factors. *FAO Fish. Rep.,* 3 (6): 979-1009.

ZENKEVICH, L. 1956. Biological appraisal of the ocean, and the problem of acclimatization. *In:* Papers Presented at the International Technical Conference on the Conservation of the Living Resources of the Sea; Rome, 18 April to 10 May 1955; United Nations, New York, p. 127-144, illus.

ZENKEWITCH, L., V. BROTZKY, and M. IDELSON. 1928. Materials for the study of the productivity of the sea-bottom in the White, Barents and Kara Seas. *J. Cons.,* 3: 371-379.

SECTION

D

D-1

THE POSSIBLE EFFECTS OF TEMPERATURE ON THE FECUNDITY OF GRAND BANK HADDOCK

By

V.M. Hodder[1]

ABSTRACT

Observations on the fecundity of haddock were made from ovaries collected during the springs of 1957-1961. Certain year-to-year differences in fecundity of fish of the same size and age were observed. These differences are attributed to the effect of temperature at certain critical periods during the initial development and early maturation of the ova.

INTRODUCTION

During the springs of 1957-1961, in the course of surveying the haddock (*Melanogrammus aeglefinus* (L.)) population of the Grand Bank (ICNAF Subarea 3), material was collected to study the fecundity of this species. All specimens were taken from an area along the southwest slope of the Bank (Fig. 1), where haddock are usually heavily concentrated during winter and spring.

Mature haddock of the Grand Bank generally spawn during May and June, so the ovaries were collected a month or two earlier in March-April. At that time the opaque yolky eggs could be readily distinguished from the minute grey-coloured ova. Ovaries which were so advanced as to contain large translucent eggs were not used in the investigation.

The method of preservation in Gilson's fluid was essentially the same as that used by Simpson (1951) for North Sea plaice. The fecundity estimates were obtained from actual counts of yolky ova in egg samples from the ovaries. These samples were obtained by fractioning the egg contents of the ovary with a whirling vessel, the description and operation of which has been given by Wiborg (1951).

During the course of the investigation year-to-year differences in fecundity of fish of the same size and age were observed. The significance of these results is discussed in relation to the possible effects of temperature at certain critical periods during the initial development and early maturation of the ova.

RESULTS

Fecundity estimates were made for 229 Grand Bank haddock during 1957-61. The data were treated by applying a logarithmic transformation to the 2 variables and expressing the relationship between log fecundity and log length in the form

$$\log F = n \log L + \log k.$$

The observations are shown as a scatter diagram in Fig. 2 together with the fecundity-length curve for the combined data.

For any one length of fish the fecundity is shown to vary between wide limits. This variation is much greater than would be expected due to sampling errors and tends to mask any annual differences in fecundity that otherwise might be apparent. This aspect is better shown by comparing the geometric means of the fecundity-at-length data with the values taken from the fitted log-log regression (Table 1). The data of 1957, being the more substantial, follow closely the fitted curve as would be expected. The 1958 data are quite irregular for haddock between 44 and 51 cm, but only 23 observations were made in that year. The 1959 data follow closely the shape of the fitted curve but, except for the value at 48-49 cm, are consistently below it throughout its entire length. The 1960 fecundity values are in most instances greater than those calculated from the curve, while those of 1961 are irregular, being based on only 16 fish.

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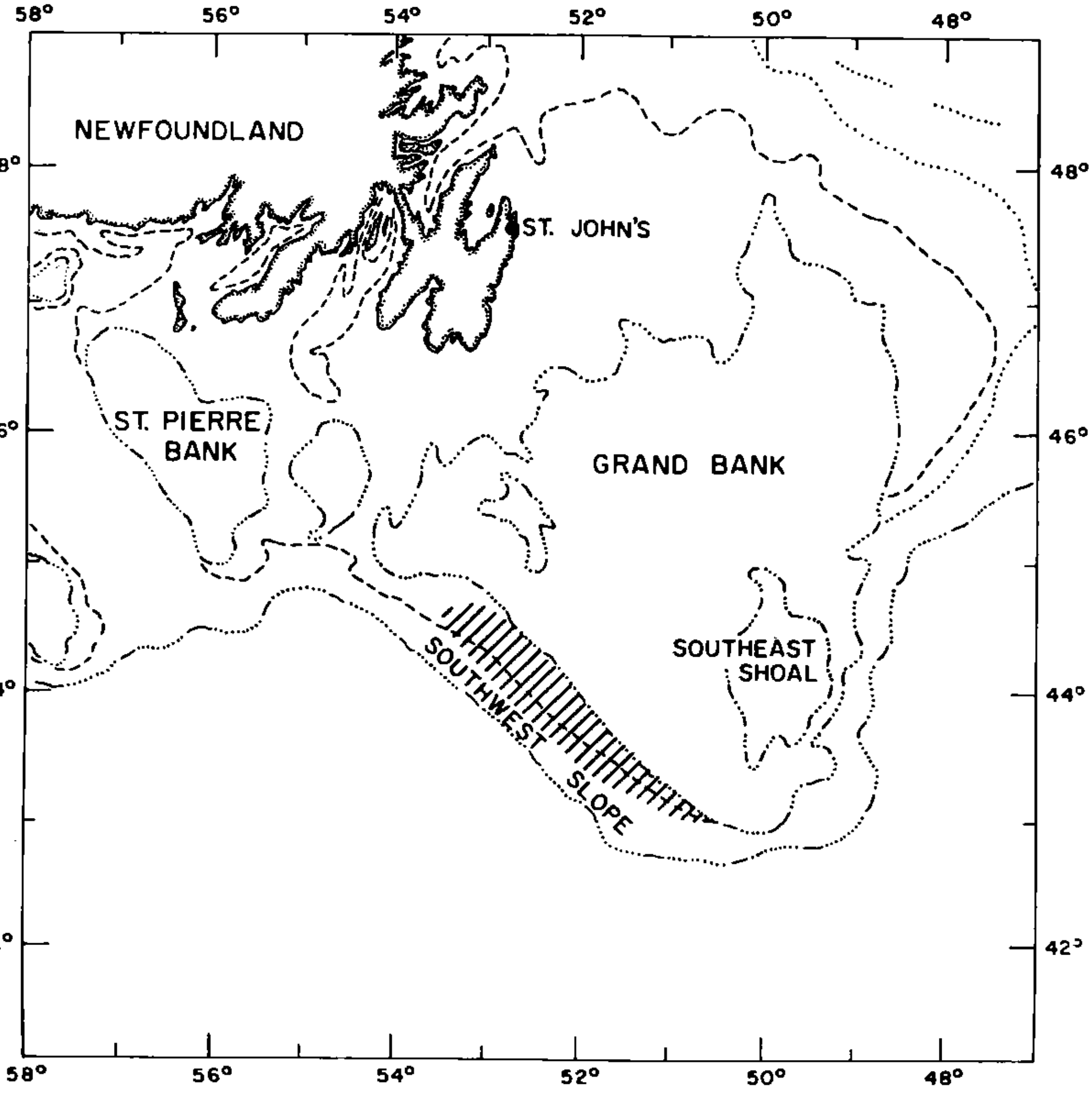

Fig. 1. Map of the Grand Bank showing the approximate location of the winter and spring concentrations of haddock.

DEPTH SCALE:
30 fathoms (55 m)___...___...___...___...
50 fathoms (91 m)___.....___.....___.....
100 fathoms (183 m)__ __ __ __ __ __ __ __
200 fathoms (366 m)......................
1,000 fathoms (1,830 m)__........___........___

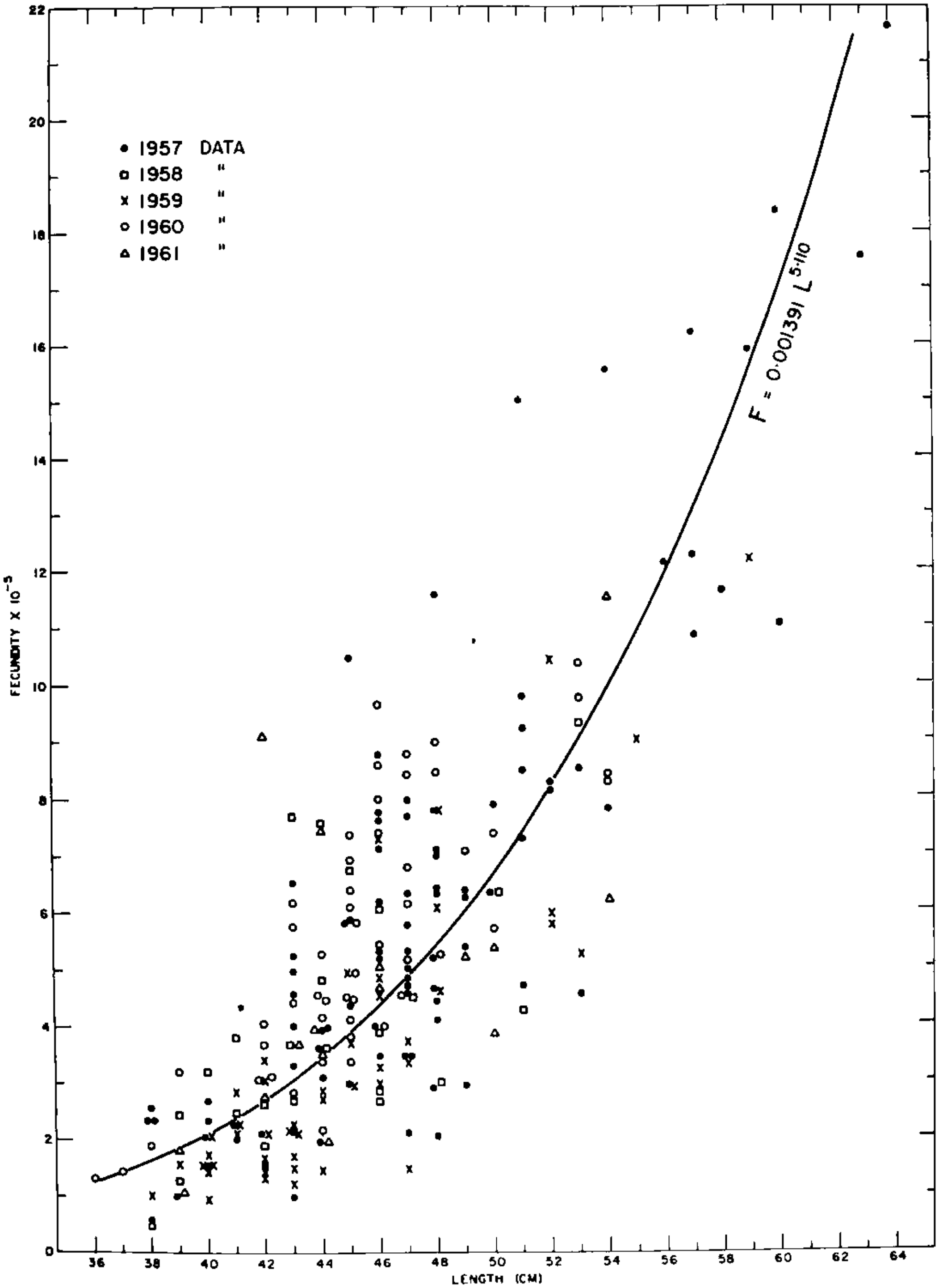

Fig. 2. Individual fecundity estimates for Grand Bank haddock by length and year of capture together with the fitted regression line.

TABLE 1. GEOMETRIC MEAN FECUNDITIES BY LENGTH AND YEAR OF CAPTURE FOR FEMALE HADDOCK OF THE GRAND BANK, 1957-61.

Length 2-cm intervals	Geometric mean fecundities in thousands of ova (Figures in parenthesis are numbers of specimens) 1957	1958	1959	1960	1961	1957-61	Range of estimates ('000)	Fecundity calculated from curve ('000)
36-37	-	-	-	137(2)	-	137(2)	131-144	134
38-39	152(5)	176(2)	127(2)	143(3)	138(2)	148(14)	48-320	176
40-41	211(6)	310(3)	175(9)	-	-	205(18)	95-380	228
42-43	306(10)	327(5)	190(12)	363(8)	450(3)	284(38)	101-909	292
44-45	415(10)	543(4)	290(6)	460(17)	375(4)	418(41)	146-1044	369
46-47	524(21)	381(5)	360(8)	666(12)	484(2)	504(48)	148-963	462
48-49	521(16)	298(1)	600(3)	727(4)	520(1)	546(25)	205-1156	572
50-51	814(8)	520(2)	-	647(2)	456(2)	680(14)	388-1500	704
52-53	713(4)	931(1)	660(4)	1002(2)	-	755(11)	455-1041	859
54-55	1100(2)	-	900(1)	834(2)	846(2)	916(7)	621-1551	1040
56-57	1269(4)	-	-	-	-	1269(4)	1085-1616	1248
58-59	1357(2)	-	1216(1)	-	-	1308(3)	1216-1588	1493
60-61	1422(2)	-	-	-	-	1422(2)	1102-1834	1773
62-63	1748(1)	-	-	-	-	1748(1)	-	2093
64-65	2158(1)	-	-	-	-	2158(1)	-	2460

N	92	23	46	52	16	229	No. of fish
n	4.913	3.635	5.724	5.515	4.110	5.110	Regression coefficient, *n*
log k	-2.5189	-0.4098	-3.9843	-3.4423	-1.2525	-2.8566	Intercept, *log k*
r	0.81	0.60	0.88	0.80	0.67	0.79	Correlation coefficient, *r*

In order to test the significance of the between-yearly differences in intercept (log fecundity adjusted to a common log body length) and in slope (rate of increase of log fecundity with log length), an analysis of covariance was used according to Snedecor(1956). The F-value derived from the ratio of mean square for adjusted means to mean square for common regression measures the significance of the sample differences in intercept. The F-value derived from the ratio of mean square for regression coefficients to mean square within samples measures the degree of variability in the regression coefficients or slopes.

No significant difference was indicated between the regression coefficients of the yearly samples, but a significant difference at the 1% level resulted when the test was applied to measure the variability in intercepts. It has already been noted that the fecundity averages for 1959 are nearly all less than the values taken from the fitted curve. In an analysis of covariance of the data, omitting the fecundity estimates for 1959, neither the regression coefficients nor the intercepts are significantly different. Similar tests were applied by omitting the data of the years 1958, 1960 and 1961 individually, but the results were essentially the same as those in the first test. Consequently the variation shown by the first test is due in large part to the inclusion of the 1959 data.

Because of the great variation in year-class survival as shown by the age distribution of the samples collected for fecundity estimates in the years 1957-61 (Table 2), an analysis of the data is rendered difficult in so far as making comparisons between years and ages are concerned. However, despite the inadequacy of the data with regard to age, some indication of the annual variation in haddock fecundity by length and age is shown in Table 2, the last three columns of which give the geometric mean lengths of fish and fecundity estimates by age together with the corresponding fecundity values as calculated from the curve of Fig. 2. The similarity of the observed and calculated fecundity values for 1957 and 1958 must be noted. In 1960 the observed fecundity values for ages 5-11 are considerably greater than those calculated from the curve. In 1961 except for age 8, the observed and calculated values are reasonably similar considering the small numbers of observations involved.

TABLE 2. GEOMETRIC MEAN FECUNDITIES BY YEAR OF CAPTURE, AGE AND LENGTH FOR FEMALE HADDOCK OF THE GRAND BANK, 1957-61.

Year of capture	Age (yr)	Geometric mean fecundities in thousands of ova by 4-cm length intervals (figures in parenthesis are numbers of fish) 36-39	40-43	44-47	48-51	52-55	56-59	60-63	64-67	Geometric mean Length (cm)	Geometric mean Fecundity ('000)	Fecundity calculated from curve ('000)
1957	5	153(5)	249(10)	390(1)	-	-	-	-	-	40.5	220(16)	227
	8	-	298(6)	471(30)	605(24)	928(5)	1216(2)	1102(1)	-	47.7	550(68)	527
	11	-	-	-	-	455(1)	1267(3)	-	2158(1)	57.7	1148(5)	1380
	15	-	-	-	-	-	1588(1)	-	1791(2)	60.6	1720(3)	1780
1958	5	-	246(1)	-	-	-	-	-	-	41.0	246(1)	243
	6	176(2)	290(6)	447(3)	-	-	-	-	-	42.3	298(11)	283
	9	-	764(1)	446(6)	432(3)	931(1)	-	-	-	46.8	496(11)	480
1959	4	-	154(1)	-	-	-	-	-	-	40.0	154(1)	213
	6	127(2)	190(6)	290(3)	-	-	-	-	-	42.1	198(11)	277
	7	-	183(14)	314(10)	527(2)	578(1)	1216(1)	-	-	44.3	267(28)	360
	10	-	-	728(1)	778(1)	736(4)	-	-	-	50.9	742(6)	735
1960	4	48(1)	-	-	-	-	-	-	-	38.0	48(1)	163
	5	153(3)	402(1)	-	-	-	-	-	-	38.2	195(4)	170
	7	320(1)	326(3)	608(8)	843(1)	-	-	-	-	44.4	514(13)	363
	8	-	385(4)	481(18)	645(3)	-	-	-	-	45.2	481(25)	400
	11	-	-	731(3)	720(2)	914(4)	-	-	-	50.1	805(9)	673
1961	6	138(2)	273(1)	339(3)	-	-	-	-	-	42.3	242(6)	283
	8	-	578(2)	347(1)	536(1)	-	-	-	-	44.7	499(4)	377
	9	-	-	588(2)	449(2)	-	-	-	-	47.2	514(4)	500
	12	-	-	-	-	846(2)	-	-	-	54.0	846(2)	990

For 1959, on the other hand, the fecundity estimates as observed for ages 4, 6 and 7 are substantially below the calculated values, whereas the observed and calculated values for age 10 are similar. Examination of the catch records reveals that the 1959 specimens were taken in depths between 86 and 270 m (47 and 148 fathoms), while the samples in the other years were taken in depths between 77 and 183 m (42 and 100 fathoms). The records further reveal that most of the haddock age 7 and younger were taken in less than 183 m (100 fathoms), but most of the 10-year-olds were caught in deep water over 183 m (100 fathoms), where they probably migrated at an earlier age and where they were not as liable to be affected by the violent changes in environmental conditions that often occur at shallower depths along the southwest slope of the Grand Bank (Templeman and Hodder, this symposium). The significance of the fluctuations in fecundity observed in 1959 and 1960 is discussed in the next section.

DISCUSSION

It has been shown that considerable variation in fecundity of Grand Bank haddock may occur from year to year. In particular, the 1959 fecundity estimates for fish of the same size and age were in general substantially lower than the averages for the 5 years combined (1957-61), while in 1960 the fish appeared to be generally more fecund. Such variation in annual egg-production has not previously received much attention. The most important work in this regard is that of Bagenal (1957) on long rough dabs (*Hippoglossoides platessoides*) for the years 1954, 1955 and 1956. He points out that the fecundity in 1955 was significantly lower than that in 1954 and 1956, even after allowance was made for length differences. Similar significant differences were evident for fish condition. He does not offer any other explanation for this except to point out that the differences were not due to differences in the age structure of the population.

In discussing the variation in individual fecundity of plaice (*Pleuronectes platessa*), Simpson (1951) observes that there are at least two critical periods in which the number of eggs to be laid may be influenced: one is the period when the germinal epithelium is being laid down during the first year of life, and the other is either the time when the new primary oocytes are being formed each year or when the eggs to be laid in the next spawning season are separated from the mass of resting oocytes. He discounts the first possibility, since it might determine the fecundity potential of the fish for life. Simpson's second critical period should really be called the second and third critical periods, for a considerable period of time might elapse between the formation of the primary oocytes and the separation from the mass of resting oocytes of the batch of ova for spawning in a subsequent spawning season.

Reibisch (1899) and Franz (1910) point out that once maturity is first reached two or three years elapse between the formation of oocytes and the final liberation of the resulting eggs, the eggs to be spawned in any winter being separated from the resting oocytes during the summer immediately preceding spawning. Raitt (1933) has thoroughly reviewed the literature with regard to intra-ovarian egg-groups. From this and from his own observations on North Sea haddock he concludes that in ripening ovaries two separate groups of ova are present (opaque-yolked and transparent-yolkless eggs), the first group to be laid in the approaching spawning season and the second to be laid in the following or possibly succeeding years.

1. In the following discussion, we shall consider three possible critical periods. Assuming that the period of intra-ovarian development is two years and that the critical period is the time of formation of the oocytes, it is possible that the low fecundity of haddock in 1959 and the high fecundity in 1960 might be the result of environmental conditions existing during the springs of 1957 and 1958 respectively. Templeman (1958, 1959, 1960) from hydrographic evidence points out that during the summers of 1957 and 1959 bottom temperatures on the southern Grand Bank were unusually low, whereas in 1958 they were generally above normal. Further evidence to support this statement is given by Templeman (this symposium) for a hydrographic station (No. 27) located off St. John's in the coastward part of the Labrador Current. The mean surface to bottom (175 m; 96 fathoms) water temperatures for the period January to May of the years 1955-59 are given below. Also given for comparison are the mean January-March air temperatures at St. John's Airport as compiled from air temperature records of the Meteorological Division of the Canadian Department of Transport (Anon., 1950-62).

	Mean Temperature (°C)	
Year	Water	Air
1955	-0.62	-3.0
1956	-0.35	-2.9
1957	-1.19	-5.8
1958	-0.21	-1.1
1959	-1.03	-6.0
1950-62	-0.65	-3.3

During the winter months haddock are generally concentrated along the southwest slope of the Grand Bank in depths greater than 90 m (50 fathoms). At this time the shallower parts of the bank are completely covered with cold water of less than 1°C and often there is much water below 0°C. In a year like 1957, when an unusually large volume of cold water flowed southward along the east coast of Newfoundland and covered the Grand Bank for a longer-then-normal period, the haddock were forced deeper and became heavily concentrated along the narrow southwest slope. The resulting overcrowded conditions, in which lack of food supposedly restricts growth, as argued by Lack (1954), probably had the effect of reducing the fecundity of haddock two years later in 1959. In 1958, on the other hand, the higher-than-normal temperature conditons that existed throughout most of the area caused the haddock concentrations to be dispersed from their winter-quarters a month or more earlier than usual, thus favouring good growth in the spring and early summer and consequently greater egg-production two years later in 1960. Hydrographically, the years 1955 and 1956 were more or less typical of the average conditions in recent years. Conditions in 1959 were somewhat similar to those of 1957, but the small number of fecundity observations in 1961 are not sufficient to show whether or not the fecundity was lower than average in that year.

If, as Reibisch (1899) and Franz (1910) suggest, the eggs to be spawned in an approaching spawning season are separated from the resting oocytes during the preceding summer, and if we consider this period as the critical one, then the environmental conditions existing in 1958 and 1959 may have been responsible for the low fecundity of 1959 and the higher-than-average estimates for 1960. Assuming that, for a particular ovary, the surface area of the lamellae on which egg growth takes place is limited (by the size of the ovary), it follows that the number of eggs for spawning in the following spring is related not only to the size of the ovary but also to the size of the eggs at the time when the limit of coverage of the basic surface area of the lamellae is reached. If this is so, fecundity might be related to the function of growth which these eggs undergo during the period in the summer when they are being separated from the resting oocytes. Therefore, in a year when growth conditions are favourable (*e.g.* 1958), it is possible that fewer large oocytes will occupy the available surface area of the ovarian lamellae and result in lower fecundity at spawning time of the following year. If conditions are unfavourable, thus restricting egg growth, a larger number of small oocytes may now occupy the surface area of the ovarian lamellae with the end result of higher fecundity in the next spawning season.

3. Perhaps the egg-production of individual fish in any one spawning season is the result of environmental conditions during the few months immediately preceding spawning. Vladykov (1956) for speckled trout (*Salvelinus fontinalis*) in Quebec lakes says that an abundant food supply for adults during several months preceding spawning resulted in higher fecundity at spawning time. Scott (1962) carried out experimental diet restriction on rainbow trout (*Salmo gairdneri*) and found that starvation during the months preceding spawning influenced the number of eggs by increasing the rate of atresia. Although there is no evidence at present to indicate that follicular atresia plays a very important role in the fecundity of those marine fishes which produce large numbers of small pelagic eggs, it is possible that severe food restriction during a period of several months preceding spawning may induce some reabsorption of ova. To this extent overcrowding during the winter and spring of 1959, caused by the abnormally-low temperature conditions, may have resulted in low fecundity at spawning time in that year. However, the unusually low temperature conditions in 1957 cannot by this hypothesis be related to the normal fecundity estimates for that year.

Much of the above discussion is speculative, since the effect of such factors as temperature on the processes of growth and reproduction is not fully understood.

REFERENCES

ANONYMOUS. 1950-1962. Monthly record, meteorological observations in Canada. Canada Department of Transport, Meteorological Divison.

BAGENAL, T.B. 1957. Annual variations in fish fecundity. *J. Mar. biol. Ass.,U.K.*, 36: 377-382.

FRANZ, V. 1910. Die Eiproduktion der Scholle *Pleuronectes platessa* (The fecundity of the plaice *Pleuronectes platessa*). *Wiss. Meeresuntersuch.*, 9: 59-141.

LACK, DAVID. 1954. The natural regulation of animal numbers. Oxford Univ. Press, 343 p.

RAITT, D.S. 1933. The fecundity of the haddock. *Fish. Bd. Scotland, Sci. Invest., 1932*, No. 1: 1-42.

REIBISCH, J. 1899. Ueber die Eizahl dei *Pleuronectes platessa* und die Altersbestimmung dieser Form aus den Otolithen (On the fecundity of *Pleuronectes platessa* and age determination of this species from otoliths). *Wiss. Meeresuntersuch.*, Kiel, 4: 231-248.

SCOTT, D.P. 1962. Effect of food quantity on fecundity of rainbow trout (*Salmo gairdneri*). *J. Fish. Res. Bd. Canada*, 19(4): 715-731.

SIMPSON, A.C. 1951. The fecundity of the plaice. *Fish. Invest., Lond (2)*, 17(5): 1-27.

SNEDECOR, G.W. 1956. Statistical methods (fifth edition). Iowa State College Press, 534 p.

TEMPLEMAN, W. 1958. Canadian Research Report 1957. *Annu. Proc., int. Comm. Northw. Atlant. Fish.*, 8: 19-22.

1959. Canadian Research Report 1958. *Annu. Proc., int. Comm. Northw. Atlant. Fish.*, 9: 20-26.

1960. Canadian Research Report 1959. *Annu. Proc., int. Comm. Northw. Atlant. Fish.*, 10: 19-25.

1964. Temperature anomalies at Station 27 off St. John's, 1950-62. *This symposium, Contribution No. H-2.*

TEMPLEMAN, WILFRED, and V.M. HODDER. 1964. Distribution of haddock on the Grand Bank in relation to season, depth and temperature. *This symposium, Contribution No. A-8.*

VLADYKOV, VADIM D. 1956. Fecundity of wild speckled trout (*Salvelinus fontinalis*) in Quebec lakes. *J. Fish. Res. Bd. Canada*, 13(6): 799-841.

WIBORG, K.F. 1951. The whirling vessel. *Fiskeridir Skr. Havundersøk.*, 9 (13): 1-16.

D-2

RELATION OF PERIODS OF SUCCESSFUL YEAR-CLASSES OF HADDOCK ON THE GRAND BANK TO PERIODS OF SUCCESS OF YEAR-CLASSES FOR COD, HADDOCK AND HERRING IN AREAS TO THE NORTH AND EAST

By

Wilfred Templeman[1]

ABSTRACT

In the period 1942-58 for which information is most complete, there were years or two or three adjacent years when successful year-classes of cod, haddock and herring were produced in Greenland, Iceland and the Norwegian to Barents Sea area. There were also intervening years or groups of years when successful year-classes were relatively scarce. The more scanty data for cod and herring from previous years back to 1912 also indicate that certain years or adjacent years were more favourable than others for the production of good year-classes throughout this region.

For cod in the years 1912-45, good year-classes occurred at West Greenland in the same years which also produced successful year-classes at Iceland. In more recent years, good year-classes of cod at West Greenland may often occur independently to or may occur one year later than good year-classes at Iceland.

For the years since 1942, successful year-classes of West Greenland and East Greenland cod usually have occurred one year after a successful year-class of Grand Bank haddock. For this period, also, Icelandic cod, haddock and herring tended to have good year-class survival in the same year as Grand Bank haddock with a tendency, also, for equally successful year-classes of haddock and herring and smaller year-classes of cod to occur one year and occasionally two years later than successful year-classes of Grand Bank haddock.

Arcto-Norwegian cod, haddock and herring in recent years generally had successful year-classes one or two years after Grand Bank haddock. The haddock year-class relationships between the two areas were closest and were generally one year apart. In an earlier period, 1912-44, when West Greenland cod may have been largely derived from Icelandic spawning, good year-classes of Atlanto-Scandian herring usually occurred one year after a good year-class of West Greenland cod. In more recent years, with the success of West Greenland year-classes of cod more dependent on spawning in West Greenland waters, the tendency has been for successful year-classes of Atlanto-Scandian herring to occur in the same year as a successful year-class of West Greenland cod.

In recent years successful year-classes of Grand Bank haddock, with one exception, have occurred only in years with low iceberg numbers.

A complete explanation of all the relationships described cannot be offered at present and some of the inter-related occurrences appear to be too close together in time. However, the occurrence of good year-classes of different species over such a wide area, usually in the same sequence of years, indicates more than unrelated local phenomena and argues for an inter-relationship through and variations in the Gulf Stream which may affect the southern Grand Bank through eddies and intermingling with Grand Bank-Labrador Current water and through its North Atlantic Current branches affect the Icelandic, Greenland and the Norwegian-Barents Sea areas.

INTRODUCTION

The haddock of the southern Grand Bank are at the northern extremity of their spawning range on the continental shelf in this area and are subject to great variations in year-class strength. It is the purpose of this paper to compare the timing of the successful year-classes of haddock on the southern Grand Bank with that of successful year-classes of cod, haddock and herring in Greenland, Iceland and the Arcto-Norwegian area.

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Much of the information on year-class strength has been obtained from the following papers: for cod and haddock, Tåning (1931, 1936), Sund (1936), Raitt (1936, 1948), Thompson (1929, 1939), Rollefsen (1954), Hansen (1939, 1949, 1954), Jónsson (1954), Baranenkova (1960), and for herring, Sund (1943).

The remaining information on year-class success especially in recent years has come mainly from papers too numerous to mention in detail in such a short paper, by many authors in many years in Annales Biologiques and ICNAF Proceedings. Among these the following authors have supplied most of the information: for West Greenland cod, Hansen, Jónsson, Rasmussen, Meyer, Rúivo, and Quartin, and Bratberg; for East Greenland cod, Meyer, Hansen and Jónsson; for Icelandic cod, Fridriksson and Jónsson; and for Arcto-Norwegian cod, Rollefsen, Lundbeck, Meyer and Maslov.

For haddock, additional year-class information, mainly from Annales Biologiques, has been obtained for Iceland from Baranenkova, Meyer and Fridriksson; and for the Arcto-Norwegian area from Baranenkova, Maslov, Meyer, Lundbeck and Saetersdal.

For herring, the information has come mainly from papers in Annales Biologiques by Fridriksson for the Icelandic area and by Devold for the Norwegian area.

The iceberg numbers south of 48°N in the eastern Newfoundland area in Table 1 are from the various Bulletins of the U.S. Coastguard giving the Ice Patrol Reports for the years 1902-61.

The following people have assisted by giving their opinions on year-class strengths for certain of the species and areas: Dr Paul Hansen, Mr Jón Jónsson, Mr Jakob Jakobsson, Mr Steinar Olsen, Mr O.J. Østvedt, Mr John Corlett and Mr John Gulland.

It is inevitable, however, that there will be some errors in the list of year-class strengths both from failure to have or to assess the complete information. For the Arcto-Norwegian cod data, apart from the most recent years, we have depended largely on Norwegian assessments based chiefly on the skrei, but in recent years there has been an increasing proportion of this Arcto-Norwegian stock caught as immature fish. There are differences in our list of successful year-classes of this stock and that of Seryakov (MS, 1962) and an unpublished list by Mr John Gulland. Our list will doubtless need correction at some future date when there are enough published data to make a critical comparison.

RELATION OF OCCURRENCE OF SUCCESSFUL YEAR-CLASSES OF COD, HADDOCK AND HERRING IN VARIOUS AREAS

1: Haddock, Grand Bank

Only for recent years since 1942 is a good approximation possible of the relative success of haddock year-classes in the Grand Bank area. In this period there have been two very successful year-classes, 1949 and 1955, three moderately successful, 1942, 1946 and 1952 and three of modest survival, 1947, 1953 and 1956. In the remaining years only small or very small numbers of young haddock survived.

2: Cod, Haddock and Herring, West Greenland — Barents Sea since 1942

For the period 1942-58 there are years, or two or three adjacent years, when successful year-classes of cod, haddock and herring are produced over much of the area under discussion from West Greenland to the Barents Sea. There are, also, intervening years or groups of years when successful year-classes are relatively scarce. Especially is this true if only the abundant and very abundant year-classes are considered (Table 1).

Two especially successful years for survival of young were 1950 and 1956 with, especially for 1950, some success in each adjacent year. There was, also, fair success in 1942, 1945, 1947, 1948 and 1953.

The 1950 and 1956 successes in year-class survival occurred one year after the production of the two most successful and very abundant year-classes of haddock on the Grand Bank. The 1947, 1948, 1953 and 1957 years of moderately successful survival occurred one year after an abundant or moderately abundant survival of haddock year-classes on the Grand Bank. The moderate success in

TABLE 1. SUCCESSFUL YEAR-CLASSES.

*	moderately abundant
**	abundant
*** etc.	very abundant

		Cod				Haddock		Herring				Relative total year-class strengths all species -not including G. Bank	
Year-class	Grand Bank haddock	West Green-land	East Green-land	Iceland	Arcto-Norwe-gian	Iceland	Arcto-Norwe-gian	Icelandic spring spawners	Icelandic summer spawners	Atlanto-Scandian stock	Ice-berg num-bers south of lat. 48°N Nfld. area	Total	Total abundant to very abun-dant only
1962	...	...	...	...	***?	...	...	...	...	...	...		
61	...	...	...	...	...	...	***?	...	...	...	115		
1960	...	*?	...	...	...	...	...	...	...	**(*?)	253		
59	...	...	...	...	**?	...	*	...	...	**(*?)	693		
58	...	*	...	...	*	...	...	...	...	...	1	2	0
57	...	**	...	...	*	**	*	...	...	...	931	6	4
56	*	**	**	*	**	**	**	**	***	...	80	16	15
55	****	...	...	***	...	*	...	...	*	...	61	5	3
54	...	...	...	...	*	...	*	...	...	...	312	2	0
53	*	**	**	...	*	...	**	...	...	...	56	7	6
52	**	...	*	...	...	*	...	...	*	...	14	3	0
51	...	...	*	...	*	**	...	**	**	...	6	8	6
1950	...	**	**	*	***	**	****	**	*	*****	460	22	20
49	****	...	*	*	**	***	...	*	**	...	47	10	7
48	...	...	...	...	**	...	***	...	...	...	523	5	5
47	*	***	**	...	*	...	...	...	...	*	63	7	5
46	**	...	...	...	...	**	...	...	...	...	430	2	2

(continued next page)

TABLE 1. cont'd.

		Cod				Haddock		Herring				Relative total year-class strengths all species -not including G. Bank	
Year-class	Grand Bank haddock	West Green-land	East Green-land	Iceland	Arcto-Norwe-gian	Iceland	Arcto-Norwe-gian	Icelandic spring spawners	Icelandic summer spawners	Atlanto-Scandian stock	Ice-berg num-bers south of lat. 48°N Nfld. area	Total	Total abundant to very abun-dant only
1945	...	**	*	****	...	**	...	*	*	...	1,087	11	8
44	...	...	...	*	*		...	...	...	*	700	3	0
43	...	...	...	*	*		...	...	...	**	840	4	2
42	**	**	**	***	*		...	...	...	...	30	8	7
41	...	...	...	...	...		...	...	...	...	2	0	0
1940	*?	...	...	...	...		...	*	...	...	10[a]	1	0
39	...	...	...	...	...		...	...	...	...	850[a]	0	0
38	...	...	...	...	...		...	...	...	*	660[a]	1	0
37	...	...	...	...	***		***	...	...	**	470	8	8
36	*?	***	...	**	*		...	...	...	...	22	6	5
35	*?	...	...	**	*		...	...	...	...	875	3	2
34	*?	***	...	**	*		...	...	...	**	576	8	7
33	*?	...	...	**	*		...	...	...	*	216	4	2
32	...	*	...	**	*	*	...	...	...	*	514	6	2
31	...	*	...	**	*	**	...	...	...	...	13	6	4
1930		...	...	...	**	...	...	...	...	**	475		
29		...	...	...	**	...	...	...	...	...	1,351		
28		...	...	...	*	...	...	...	...	...	515		
27		...	...	...	*	...	...	...	...	...	389		
26		**	...	*	*	...	...	...	...	...	345		
25		...	...	...	...	**	...	...	...	*	109		
24		**	...	***	...	*	...	...	...	...	11		

TABLE 1. cont'd.

Year-class	Grand Bank haddock	Cod				Haddock		Herring			Iceberg numbers south of lat. 48°N Nfld. area	Relative total year-class strengths all species -not including G. Bank	
		West Greenland	East Greenland	Iceland	Arcto-Norwegian	Iceland	Arcto-Norwegian	Icelandic spring spawners	Icelandic summer spawners	Atlanto-Scandian stock		Total	Total abundant to very abundant only
1923		...	...	...	...	...	...	...	...	**	236		
22		***	...	****	*	**	...	...	...	...	523		
21		...	...	...	*	*	...	...	...	...	746		
1920		...	...	...	*	...	...	...	...	...	445		
19		...	...	*	***	...	...	...	...	...	317		
18		...	...	...	***	...	...	...	...	*	199		
17		**	...	*	***	...	...	...	...	...	38		
16		...	...	...	...	*	...	...	...	...	54		
15		...	...	*	**	...	...	...	...	...	468		
14		...	...	...	...	...	...	...	...	...	731		
13		...	...	*	...	...	...	...	...	*	550		
12		*?	...	*	**	...	...	...	...	...	1,019		
11		...	...	...	...	...	...	...	...	...	396		
1910		...	...	...	...	...	...	...	...	...	50		
09		*?	...	...	...	...	...	...	...	...	1,024		
08		...	...	...	...	...	...	...	...	...	222		
07		...	...	...	...	*	...	...	...	...	638		
06		...	...	...	...	...	...	...	...	...	405		
05		...	...	...	...	...	...	...	...	...	845		
04		...	...	...	**	*	...	...	...	*****	265		
03		...	...	...	...	*	...	...	...	...	802		
02		...	...	...	...	...	...	...	...	...	41		

a = approximate from figure.

1942 and 1949 was in the same year with an abundant survival of haddock on the Grand Bank and in 1951, two years after a very abundant haddock year-class on the Grand Bank. Only the 1945 success in the Greenland and Icelandic areas appears to be unrelated to a recent successful haddock survival on the Grand Bank.

2.1 West Greenland and East Greenland Cod. In recent years there is an excellent relationship between the occurrence of an unusually successful year-class of cod in West Greenland and the success of survival of Grand Bank haddock. All five abundant to very abundant year-classes of West Greenland cod since 1946 came the year after a moderately abundant to very abundant year-class of Grand Bank haddock. Four of these came one year after an abundant to very abundant Grand Bank haddock year-class and only one of three moderately abundant Grand Bank haddock year-classes was followed by an abundant year-class of cod in West Greenland.

One successful year-class of West Greenland cod, that of 1942, occurred in the same year as a successful year-class of Grand Bank haddock and another, that of 1945, was apparently not related to a successful year-class of Grand Bank haddock.

All the abundant year-classes of East Greenland cod have occurred in years when there was also an abundant survival of West Greenland cod but there have been other years of moderate survival, two of three being in the same year as an abundant to very abundant year-class of Grand Bank haddock. Cod of the East Greenland area have not been so intensively investigated as those of West Greenland and the year-classes cannot be assessed with as great accuracy.

2.2 Icelandic Cod, Haddock and Herring. In recent years since 1942 better than average year-classes of Icelandic cod have some tendency to occur in the same year and magnitude as successful year-classes of Grand Bank haddock, and usually moderately abundant year-classes occur the year afterward (in 1944, two years afterward). The very abundant 1945 year-class appears to be unrelated to the success of a year-class of Grand Bank haddock.

The recent information on year-classes of Icelandic haddock begins with 1945. Although these haddock usually have better than average year-classes in the same years as the Icelandic cod and in the same years with good survival of haddock on the Grand Bank, there is also a tendency in some cases for Icelandic haddock, like the Greenland cod, to have a successful year-class one year later than that for Grand Bank haddock (in 1951, two years later).

Icelandic herring show some tendency, but more for the summer than for the spring spawners, to have successful year-classes in the same year as the Grand Bank haddock but there is also some tendency for a good year-class to occur a year later and in one case two years later. The year-class of 1945, generally successful in the Greenland and Icelandic area and not represented by haddock success on the Grand Bank, was also moderately successful for Icelandic herring. In the Icelandic area the success of survival of herring, although having some relationship to that of cod, has still more agreement with that of haddock. There appear, however, to be less good year-classes of herring, unless different criteria are used for judging herring. It is especially close to the time of the very abundant Grand Bank haddock year-classes of 1949 and 1955 that unusually successful year-classes of herring appeared at Iceland. Lesser year-classes of haddock on the Grand Bank were not followed by exceptional year-classes of Icelandic herring.

2.3 Arcto-Norwegian cod and haddock and Atlanto-Scandian herring. The variations in survival of the Arcto-Norwegian cod do not seem to be as extreme as those of West Greenland cod, or there is a tendency to assess more of the year-classes of Arcto-Norwegian cod as moderately abundant. The moderately abundant to very abundant year-classes of Arcto-Norwegian cod in recent years between 1942 and 1958 usually occurred one or two years after a moderately abundant to very abundant year-class of Grand Bank haddock.

All six moderately abundant to very abundant year-classes of Arcto-Norwegian haddock between 1948 and 1957 occurred one year after a moderately abundant to very abundant year-class of Grand Bank haddock. In all cases except one there is a qualitative relationship, the moderately abundant and the more abundant year-classes of Norwegian haddock following one year after moderately abundant and more abundant year-classes, respectively, of Grand Bank haddock. In the remaining case the 1948 very abundant year-class of Arcto-Norwegian haddock can be considered either as following one year after the moderately abundant year-class of Grand Bank haddock or two years after an abundant year-class, that of 1946.

For the Atlanto-Scandian herring the 1904 and the 1950 year-classes were so large that all other year-classes suffer by comparison and for nine and eight years respectively after these two year-classes no even moderately abundant year-class appeared. Between 1942 and 1950, however, the four moderately abundant to very abundant year-classes of Atlanto-Scandian herring appeared one to two years after an abundant to very abundant year-class of Grand Bank haddock.

3: Successful Year-classes before 1946

For the period earlier than 1942 the years when successful year-classes of Grand Bank haddock occurred are in doubt since the information is too general. Information on year-class strengths is also lacking for many of the other areas and species. There is good information for West Greenland, Icelandic and Arcto-Norwegian cod and Atlanto-Scandian herring and some for Icelandic haddock.

All eleven moderately abundant to very abundant year-classes of West Greenland cod between 1912 and 1945 occurred in the same year as a moderately abundant to very abundant year-class of Icelandic cod, but not all successful year-classes at Iceland were also exceptional year-classes at West Greenland. Of 12 moderately abundant to abundant year-classes of Atlanto-Scandian herring between 1912 and 1944, eight occurred one year after, one occurred in the same year (or two years after) and two two years after the occurrence of a moderately abundant to very abundant year-class of West Greenland cod. In the period since 1944 when the success of cod year-classes in West Greenland has depended more on spawning in West Greenland, of four successful year-classes of Atlanto-Scandian herring three have occurred in the same year as a successful year-class of West Greenland cod.

ICEBERG NUMBERS AND SUCCESS OF YEAR-CLASSES OF GRAND BANK HADDOCK

Seven out of eight moderately abundant to very abundant year-classes of Grand Bank haddock since 1942 occurred in years when there were low iceberg numbers (less than 100) passing south of 48°N in the eastern Newfoundland area (Table 1). The exception, 1946, had an average iceberg number (430). Nine of the years between 1942 and 1960 were low iceberg years (1-80) and seven of these had moderately abundant to very abundant year-classes of Grand Bank haddock. Ten of the years between 1942 and 1960 were moderate to high iceberg years (253-1,087) and only one of these years had a successful haddock year-class on the Grand Bank.

DISCUSSION AND CONCLUSIONS

1: Introduction

As near as we can determine, the main periods of spawning for the populations of fish under consideration are:

Grand Bank haddock	May - June
West Greenland cod	March - <u>April</u> - May
East Greenland cod	April - May
Icelandic cod	Mid-March - mid-April
Icelandic haddock	Mid-April - mid-May
Icelandic spring spawning herring	March - April
Icelandic summer spawning herring	July - August
Arcto-Norwegian cod	Late February - <u>March</u> - mid-April
Arcto-Norwegian haddock	May and presumably earlier
Atlanto-Scandian herring	February - March

Tåning (1931) remarked on the apparent agreement between Norway, Iceland and West Greenland in the years when dominant year-classes of cod were produced, except that not all of the dominant year-classes in the other two areas were also dominant at West Greenland.

The apparent interrelationships of the occurrence of good year-classes in the Greenland, Iceland and Norwegian to Barents Sea areas in the year or two following, or in the case of Iceland sometimes in the same year as, a good year-class survival of Grand Bank haddock suggests a hydrological or meteorological sequence of favourable situations for survival in these areas.

Success of year-classes will also depend especially on drift and survival for several months following spawning.

Mr Floyd M. Soule (personal communication, 6 March 1963) says that if the oceanographic conditions on the Grand Bank are affected by the North Atlantic eddy, conceivably conditions off southwest Greenland might be affected a year later subject to the many opportunities for modification en route. Hermann (1951; MS, 1961) found a correlation between successful year-classes of cod in West Greenland and higher than usual bottom temperatures on Fylla Bank in June. Kislyakov (1961) found a correlation between success of year-class survival of Arcto-Norwegian cod and the mean temperature and also the surface temperature of the water mass on the spawning grounds off the west coast of Norway. Higher-than-usual temperatures produced the more successful year-classes. These correlations may indicate a direct relationship between temperature and survival, or it may be that the higher temperatures are indicative of some other factor such as water transport acting directly or in concert with temperature.

2: Drifts across the Atlantic

Five of the surface drift bottles liberated in and near the Gulf of Maine in July and August 1922-23 were found on the European side of the Atlantic in the Azores, France, Ireland and England 12-14 months later (Bigelow, 1927).

In the Annual Reports of the Newfoundland Fisheries Research Commission (1934) and of the Newfoundland Fisheries Research Laboratory (1936) surface drift bottles liberated in the Newfoundland area in 1932-33 at southern Labrador, northern Grand Bank and the mid-east coast of Newfoundland were reported from Ireland (2) and from Scotland (1) in 343, 371 and 339 days after liberation. Others liberated in the Newfoundland area in 1932-34 were recovered in Ireland (4), Scotland (5) and the Azores (1) in 421-470 days and at the Faroes (1) 436 days, and in Norway (2) 470 and 511 days after liberation.

Dr R.W. Trites of the Fisheries Research Board of Canada's Atlantic Oceanographic Group, has supplied (20 June 1963) information on periods between release of surface drift bottles in the Canadian Atlantic area by the Fisheries Research Board of Canada Biological Station, St. Andrews, N.B. and recovery in some of the countries on the European side of the Atlantic. Omitting occasional abnormally short and unusually long periods the average times between release and recovery of these bottles were as below:

Area	Number drift bottles	Avg days release to recovery		
		1st 25%	1st 50%	All bottles
Ireland	54	228	246	356
Scotland	15	302	339	393
Iceland	9	328	374	417
Norway	18	383	452	537

These average periods are maximal since some bottles would not be recovered immediately they drifted ashore. Dr Trites estimates that with drift bottles ballasted so that they barely float the speed of drift is probably not more than 20% in excess of the speed of the upper metre of water and that the average times of transatlantic passages of drift bottles indicated above are reasonably representative of water motion in the upper metre.

Dodimead and Hollister (1958) for drift bottles liberated in the Eastern Pacific found that the current speeds estimated from drift bottles were generally comparable to the average speeds calculated from the geopotential topography.

The leptocephali of the European eel (*Anguilla vulgaris*) take two years to drift from the Western Atlantic west of 50°W (the longitude of the southern tip of the Grand Bank but with the main distribution 10-15° of latitude further south) to the coastal banks of Europe west of the British Isles (Schmidt, 1925).

Helland-Hansen and Nansen (1909) say that the temperature effect of a large amount of warm Atlantic water should appear off Lofoten one year later and in the Barents Sea two years later than off Sognefjord in southwestern Norway.

3: Relation of Relative Year-class Successes to Speed of Current Drift

It is apparent from the foregoing that it is possible that a hydrological effect due to the Gulf Stream system effect on the southern Grand Bank such as a greater volume transport of this warm water may affect the Icelandic area a little over a year later, the Norwegian area approximately two years later and the western Barents Sea area over which the Arcto-Norwegian cod and haddock stocks drift about three years later than the Grand Bank effect. It is possible that there may be also some persistence of the effect for a later period and that on the Grand Bank the effect may both begin much earlier and continue considerably later than the time of its actual main effect on haddock year-class survival.

The occurrence in recent years of good year-classes of cod in West Greenland one year after those of Grand Bank haddock (actually a little less than one year since West Greenland cod spawn more than a month earlier than Grand Bank haddock) seems to allow a minimal time for transfer of warm water from the Gulf Stream system. The occurrence of some good year-classes of cod, haddock and herring at Iceland and more occasionally in West and East Greenland in the same year as the success of year-class survival of Grand Bank haddock is unlikely to be due to transport of the same water which led to the haddock success unless the beginning of the build-up of the passage of suitable water south of the Grand Bank occurred in the year previous to the year of the successful Grand Bank year-class. The Icelandic year-class successes in haddock and herring one and sometimes two years after the Grand Bank success could presumably be due to water transfer between the two areas.

The occurrence of good year-classes of Arcto-Norwegian cod and haddock, and to a lesser degree Atlanto-Scandian herring, one year after a good year-class of Grand Bank haddock again seems to be too short a time for actual water transport between the two areas unless the actual water mass changes south of the Grand Bank begin many months previously to the May-June-August period when Grand Bank haddock year-class survival is likely to be affected. The relationship of the year-class survivals in the Grand Bank and Norwegian areas which are separated by two years has a greater probability.

The occurrence of abundant to very abundant year-classes of Grand Bank haddock had such a regular periodicity of three years between 1946 and 1955, with a four-year period between 1942 and 1946, that instead of a Greenland-Barents Sea relationship of successful year-classes of cod, haddock and herring usually one to two years after the occurrence of a successful year-class of Grand Bank haddock (with often successful year-classes of these fish at Iceland and of Grand Bank haddock in the same year), the relationship might be that of a good year-class occurrence in the West Greenland-Barents Sea areas three to five years after a Grand Bank haddock success.

Opposed to this view is the occurrence of the best groups of year-classes in the West Greenland-Barents Sea areas one year after the most successful Grand Bank haddock year-classes of 1949 and 1955. However, the presumption that the related effect is one to three years after a Grand Bank success would transfer most of the cases of year-class success at Iceland and Greenland occurring in the same year as a Grand Bank success to an occurrence three or two years after a Grand Bank success, and would also provide a relationship between the 1945 successes at Iceland and Greenland and the 1942 success on the Grand Bank.

The occurrence between 1912 and 1945 of good year-classes of cod at West Greenland, always in the same, but not in all, years when there were good year-classes of cod at Iceland, may often be due to the drift of cod larvae from Iceland (Tåning, 1934, 1937; Hansen, 1949, 1954) and argues for a stronger water and cod egg and larval transport from Iceland to West Greenland in some years than others.

During the period when cod year-class success at West Greenland coincided with and often, at least, largely depended on cod year-class success at Iceland, the success of year-classes of Atlanto-Scandian herring (occurring usually one but sometimes two years after a year-class success of West Greenland cod) could be due, also, to the same stronger than usual (or otherwise more suitable than usual) North Atlantic water transport which produced the successful West Greenland year-classes of cod. Due to the longer time required for water transport to Norway than to Iceland the Norwegian herring development and larval drift area is affected a year and occasionally two years later. In recent years, with a greater dependence of the West Greenland cod stock on spawning in West Greenland itself (Hansen, 1954), there is more coincidence in year-class success in the same year for West Greenland cod and Atlanto-Scandian herring. This agrees with the idea that water transported from a common source will arrive later on the West Greenland than on the Icelandic cod spawning grounds, and may arrive off Norway at approximately the same time as off West Greenland.

A complete explanation of all the relationships described cannot be offered at present and some of the interrelated occurrences appear to be too close together in time. However, the occurrence of good year-classes of different species over such a wide area in the same years and groups of years indicates more than unrelated local phenomena and argues for an interrelationship through the Gulf Stream which may affect the southern Grand Bank through eddies and intermingling with Grand Bank-Labrador Current water and through its North Atlantic Current branches affect the Icelandic, Greenland and the Norwegian-Barents Sea areas.

It is possible that in the periods of change in water transport and temperature the favourable effect on year-class survival may be at or near the peak of transport or temperature in one area and also before and after the peak in another area and that thus the apparent timing differences in year-class survival may be explained. Although the main effects appear to be related there are also likely to be some local effects which will occasionally produce or interfere with the production of a successful year-class in a local area.

Often in fisheries research what has appeared to be a good correlation has shown no correlation at a later period. Thus, our confidence cannot be too great in the apparent correlations in year-class timing and in year-class iceberg relationship discussed in this paper. However, the greater tendency for successful haddock year-classes on the southern Grand Bank to appear in low rather than in high iceberg years seems to occur too often to be fortuitous. Mr Floyd Soule (personal communication 6 March 1963) says that there are great year-to-year variations in the numbers of bergs calved in West Greenland. Once calved they are affected in varying degrees by the factors which prevent 98 to 99% of them from reaching positions south of 48°N in the vicinity of Newfoundland. In addition to variations in the transportation system such factors as stranding and melting are important. Each of these is the result of a number of interrelated items which still have to be evaluated. Mr Soule's best estimate of the travel time of bergs, from parent glacier point in West Greenland to the Newfoundland area, is three years.

It is not possible at the present time to say why iceberg numbers south of 48°N ahould be related to the success of haddock year-classes on the southwestern Grand Bank. Schell (1962) showed that stronger than usual northwesterly winds off the Newfoundland and Labrador coasts and relatively low temperatures over Newfoundland in the months from December to March produce greater than average berg counts off Newfoundland in the following months, mainly April to June. The opposite conditions - lighter northwesterlies and higher temperatures are related to lower than average berg counts. Thus temperature and related winds may be factors in haddock year-class survival on the Grand Bank.

REFERENCES

BARANENKOVA, A.S. 1960. The results of young cod and haddock surveys in the Barents Sea in the period 1946-1959, p. 267-275. In *Soviet Fisheries Investigations in North European Seas, Moscow.*

BIGELOW, HENRY B. 1927. Physical oceanography of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, 40(2): 511-1027.

DODIMEAD, A.J. and H.J. HOLLISTER. 1958. Progress report of drift bottle releases in the Northeast Pacific Ocean. *J. Fish. Res. Bd. Canada*, 15(5): 851-865.

HANSEN, PAUL M. 1939. The age composition of the cod in West Greenland waters in the years 1924 to 1938. *Rapp. Cons. Explor. Mer*, 109: 60-65.

1949. Studies on the biology of the cod in Greenland waters. *Ibid.*, 123: 1-77.

1954. The stock of cod in Greenland waters during the years 1924-52. *Ibid.*, 136: 65-71.

HELLAND-HANSEN, BJORN and FRIDTJOF NANSEN. 1909. The Norwegian Sea, its physical oceanography based on the Norwegian researches 1900-1904. *Rept. Norweg. Fish. Mar. Invest.*, 2(2): 1-390.

HERMANN, FREDE. 1951. Hydrographic conditions off the west coast of Greenland 1950 with remarks on the influence of temperature on cod year-classes. *Ann. biol., Copenhague*, 7: 21-24.

1961. Some considerations about correlations between the West Greenland stock of cod and environmental factors. *Annu. Meet. int. Comm. Northw. Atlant. Fish.*, 1961. Doc. No. 34, Serial No. 898 (mimeographed).

JONSSON, JON. 1954. On the Icelandic stock of cod during the years 1928-1953. *Rapp. Cons. Explor. Mer*, 136: 51-57.

KISLYAKOV, A.G. 1961. The connection between hydrological conditions and fluctuations in the abundance of year-classes of cod. *Trudy Soveshchanii*, No. 13, 260-264.

NEWFOUNDLAND FISHERIES RESEARCH COMMISSION. 1934. *Ann. Rept. 1933*, 2(2): 1-117.

NEWFOUNDLAND FISHERIES RESEARCH LABORATORY. 1936. *Ann. Rept. 1935*, 2(5): 1-95

RAITT, D.S. 1936. The haddock stocks of the North-east Atlantic, 1916-1935. *Fish. Bd. Scot., Sci. Invest. 1936*, No. 1, p. 1-32.

1948. The haddock at Iceland with special reference to Faxa Bay. *Rapp. Cons. Explor. Mer*, 120: 52-53.

ROLLEFSEN, GUNNAR. 1954. Observations on the cod and cod fisheries of Lofoten. *Rapp. Cons. Explor. Mer*, 136: 40-47.

SCHELL, IRVING I. 1962. On the iceberg severity off Newfoundland and its prediction. *J. Glaciol.*, 4(32): 161-172.

SCHMIDT, JOHS. 1925. The breeding places of the eel. *Rept. Smithson. Instn. for 1924*, p. 279-316.

SERYAKOV, E.I. MS, 1962. On the possibility of forecasting the thermal conditions of the waters in the ice-free part of the Barents Sea for five-year periods. *I.C.E.S. C.M. 1962, Hyd. Comm.* No. 126, p. 1-6.

SUND, OSCAR. 1936. The fluctuations in the European stocks of cod. *Rapp. Cons. Explor. Mer*, 101(3): 1-18.

1943. The age-composition of the Norwegian spawn-herring observed during 36 years. *Ann. biol. Copenhague*, 1: 45-49.

TÅNING, Å. VEDEL. 1931. Fluctuations in the stock of cod in Icelandic waters. *Medd. Danm. Fisk. Havundersøg*, 9(3): 1-43.

1934. Survey of long distance migrations of cod in the northwestern Atlantic according to marking experiments. *Rapp. Cons. Explor. Mer*, 89(3): 5-11.

1936. Review of the fluctuations in the stock of cod at Greenland, Iceland, the Faroes and in Danish waters. *Ibid.*, 101(3): 19-21.

1937. Some features in the migrations of cod. *J. Cons.*, 12(1): 3-35.

THOMPSON, HAROLD. 1929. General features in the biology of the haddock (*Gadus aeglefinus* L.) in Icelandic waters in the period 1903-1926. *Fish. Bd. Scot., Sci. Invest. 1928*, No. 5, p. 1-63.

1939. The occurrence and biological features of haddock in the Newfoundland area. *Nfld. Dept. Nat. Res., Res. Bull.* No. 6, p. 1-31.

U.S. COASTGUARD, 1915-1963. *Reports of the International Ice Patrol Service in the North Atlantic Ocean, seasons of 1914-1961.* Bull. No. 3-47.

D-3

CHANGES IN GROWTH, FEEDING AND DENSITY OF GULF OF ST. LAWRENCE COD[1]

By

A. Carl Kohler[2]

ABSTRACT

Growth rates of southwestern Gulf of St. Lawrence cod increased from 1952 to 1955 and decreased from 1957 to 1959. Laboratory studies showed that within limits food consumption increases with increasing water temperature and growth increases with increasing food consumption. Field studies showed no major changes in water temperature in the period 1952-59, but during the fast-growth years there was a lower density of large cod (herring eaters) and greater availability of food for cod in the form of moribund herring due to an epizootic. The changes in growth rate were related to the latter two environmental factors.

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D-4

TEMPERATURE AND GROWTH OF COD IN ICELANDIC WATERS

By

Jon Jonsson[1]

ABSTRACT

The hydrographical conditions around Iceland are characterized by a gradual decrease in temperatures along the coast, the temperature being highest off the south coast and lowest off the east coast. This very much affects the growth and distribution of marine animals in these waters.

The immature cod in Icelandic waters provides a good example of a strong positive correlation between temperature and growth.

Four stations with a range in temperature from 3.57°C to 8.51°C are analyzed and the temperature differences are correlated to differences in the lengths of the various agegroups. The temperature coefficients found this way are in agreement with values found by laboratory tests.

Numerous tagging experiments have shown that the Icelandic cod is rather stationary during its first years of life and does not undertake extensive migrations until it reaches maturity. The main spawning areas are located in the warm waters off the south and southwest coasts, and from there the eggs and larvae drift clockwise around the Island. The fish in the various coastal areas are therefore practically all derived from the same spawning population.

There is a gradual decrease in temperature from highest off the southwest coast to lowest off the northeast and east coast. In August the mean temperature at 50 m is about 9°C in Faxa Bay (southwest coast), but below 5°C off the east coast. This difference in temperature greatly affects the distribution and growth of marine organisms in the various coastal areas.

The growth of the cod in Icelandic waters is a good example of this and in order to examine this problem further we shall analyse some samples of cod taken by the R/V *Maria Julia* in 1950. All the stations were worked during the period 14 to 31 August. Figure 1 shows the location of the stations. Table 1 shows the average lengths of the age groups with the average temperature at 50 m in July-August of 1948-50 at four fixed hydrographical sections nearest the locality where the fish were caught. These averages should therefore give, as far as temperature is concerned, the differences in the environment in which the fish has lived the past three years before capture.

Figure 2 shows a very strong positive correlation between temperature and growth. It therefore does not seem unreasonable to view the data as resulting from a huge experiment conducted by Nature to rear fish under different temperature conditions.

Tackling the problem from this point of view, we can see if our data are in any agreement with laboratory experiments about the effect of temperature on the growth of living organisms. We have to assume, among other things, that the availability of food has been the same in all areas and there is no reason to believe otherwise.

Van't Hoff has shown that the rate of an inorganic process increases exponentially with increasing temperature, *i.e.* the rate of the process increases as x^n, n being the difference in temperature and x the socalled *temperature coefficient*. Generally we can say that when $n=10$, then $x=2$, *i.e.* the speed of the process is doubled with an increase of 10°C in temperature.

Numerous investigations made on the effect of temperature on the rate of growth in living organisms have shown a similar effect of temperature as stated by Van't Hoff.

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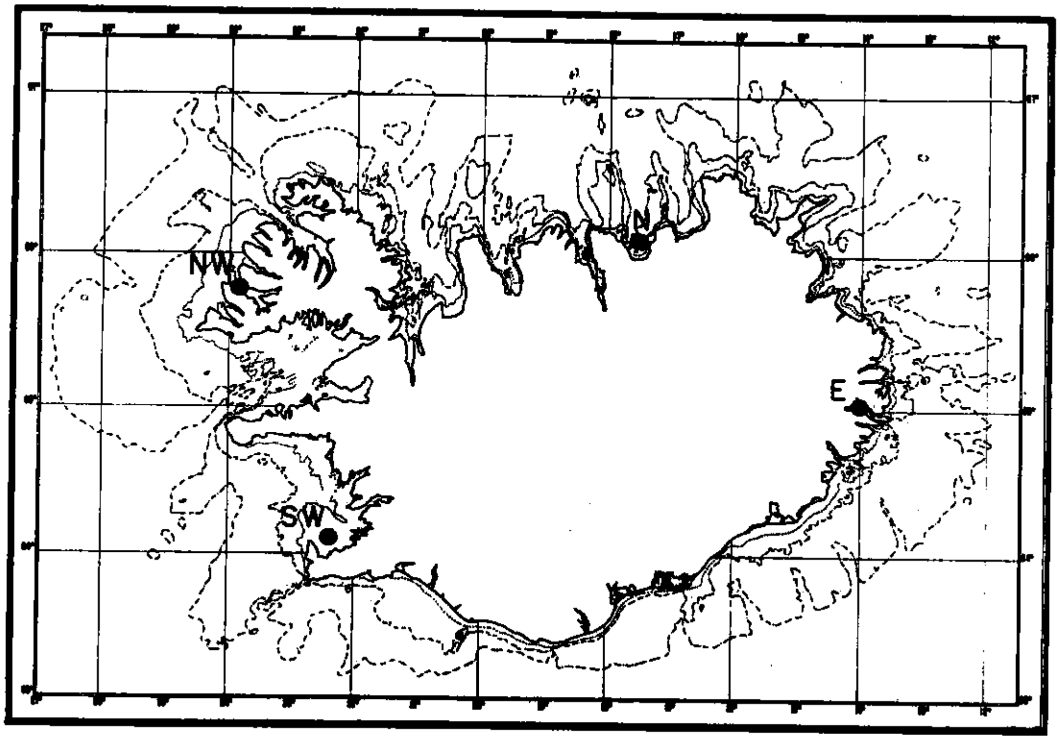

Fig. 1. Location of stations where otolith material was collected.

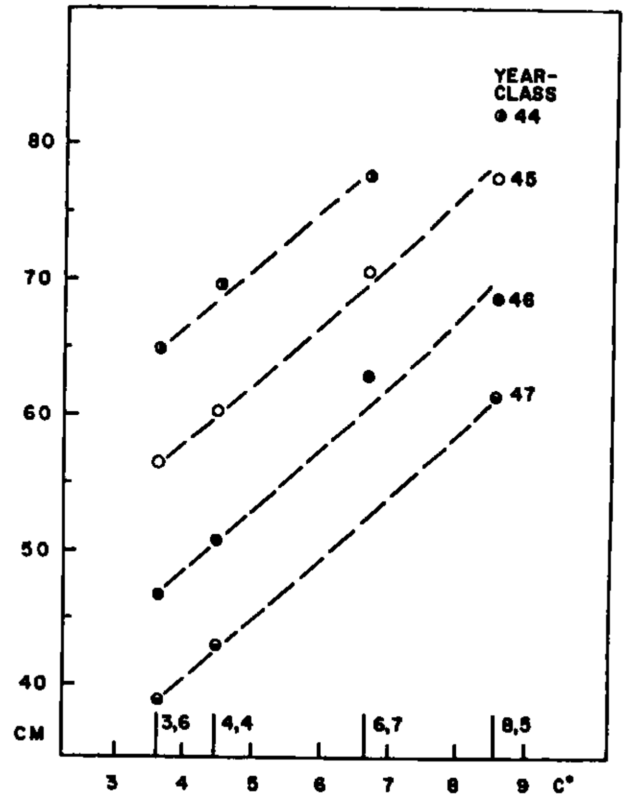

Fig. 2. Average temperatures at 50 m in July-August 1948-1950 and the lengths of the age-groups 3-6 (1944-1947 year-classes) of cod in August 1950.

From Table I we can calculate the Q_1, or the temperature coefficient for one centigrade and make use of the following equation:

$$\frac{V_{(t+n)}}{V_t} = x^n \text{ or } \log V_{(t+n)} - \log V_t = n. \log x$$

As an example we can compare the lengths of age-group 4 from the areas N and SW and get the following:

$$\frac{\log 68.7 - \log 51.0}{4.07} = \log x, \quad \log x = 0.0318, x = 1.07$$

In the same way we can compare other temperatures and other age-groups, and the values for Q_1 thus found are shown in Table 2.

The table shows, first, that the Q_1 is highest for the younger age-groups, and decreases for the older ones. This may be explained by the fact that a part of the older fish is already mature and the effect of maturity has set in. Second, we see that the values of Q_1 are relatively higher when we compare the lower temperature areas, *i.e.* the change in temperature in the cold water seems to have a greater effect than in the warm waters.

In his work on growth and form, D'Arcy Thompson (1942) gives some values for the Q_1 found

TABLE 1.--TEMPERATURE (°C) AND THE LENGTH (CM) OF THE AGE-GROUPS 3 TO 6 AROUND ICELAND IN AUGUST 1950.

Areas	Mean temp. °C	Age-groups 3	4	5	6
SW	8.51	61.6	68.7	77.6	81.2
NW	6.66	-	58.0	70.5	77.8
N	4.44	43.4	51.0	60.5	68.7
E	3.57	39.2	46.9	56.6	65.0

TABLE 2.--VALUES OF Q_1 FOUND FOR VARIOUS TEMPERATURE DIFFERENCES AND VARIOUS AGE-GROUPS.

Areas	Diff. in temp.	Age-groups 3	4	5	6	mean for 4-6
SW and E	4.94	1.095	1.080	1.066	1.046	1.064
SW and N	4.07	1.090	1.076	1.063	1.041	1.060
NW and E	3.09		1.071	1.074	1.060	1.068
NW and N	2.22		1.060	1.071	1.058	1.063
SW and NW	1.85		1.096	1.053	1.023	1.057
N and E	0.87	1.124	1.101	1.080	1.066	1.082
Avg		1.103	1.081	1.068	1.049	1.066

by laboratory experiments in various plants and animals. The following figures are taken from his work (page 231):

Yeast 1.13, lupin 1.16, maize 1.20, pea 1.09, echinoids 1.08, drosophila 1.12, frog (segmentation) 1.08, frog (tadpole) 1.13. The average for these experiments is 1.12.

We therefore say that our "natural experiment" without any scientific control is in a rather good agreement with laboratory tests.

This material was not originally collected with such calculations in view and the number of fish in some age-groups is rather small. Laboratory experiments on Q_1 have been criticised by some workers and the problem is of course very difficult, but without taking the figures found for Q_1 too seriously, we certainly must admit that they give us the strongest impression of the relationship between the growth of the fish and their environment. Other factors, of course, may influence the growth, but at present only the temperature can be expressed by numerical values.

REFERENCES

THOMPSON, D'ARCY W. 1942. On Growth and Form . Cambridge 1942.

D-5

SOME PROBLEMS OF ZOOPLANKTON PRODUCTION AND THE PROBLEMS OF FISHERIES

By

Wladyslaw Mankowski[1]

ABSTRACT

From observations made on zooplankton production in the Southern Baltic and on the biology of two plankton-eating fish, sprat and herring, from 1951-62, the author shows that the amount of fat in sprat, the length of herring in its first and second year of life, the rate of growth of both species and the condition of herring depend on production of zooplankton. These relationships were most conspicuous in the years 1955-1957. Hydrological conditions, particularly the temperature of water, seem to be the factor regulating these phenomena. After severe winters the production of zooplankton and the amount of fat in sprat, condition of herring and the rate of growth are poor; after mild winters they are good.

Studies, carried out for many years on production of zooplankton in the southern Baltic, though sometimes based on incomplete annual cycles, enabled us to establish the course of zooplankton production in particular years. As a further step an attempt was made to compare acquired data with some elements of the biology of the plankton-eating fish, sprat and herring. The following elements were taken into consideration:

(1) Fat contents (for sprat);

(2) Length (L_1, L_2) and the rate of growth

(t_2 for herring and t_2, t_3 , t_4 for sprat);

(3) Condition (Fulton's weight-growth coefficient for herring).

The observations cover the period of twelve years (1951-62). It was impossible to obtain the same data for all the elements shown above.

The first few years of the period (1951-54) do not show anything particular. The production of plankton (Fig. 1) and such elements of the biology of the above mentioned fish, which were recorded from the observations, *i.e.* fat contents of sprat, the length of herring (L_1 and L_2 - Fig. 2 and 3) and Fulton's coefficient K, remain on an average level.

The years 1955-58 are the most interesting period. Plankton production reached its highest and lowest values and was followed by similar fluctuations in values of some of biological features of plankton-eating fish.

The first year, 1955, must be considered a good one. Good production of plankton caused considerable accumulation of fat in sprat and good condition of herring, as well as good growth rate of both species.

Lowest plankton production was in the year 1956. It was characterised by a continuing and considerable fall of fat contents of sprat, which at the beginning of 1956, with an accumulation from 1955, was large. The decrease of fat contents of sprat lasted unusually long, and in July had dropped to a very low value, the lowest one in the whole period of observations (about 3%). The

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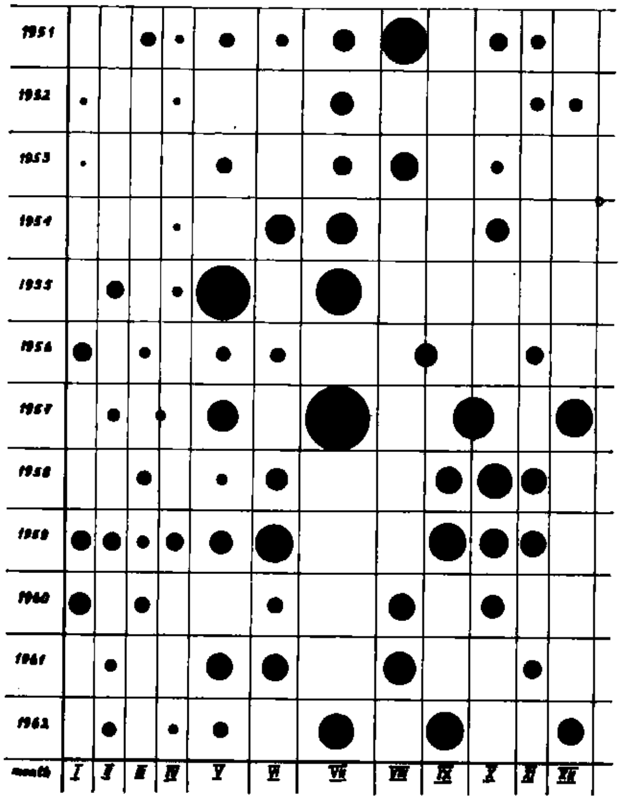

Fig. 1. Mean biomass of the plankton in Gdansk region in g/lm^2 of the sea surface.

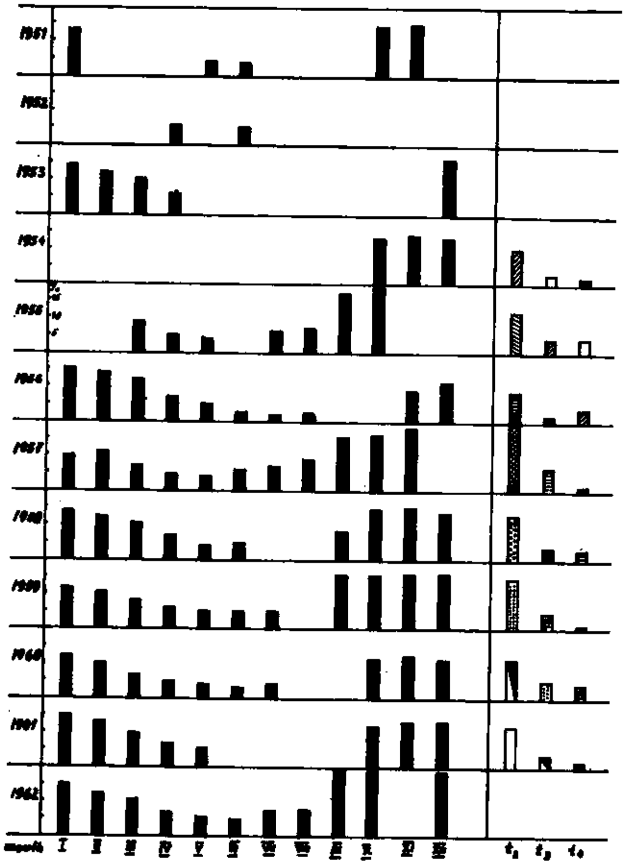

Fig. 2. Fat content (in %) and rate of growth (t_2, t_3, t_4) of sprat in the southern Baltic.

delayed restoration of fat and the small quantities of plankton resulted in the fat content of sprat reaching (towards the end of the year) only 12%, quite small in view of the recorded 19% in 1955. Also the rate of growth in 1956 was smaller than the rate in both preceding and following years.

Similar behaviour was observed in 1956 for both the spring and autumn spawning herring. The coefficient K dropped to its lowest value. The same was true for the length reached by herring from the autumn spawning of the previous year and spring spawning of 1956. Thus the length increase of this herring was small.

This year of poor nourishment, 1956, was followed by the best one in plankton production, the year 1957. The amounts of plankton were enormous. All the biological indexes of plankton-eating fish reached their highest values. The fat contents of sprat in spite of their low level (12%) at the beginning of the year decreased only to about 5%. This decrease stopped in May and fat restoration on the basis of the rich plankton reached 18% towards the end of the year. The highest value was also recorded for length increase of sprat of the first and second age-group (t_2 and t_3).

Herring reacted in a similar way to the amount of nourishment. The fish of zero group reached good growth, whereas the fish of group I reached the average long-term length, owing to an exceptionally fast length increase, which made up for the losses in 1956. Of particular interest was the increase of the coefficient of condition of herring to the highest value during the period of observations.

In the next period the values for plankton production were rather average, which was evidenced by the good fat contents (to 16%) and the average length increase of sprat. Herring size and coefficient of condition showed similar values.

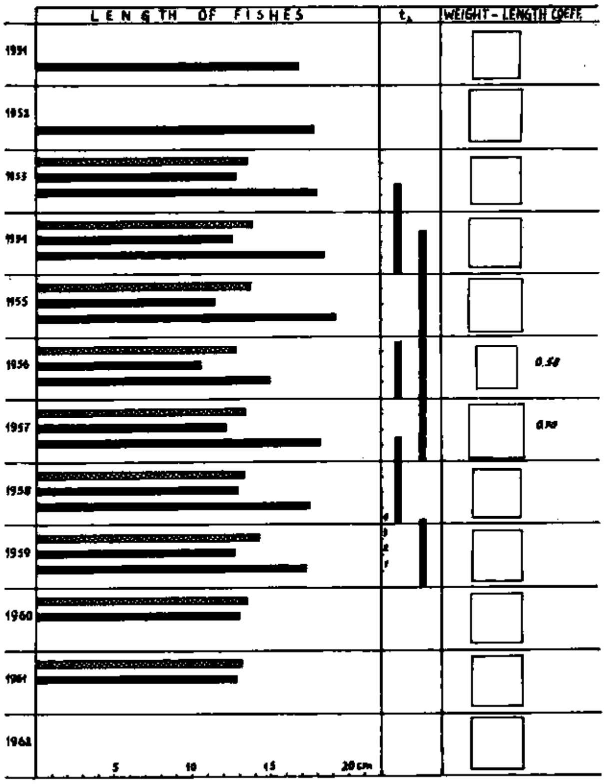

Fig. 3. Length (L), rate of growth (t_2) and weight-length coefficient of spring (solid black) and autumn (cross hatched) herring in the southern Baltic.

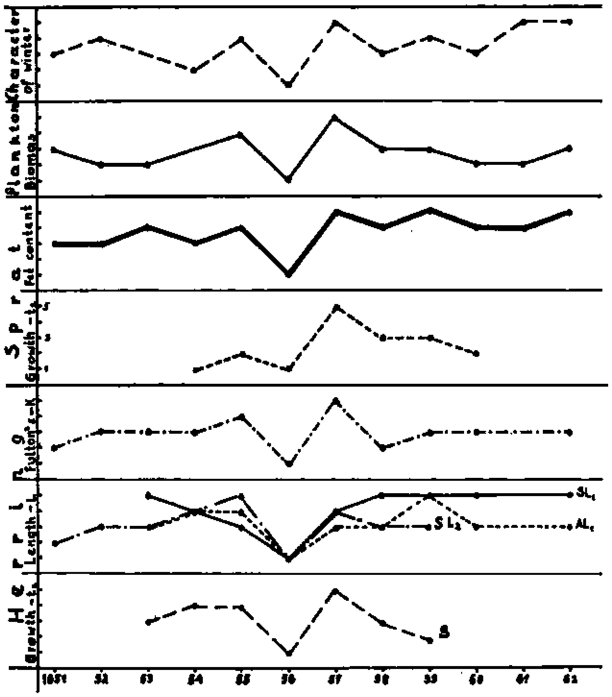

Fig. 4. Plankton production in the southern Baltic and its effect on the biology of the sprat and herring. Scale for the character of winter: 1-very cold; 2-cold; 3-mean; 4-mild; 5-very mild. Scale for the other features: 1-very small; 2-small; 3-mean; 4-good; 5-very good.

The mean biomass of zooplankton and the above elements have been brought into a five-grade scale (Fig. 4), in which the lowest and the highest values were taken as the lowest and the highest grades of the scale. It was possible in this way to bring all the elements into a common diagram. Such tabulation allows quick comparison and shows the relation between plankton production and biology of plankton-eating fish.

The question arising from this analysis, is: what is the basic source of the plankton production? Characteristic winter conditions in the sea are shown in Fig. 4 and the following table

WINTER SEA WATER TEMPERATURES

Depth m	25 March 1956 °C	5 April 1957 °C	18 March 1958 °C
0	-0.20	4.90	1.15
10	-0.15	3.20	1.15
20	-0.28	3.20	1.18
30	-0.15	2.90	1.10
40	-0.20	2.80	1.10
50	-0.20	2.60	1.22
60	-0.30	2.80	1.25
70	4.70	2.80	1.62
80	5.40	4.40	2.00
90	5.27	4.40	2.10
100	5.50	5.00	3.20

points to the fact that the most severe winter was in 1956, whereas the mildest winters were in 1955 and 1957. Is temperature of the waters the main and direct factor regulating all the above phenomena, or are we witnessing only their coincidence? Is water temperature an indirect factor which affects the balance of biogenic salts in the sea, which in turn affect the basic production and further links of life? These questions require further and thorough analysis.

REFERENCES

MANKOWSKI, W. 1957. Initial Researches on the Production of the Plankton in Southern Baltic. ICES Baltic-Belt Seas Committee, Paper No.28.

1960. Continued Investigation on the Production of the Southern Baltic Plankton. ICES Plankton Committee, Paper No.71.

MANKOWSKI, W. and J. POPEIL. 1961. The Plankton Production in the South-Eastern Baltic and its Effect on the Biology of Herring. ICES Herring Committee, Paper No.29.

MANKOWSKI, W., J. ELWERTOWSKI, and J. MACIEJCZYK. 1961. Plankton Production in the Southern Baltic and its Effect on the Sprat Biology. ICES Sardine Committee, Paper No.32.

D-6

COD GROWTH AND TEMPERATURE IN THE NEWFOUNDLAND AREA

By

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ABSTRACT

Growth of cod from various parts of the Newfoundland-Labrador area is described by the von Bertalanffy growth equation. Variations in growth are related to the varying influence of the Labrador Current in terms of increasing surface temperatures and decreasing volume of cold water (less than 0°C) from north to south. Values of the growth parameters K and L_∞ are shown to be related to latitude. The highest values of K and lowest values of L_∞ are found in the cooler waters of higher latitudes, while the reverse is true in warmer waters to the south. This does not conform to most of the findings in the fisheries literature. Some possible reasons for these differences are discussed.

INTRODUCTION

Annual growth of fishes represents the excess of food intake over that necessary for general maintenance requirements and, in the case of mature individuals, for production of the genital products. As such, the yearly growth increment is governed by the complex interaction of factors influencing availability of food and its assimilation to form new somatic tissue in the organism. The former category includes those factors which govern distribution and abundance of predator and prey, while the latter includes those affecting metabolism. Temperature makes its effects felt in both directions and has probably received most attention, both in the laboratory and in nature.

While the effects of temperature on growth can be observed with relative ease in controlled laboratory experiments, they are difficult to isolate in studies of natural populations. Of all the physical and biotic factors which influence growth, temperature is certainly the one most easily measured, and the one for which the greatest amount of accurate and long-term data is available. Even so, a study relating temperature to growth in the sea may be little more than qualitative because of the difficulty of obtaining a temperature measure which is representative of an oceanic area and, particularly, of the immediate thermal environment of the fish which inhabit that area. Taylor (1958, 1959, 1960) has approached the problem by using mean annual air and surface temperatures as indicators. Experimental evidence relating temperature and growth has been reviewed by Brown (1957).

In the present study geographical variations in growth of cod from the Newfoundland-Labrador area are related to temperature differences in the various localities under consideration.

MATERIALS AND METHODS

The assembled growth data cover at least eight more or less distinct stocks of cod, as reviewed by Templeman (1962*b*), occupying ICNAF Subareas 2 and 3 as well as Division 4R. These include the Labrador-Newfoundland stock, the Flemish Cap stock, the Grand Bank stock, the Avalon-Burin stock, north and south St. Pierre Bank stocks, the Borgeo Bank stock and the West Newfoundland stock. The geographical limits, seasonal distribution and migration routes of these are illustrated in Fig. 5 of Templeman (1962*b*).

In the present study, since it was not always possible to separate data relating to the various stocks, the analysis has proceeded on an area rather than a stock basis. In fact, these criteria have similar effect except for the Newfoundland south coast area where intermingling of several stocks is known to occur at various times throughout the year.

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The otolith collections and length data include both inshore and offshore material collected during the period 1960-62 (Table 1). The offshore data represent random samples of research vessel catches by otter trawl having the codend lined or covered with small-meshed netting. These vessels generally fished one or more series of standard depths from the shallowest depth available to at least 375 m, and sometimes to more than 700 m. The inshore collections represent random samples by various gears from the inshore commercial catches at fishing centres along the Newfoundland and Labrador coasts (Fig. 1). Where both inshore and offshore material were available only the offshore

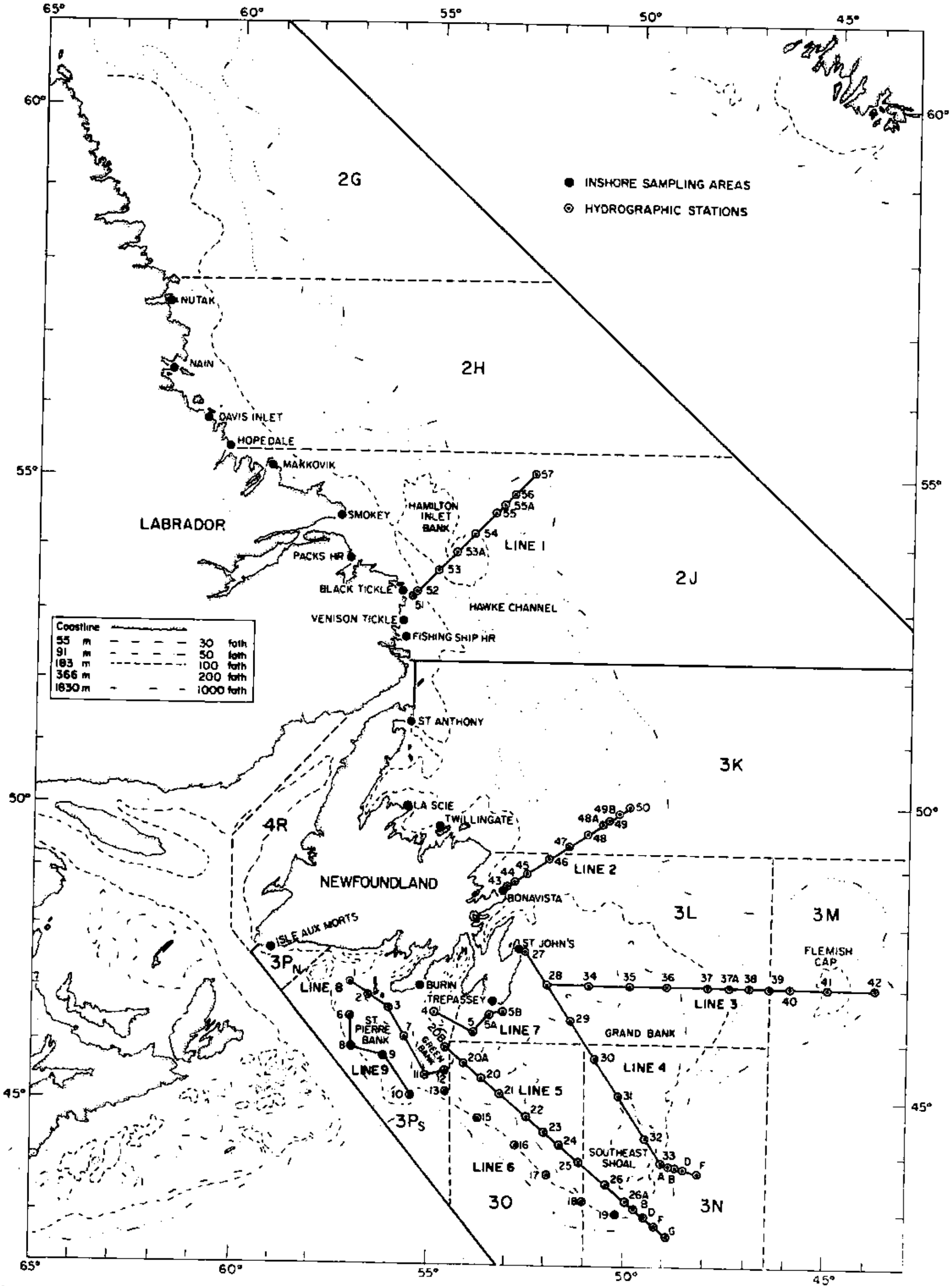

Fig. 1. Area map showing ICNAF Divisions, hydrographic stations, inshore sampling stations and place names mentioned in the text.

data were used to compute mathematical growth curves, with the exception of Division 3Ps where the offshore data were scanty for the older ages.

TABLE 1. OTOLITH COLLECTIONS DURING 1960-62 IN THE NEWFOUNDLAND AREA REPRESENTED IN THE LENGTH-AT-AGE PLOTS OF FIG. 2.

ICNAF Division	Stocks	Pairs of otoliths Inshore	Pairs of otoliths Offshore	Ages used to fit growth curve
2H	Labrador-Newfoundland	1,149	1,176	3-15
2J	Labrador-Newfoundland	1,870	1,580	3-15
3K	Labrador-Newfoundland	3,792	1,004	3-15
3L	Labrador-Newfoundland, Grand Bank, Avalon-Burin	2,596	1,279	2-14
3M	Flemish Cap	-	522	2-8
3N-O	Grand Bank	-	2,560	2-14
3Ps	St. Pierre Bank, Avalon-Burin, Burgeo Bank	2,340	684	3-14
3Pn	West Newfoundland, Burgeo Bank, Avalon-Burin	901	-	5-14
		12,648	8,805	

Lengths were measured to the nearest centimetre from snout to mid-fork. Ages were determined from otoliths, supplemented by scales in some doubtful cases. Most of the age reading was done by the authors, working on an area basis. The age reading technique is described in the summary by Keir (MS, 1960). An intramural otolith exchange programme revealed that no consistent differences in interpretation existed among the group and, in fact, that each age reader obtained best results for the area for which he was responsible, and therefore most familiar.

The collections were made at various times throughout the year in the various areas, though in most areas mainly between April and September. In such cases the age has been regarded as one-half year above that read from the otolith, since we have adopted the convention of using 1 January as the "fish's birthday". However, the collections in Divisions 3M and 3Pn were almost entirely in the January-June period, and for these areas no adjustment has been made.

Growth in each area has been described by the von Bertalanffy (1938) growth curve (Fig. 2) using the "trial L_∞" approach as described by Ricker (1958), P. 194-196. Aberrant averages at the younger ages and averages based on less than 10 fish have not been used in computing the curves.

The temperature sections of Fig. 4 and 5 are based on annual hydrographic surveys in July-August by research vessels of the St. John's Biological Station.

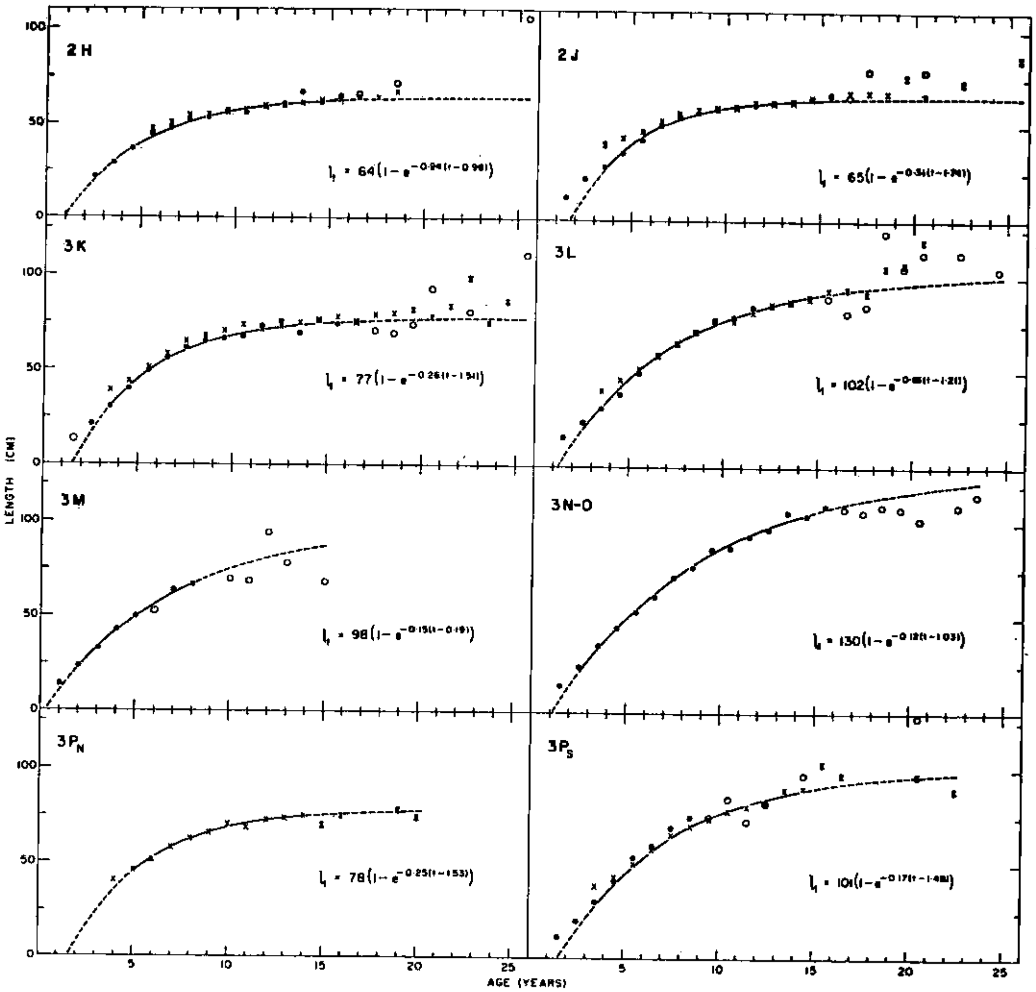

Fig. 2. Plots of average length at age and fitted von Bertalanffy growth curves for various areas. The curves are fitted to the offshore data only except in Divisions 3Pn and 3Ps. The circles represent offshore averages and the crosses inshore averages. Open circles, and crosses with a vertical stroke indicate averages based on less than 10 fish. The solid part of each curve represents the range of data on which the mathematical fit was based.

GROWTH OF COD

Plots of average length at age for each area under consideration are shown in Fig. 2. Inshore averages from mixed gear collections and offshore averages from research otter-trawl collections are shown separately. The von Bertalanffy growth curve is given for each area in the form

$$l_t = L_\infty\ (1-e^{-K(t-t_0)})$$

where l_t is length at age t, L_∞ is the theoretical maximum length, K is a constant determining the rate of change in length increment and t_0 is the hypothetical age at zero length. The various equations provide an adequate description of growth over the range of ages used to derive them.

Average lengths at the youngest ages represented in the inshore data tend to be artificially high because of selection by the various inshore gears (traps, longlines, handlines, jiggers and gillnets). Apart from this, and except for Division 3Ps, the inshore average lengths in those areas bordering the coastline are similar to those derived from the offshore data in the same areas. Thus the curves derived from the offshore data provide an adequate representation of the inshore material as well, lending evidence to the hypothesis (Templeman, 1962*b*) that there is no inshore-offshore stock separation in the areas concerned. With the exception of the youngest ages the offshore averages in Division 3Ps are generally higher than those inshore. These differences are undoubtedly a reflection of the fact that several stocks inhabit this area. Since the offshore (St. Pierre Bank) growth data were very scanty beyond age 7 we have not considered this area separately. Again, the Flemish Cap data were scarce beyond age 8, but it is reasonably certain that the isolated cod population in this area does not alter significantly in composition throughout the year. However, the values of K and L_∞ calculated for the Flemish Cap stock must be regarded as provisional.

The offshore data almost always include some fish at the youngest ages, but the averages for ages 1 and 2, at least, are considered to be artificially high. Fish of these young ages are probably not distributed randomly on bottom, and the trawl probably would select the largest individuals which might tend to be distributed closer to bottom than the smallest. Thus the fish at age 1 have not been used in computing the growth curves, and those at age 2 used only where large numbers were available.

It is evident from Fig. 2, that with the exception of Divisions 3N-O and 3Pn, the very old fish, having values of average length at age consistently greater than the calculated value of L_∞, do not adhere to the theoretical pattern of growth as described by the von Bertalanffy equation. Although the average lengths at these ages are often based on very few fish, the pattern is consistent enough that it cannot be dismissed as random variation in the data. Further, such a phenomenon has previously been reported from the Newfoundland area by Fleming (1960), and for other areas by Poulsen (MS, 1957). Elucidation of this phenomenon requires further investigation, but it may possibly be related to a change in diet beyond a certain size (Fleming, 1960; Templeman, this symposium). Also, since it is more evident in the northern areas, the possibility of north-south separation of fast- and slow-growing old fish is indicated.

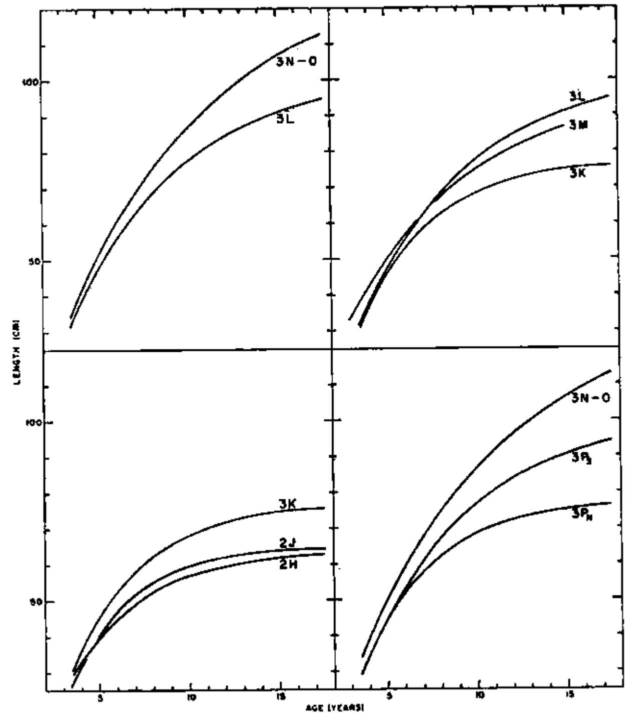

Fig. 3. Comparison of growth curves from the various areas.

The fitted curves are shown in relation to each other in Fig. 3. The curves cross over only at the youngest ages, and the general decline in average length at age proceeding from south to north is obvious. The curves for Divisions 3K and 3Pn are seen to be closely similar, as are those for Divisions 3L and 3Ps (see also the equations of Fig. 2).

TEMPERATURE DISTRIBUTION

The single major factor influencing the hydrography of the greater part of the area under consideration is the effect of the Labrador Current. The origins, extent and structure of the Labrador Current are well documented (Smith, *et al.*, 1937; Dunbar, 1951; Bailey and Hachey, 1951; Hachey, *et al.*, 1954). The shoreward portion of this current, containing cold water of Arctic origin, extends from the coastline to the edge of the continental shelf, causing bottom temperatures in summer in most areas (and except where solar warming occurs close inshore) to be less than 3°C in depths less than 300 m (Fig. 4 and 5). The cold, central core of the current tends to diminish in volume to seaward. The seaward portion of the Labrador Current, extending to depths of 1,000 m or more over the continental slope, contains warmer water of West Greenland origin. Since most of the cod stocks in the area spend their lives in water of Labrador Current origin, any growth variations with temperature between areas should be closely related to geographical variations in temperature structure of the Labrador Current.

The difficulty of obtaining a temperature measure to represent the thermal environment of a species has previously been noted. Ideally one would need to know the geographical and depth distribution of a stock at all times throughout the year, and to obtain growth and hydrographic data at regular intervals and as changes in distribution occur. This is almost a physical impossibility, especially as in this area much of the ocean is covered by ice for part of the year.

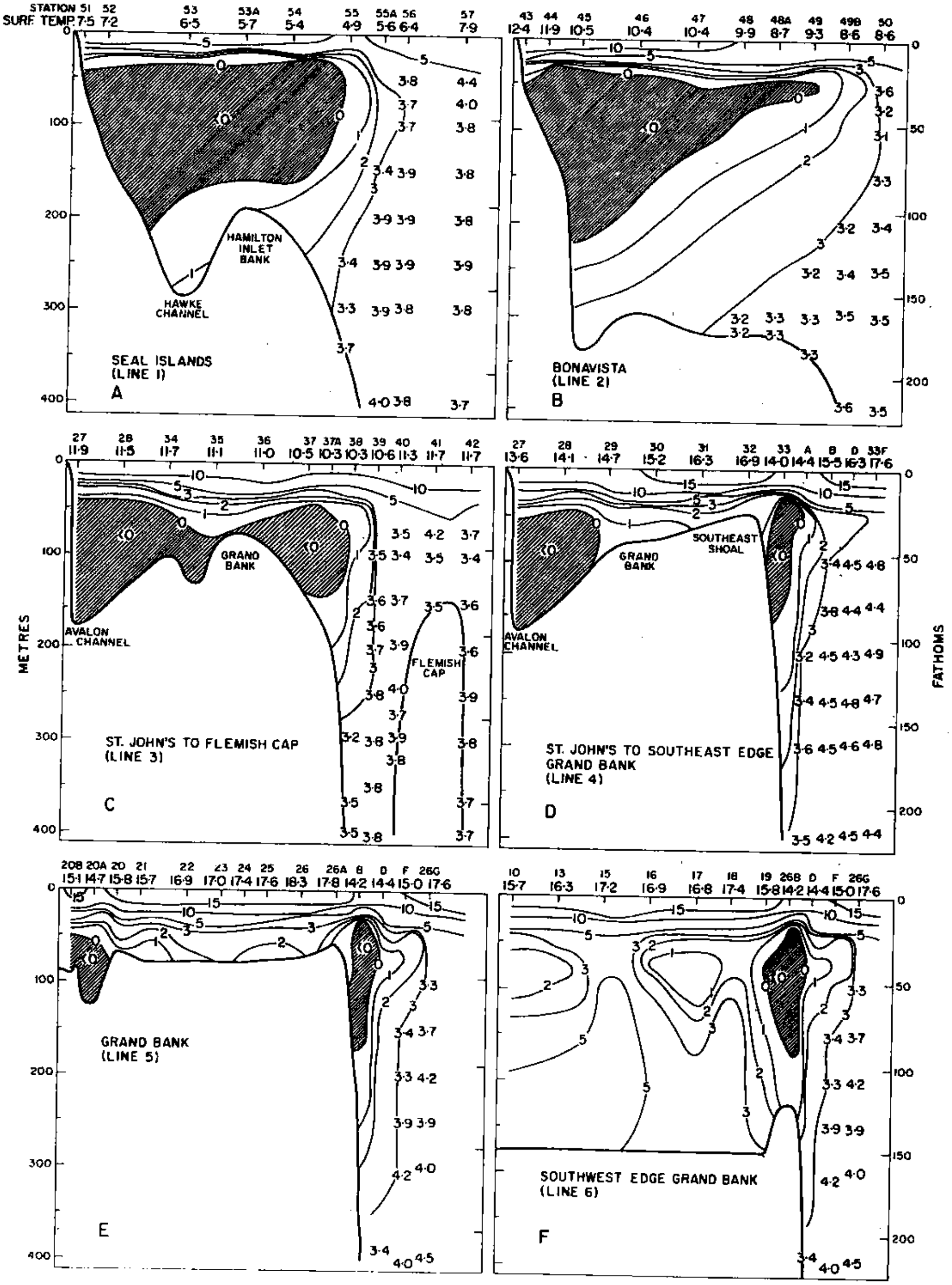

Fig. 4. Average temperature profiles for July-August, 1959-63, over the continental shelf off Labrador and Newfoundland. The station positions are shown in Fig. 1.

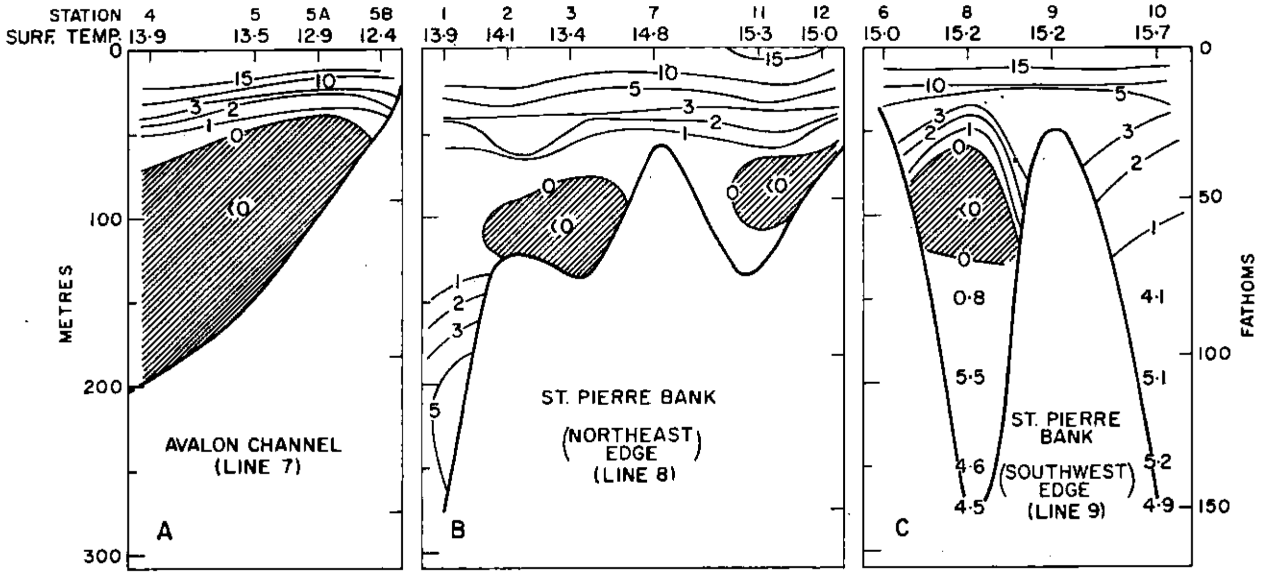

Fig. 5. Average temperature profiles for August, 1959-63, in the Avalon Channel-St. Pierre Bank area. The station positions are shown in Fig. 1.

It can be shown that the volume of very cold water in the Labrador Current declines from north to south in the area under consideration. Vertical temperature profiles during July-August for most of the lines of hydrographic stations shown in Fig. 1 (Templeman, 1960, 1961, 1962*a*; MS, 1963) illustrate these points. For present purposes temperatures at standard depths in these profiles have been averaged for the period 1959-63, and the resultant average profiles are shown in Fig. 4 and 5. The shaded portion of each profile represents water of temperature less than 0°C.

Figure 4A gives the vertical temperature distribution from the coast of Labrador in a northeasterly direction across the Hawke Channel and Hamilton Inlet Bank. Water of temperature less than 0°C extends from depths of less than 50 m to more than 150 m from near the coast to the eastern edge of Hamilton Inlet Bank. Bottom temperatures on the bank in depths to 300 m are less than 3°C. Some solar warming is evident, though temperatures greater than 5°C are generally to be found only in the upper 15 m.

In the section extending northeast from Cape Bonavista (Fig. 4B) the 5-degree contour is a little deeper, mainly between 15 and 25 m, and temperatures above 10°C are present in the upper 10-15 m. The volume of cold water on the inshore part of the section is about the same as on the Labrador line, but becomes progressively less offshore.

On the section extending from St. John's to Flemish Cap (Fig. 4C), solar warming has pushed the 5-degree contour to 20-35 m over the Grand Bank and to 55 m over Flemish Cap. The 10-degree contour extends between 15 and 25 m. Solar warming over the shallower parts of the Grand Bank causes the 0-degree contour to approach very close to the bottom. Also the Labrador Current divides into two branches in this area, one passing westward through the Avalon Channel as seen in the inshore part of the section, and the other sweeping around the eastern edge of the Grand Bank, as evidenced by the volume of cold water between 50 and 150 m over the edge of the bank. The colder inshore part of the Labrador Current does not extend to Flemish Cap, and fairly uniform temperatures (3.5 to 4.0°C) are seen to be present at all depths below 100 m.

The section from St. John's to the southeast edge of the Grand Bank (Fig. 4D) again shows the Avalon Channel branch of the Labrador Current as the volume of cold water on the inshore part of the section, but the amount of cold water along the eastern edge of the bank is much reduced, and bottom temperatures on the bank are higher than in the previous section (Fig. 4C). Temperatures in excess of 15°C are present in the upper 15 m. A similar pattern is present in the Grand Bank section of Fig. 4E, but with bottom temperatures over the shallower part of the bank about 1°C warmer. It should be noted here that these two sections (Fig. 4D and 4E) and those of Fig. 4F and 5, are occupied 2-3 weeks later than the more northerly sections. Thus at stations 27 and 28 (Fig. 4C and 4D) the average surface temperatures are seen to be higher in the later period (by 1.7°C and 2.6°C respectively), and at station 27 and 0-degree contour is about 10-15 m deeper.

In the section at 275 m along the southwest edge of the Grand Bank (Fig. 4F), the body of cold water is present only as an intermediate layer, representing the Labrador Current as it turns westward around the tail of the bank. Warmer water of Gulf Stream origin is present over the western part of the southwest edge.

Temperature profiles in the Avalon Channel and across the northeast and southwest edges of St. Pierre Bank are shown in Fig. 5. The Avalon Channel branch of the Labrador Current is seen to extend southward to St. Pierre Bank and cool water (less than 1°C) is present along the northeast edge for most of the area below 50 m (Fig. 5A, 5B). Temperatures in shallow water on top of the bank, and in deeper water along the southwest edge are moderately high (Fig. 5C). The core of cold water over the slope represents the Labrador Current water which flows southward from the Avalon Channel on each side of Green Bank, and turns westward around the southeast corner of St. Pierre Bank.

Comparable temperature data for the area represented by the Division 3Pn growth curve are not available, but these fish are mainly of the West Newfoundland stock, which spend most of the year (April-December) in the eastern and northeastern Gulf of St. Lawrence. A cold layer of water less than 0°C in temperature is present throughout the year in this area, having a maximum volume in spring and a minimum in autumn (Lauzier and Bailey, 1957). Comparing the temperature profiles given by these authors with those of Fig. 4 and 5, the vertical temperature distribution in this area during July-August would be most similar to that in Division 3K, as represented by the profile of Fig. 4B.

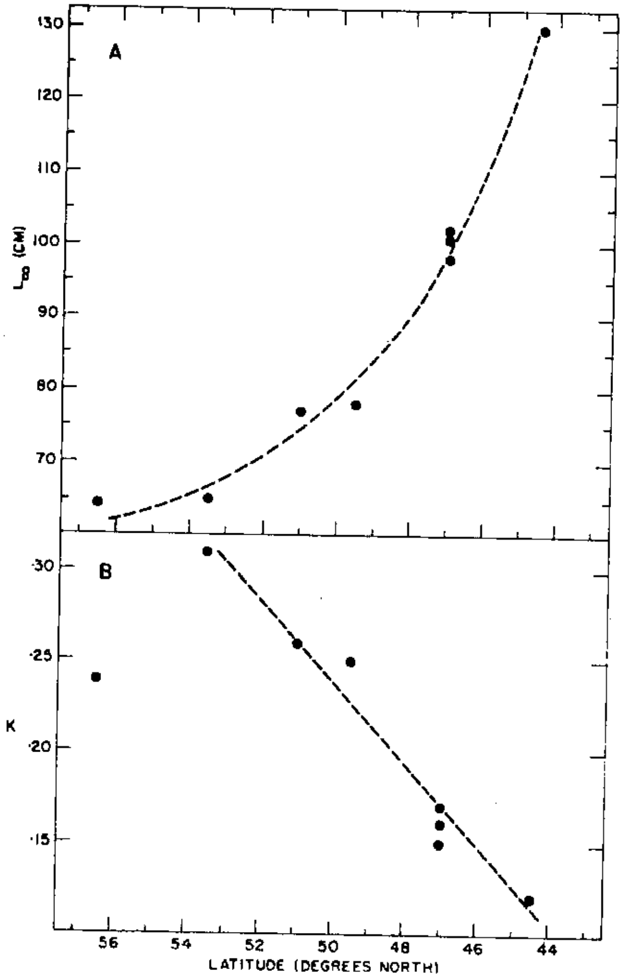

Fig. 6. Plot of data of Table 2 showing for the Newfoundland area the correlation between mid-latitude of ICNAF Divisions (except as indicated in text) and values of L_∞ and K derived from cod growth data.

RELATION OF TEMPERATURE AND GROWTH

We have seen in the previous sections that in the Newfoundland area, average length at age of cod tends to increase from north to south (Fig. 2 and 3), while the volume of cold water (less than 0°C) carried by the Labrador Current decreases in the same direction. This being so, an indirect correlation between temperature and growth appears to exist. However, lacking a temperature measure which would be comparable for all the areas considered, we have related values of L_∞ and K to the value of latitude (degrees North) which probably represents the centre of north-south distribution of the fish in each area (Fig. 6). L_∞ represents the theoretical maximum size of an average individual of the population, while K gives a measure of the average rate at which this size is reached.

We have chosen the approximate mid-latitude of each of the areas concerned except for Divisions 3Pn and 3Ps. Since fish in the former area are known to spend the summer and autumn (presumably the growing season) in the eastern and northeastern Gulf of St. Lawrence, the mid-latitude of Division 4R can be considered representative for present purposes. We have used age and length data for the inshore part of Division 3Ps to derive the growth parameters, and therefore chose the latitude of this inshore area to represent this particular group.

With the exception of the low value of K for Division 2H, the correlations of Fig. 6 are surprisingly good, and indicate, that for the area under consideration, latitude may serve as a measure of environmental opportunity for growth of the species. Stocks inhabiting similar latitudes (*e.g.* those of Divisions 3L, 3M and 3Ps) exhibit similar growth patterns, though in Division 3M it cannot be said that this is related to temperature since temperatures in this area are not similar to those in Divisions 3L and 3Ps (Fig. 4C, 5B and 5C).

It is obvious from the plots of Fig. 6 that L_∞ and K are inversely correlated. This has been found to be fairly general for a variety of species (Beverton and Holt, 1959). For the present material, this means that fish from the northern areas approach their theoretical maximum length (L_∞) more quickly (high K values) than do those of the southern areas.

DISCUSSION AND CONCLUSIONS

Allee *et al.* (1949), discussing the Bergmann rule, observe that poikilothermous terrestrial animals tend to have their species and individuals with largest size in warmer climates. Clarke (1954), in effect, makes the same observation, *i.e.* that poikilothermous animals tend to be smaller in colder climates. The present data conform to this principle.

On the other hand Taylor (1958) makes the observation that "rapid growth is, in poikilothermic animals at least, generally incompatible with a long life span and, conversely, that large size and a long life span are often associated with the cooler temperatures of higher latitudes". Holt (1959) proposes that on theoretical grounds L_∞ should decrease slowly with increasing temperature, and that fish which approach their L_∞ rapidly, seemingly tend to have shorter lives than those which approach it at a slower pace. Taylor (1962) attributes to Pütter (1920) the observation that animals at higher temperatures should show more rapid growth but a smaller final size, and that animals at lower temperatures should grow larger.

Beverton and Holt (1959) have shown for a number of species groups that a positive correlation exists between longevity and ultimate size, and also between K (the rate at which this size is approached) and mortality. In general, a negative correlation is shown to exist between K and L_∞. The present data also show a negative correlation between K and L_∞, but the lowest L_∞ (and highest K) values are found in a cool, rather than a warm environment. Further, no relation is evident between longevity (as measured by the maximum age recorded in the samples) and L_∞. Beverton and Holt (1959) state that "the clearly established exceptions to the general positive correlation between longevity and size are those species which have a much higher value of K than would be expected from their L_∞," suggesting that K, rather than L_∞, is more closely realted to longevity. Again the present data offer no evidence to support this possibility. Whether or not a positive correlation exists between K and natural mortality needs further investigation, but, in view of the foregoing this is not to be expected. It is pointed out by Beverton and Holt (1959) that the association between high values of natural mortality and K may not hold for populations of the same species in closely adjacent waters, but this does not appear relevant here.

Thus the usual relations between temperature and growth are a decrease in maximum size with increase in temperature, but an increase in the rate at which this maximum size is attained. Taylor (1958) shows for cod from various areas, but mainly European, that a positive straight line correlation exists between the logarithms of values of K and mean annual surface temperature.

The fact that these relations tend to be reversed in the present data may mean that other factors, rather than temperature, exert the primary influence on growth. It is known, for example, (Fleming, 1960) that in this area the age and size at first maturity increase from north to south, and this would certainly tend to produce differences in growth in the direction as observed. Food relations and differences in feeding are not well known, but must be of importance. Further investigation along these and possibly other lines is required to reconcile the differences we have discussed in the temperature-growth relationship.

A relationship of the type found in the present data between latitude and L_∞ is described by Jones (1962), who gives L_∞ values for areas of fast and slow growth (southern and northern North Sea) as 58.1 cm and 48.3 cm respectively, though these differences are also related to depth.

In analysis of the present material the authors have found that the estimated values of L_∞ and K are very susceptible to small changes in the observed data. This has also been noted by Jones (1962), and Taylor (1962) shows that unrealistic values of L_∞ may be obtained by the usual method of estimation (regression of length at age *t*+1 on length at age *t*). The observation by Jones (1962) applied particularly to data over a limited age range, though in the present material the authors have found that significant changes in K and L_∞ could be brought about by the choice of the age range used to fit the equation. For this reason we have adopted Ricker's (1958) suggestion that the estimate of L_∞ derived as above be used as a trial value in the expression

$$\log (L_\infty - l_t) = \log L_\infty + Kt_o - Kt$$

and that the final L_∞ value be chosen as that which gives the straightest line for a plot of log $(L_\infty - l_t)$ against t.

In view of the foregoing it is obvious that some caution must be exercised in deriving values of L_∞ and K to be used as representative of an area or a stock, particularly if the age range of the observed data is limited. Certainly some of the L_∞ values for cod (up to 200 cm) derived by Taylor (1958) from the limited age data of Saemundsson (1923) do not appear to have much biological meaning in relation to the maximum sizes found in the samples.

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REFERENCES

ALLEE, W.C., A.E. EMERSON, O. PARK, T. PARK, and K.P. SCHMIDT. 1949. *Principles of Animal Ecology.* W.B. Saunders Co., Philadelphia and London, 837 p.

BAILEY, W.B. and H.B. HACHEY. 1951. The vertical temperature structure of the Labrador Current. *Proc. N.S. Inst. Sci.*, 22(4): 34-48.

VON BERTALANFFY, LUDWIG. 1938. A quantitative theory of organic growth (inquiries on growth laws. II). *Hum. Biol.*, 10(2): 181-213.

BEVERTON, R.J.H. and S.J. HOLT. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. Ciba Foundation. Colloquia on Ageing. Vol. 5. *The Lifespan of Animals:* 142-180.

BROWN, MARGARET E. 1957. Experimental studies on growth. *In* Brown, M.E. The physiology of fishes. Vol. 1. Metabolism. Academic Press Inc., New York. 361-400.

CLARKE, GEORGE L. 1954. *Elements of ecology.* John Wiley & Sons Inc., New York. 534 p.

DUNBAR, M.J. 1951. Eastern Arctic waters. *Bull. Fish. Res. Bd. Canada*, 88: 1-131.

FLEMING, A.M. 1960. Age, growth and sexual maturity of cod (*Gadus morhua* L.) in the Newfoundland area, 1947-1950. *J. Fish. Res. Bd. Canada*, 17(6): 775-807.

HACHEY, H.B., F. HERMANN, and W.B. BAILEY. 1954. The waters of the ICNAF convention area. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 4: 67-102.

HOLT, S.J. 1959. Water temperature and cod growth rate. *J. Cons.*, 24(2): 374-376.

JONES, RODNEY. 1962. Haddock Bionomics. II. The growth of haddock in the North Sea and at Faroe. *Scot. Dept. Agr. and Fish., Mar. Res. 1962,* (2): 1-19.

KEIR, R.S., MS, 1960. Answers to the questionnaire on age reading. *Annu. Meet. int. Comm. Northw. Atlant. Fish*, 1960. Doc. No. 4, Serial No. 714 (mimeographed).

LAUZIER, L. and W.B. BAILEY. 1957. Features of the deeper waters of the Gulf of St. Lawrence. *Bull. Fish. Res. Bd. Canada*, 111: 213-250.

POULSEN, ERIK M., MS, 1957. Growth of the cod in Subarea 1. *Annu. Meet. int. Comm. Northw. Atlant. Fish*, 1957. Doc. No. 2, Serial No. 429 (mimeographed).

PÜTTER, A. 1920. Studien über physiologische Ähnlichkeit. VI. Wachstumsähnlichkeiten. *Pflügers Arch. ges. Physiol.*, 180: 298-340.

RICKER, W.E. 1958. Handbook of computations for biological statistics of fish populations. *Bull. Fish. Res. Bd. Canada*, 118: 1-300.

SAEMUNDSSON, B. 1923. On the age and growth of the cod (*Gadus callarias* L.) in Iceland waters. *Medd. Danm. Fisk. Havundersøg., Ser. Fisk.*, 7(3): 1-35.

SMITH, EDWARD H., FLOYD M. SOULE, and OLAV. MOSBY. 1937. The Marion and General Greene Expeditions to Davis Strait and Labrador Sea. Scientific Results, Part 2. Physical Oceanography. *U.S. Treas. Dept., Coast Guard Bull.*, 19: 1-259.

TAYLOR, CLYDE C. 1958. Cod growth and temperature. *J. Cons.*, 23(3): 366-370.

1959. Temperature and growth - the Pacific razor clam. *Ibid.*, 25 (1): 93-101.

1960. Temperature, growth and mortality - the Pacific cockle. *Ibid.*, 26 (1): 117-124.

1962. Growth equations with metabolic parameters. *Ibid.*, 27 (3): 270-286.

TEMPLEMAN, W. 1960. Canadian research report, 1959. A. Subareas 2 and 3. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 10: 19-25.

1961. Canadian research report, 1960. A. Subareas 2 and 3. *Ibid.*, 11: 23-31.

1962*a*. Canadian research report, 1961. A. Subareas 2 and 3. *Int. Comm. Northw. Atlant. Fish. Redbook.* 1962, Part II: 3-20.

1962*b*. Divisions of cod stocks in the Northwest Atlantic. *Ibid., Part III:* 79-123.

MS, 1963. Canadian research report, 1962. A. Subareas 2 and 3. *Annu. Meet. int. Comm. Northw. Atlant. Fish.* 1963. Doc. No. 13, Serial No. 1080 (mimeographed).

MS, 1964. Some instances of cod and haddock behaviour and concentrations in the Newfoundland and Labrador areas in relation to food. *This symposium, Contribution No. C-3.*

D-7

POSSIBLE INFLUENCE OF WATER TEMPERATURE ON THE GROWTH OF THE WEST GREENLAND COD

By

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and

Paul M.Hansen[2]

ABSTRACT

From the 1920's to the beginning of the 1950's, the average length of cod of the same age decreased steadily. From about 1955 the average length increased. The variation of the length is compared with mean surface water temperature anomalies during the life of the cod year-class in question, and significant correlation coefficients are found for the age-groups V to IX. The possible influence of overpopulation on growth is discussed. It is found most probable that the variation in growth is mainly caused by temperature variation.

VARIATION OF LENGTH OF COD OF DIFFERENT AGE-GROUPS

Length measurements and age determinations of West Greenland cod were made nearly every year since 1924. Most of the material from the coastal area consists of samples taken from the Greenlanders' landings, but material from research vessels has also been included. The material from the offshore banks was obtained from research vessels. Only Danish material is used in this paper. The conditions in three different areas are discussed separately. The first area is the coastal area from Godthåb and northwards (*i.e.* north of approximately 62°30'N). The second area includes Frederikshåb and Julianehåb districts (*i.e.* the coastal area between Cape Farewell and 62°30'N), and the third area includes the West Greenland fishing banks from Dana Bank to Store Hellefiske Bank. From the length measurements the mean lengths of each of the age-groups V to IX were calculated for each year.

Variations in the length of age-groups V, VII and IX during the years 1924 - 62 are shown in Fig. 1 a and 1 b for the northern and the southern coastal area, respectively. Mean lengths have been decreasing since about 1932 in the northern area and since about 1936 in the southern area. They reached a minimum about 1954 and have since been increasing. Length curves for the southern area show greater fluctuations than those for the northern area. In the southern area there are probably two cod populations with different growth rates which probably are not evenly represented in the different samples.

Growth rate of cod varies considerably in the Greenlandic area. Mean length from the first half of the 1930's to the first half of the 1950's decreased from about 65 cm to about 50 cm for a five-year-old cod in the northern area. This corresponds to a decrease in weight from 2.5 kg to 1.2 kg. The mean length of a five-year-old cod in the northern area around 1930 was in fact about the same as the mean length of a seven-year-old cod around 1954.

VARIATION OF SURFACE TEMPERATURE ANOMALIES

For a comparison between growth rate and sea temperature, the temperature of the water layers n which the cod live should be used. However, sufficient subsurface temperature observations and nformation about the vertical distribution of the cod are not available. The only long-term tem-erature observations available are surface temperature observations collected by the Danish Meteor-logical Institute and presented by Smed (1959) as monthly mean temperature anomalies for each year nd for selected areas. When averaged over a number of years the variation in the surface tempera-ure anomalies for the area where the cod live, should represent fairly well the mean variation in

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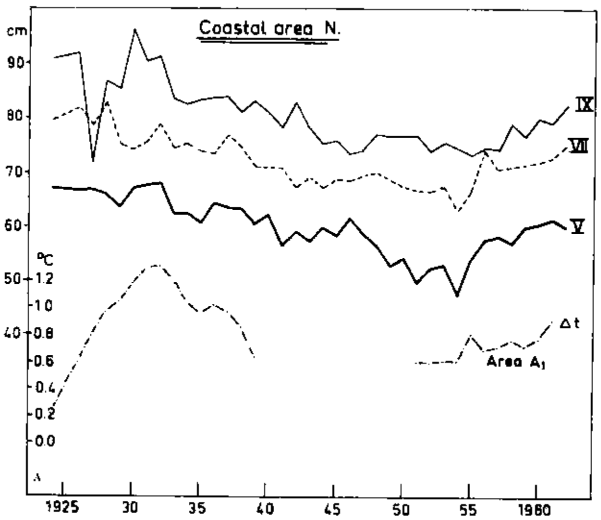

Fig. 1a. Variation in length of cod of age-groups V, VII and IX in the northern part of the West Greenland coastal area. Dotted lines mean surface temperature anomaly during the life time of age-group V.

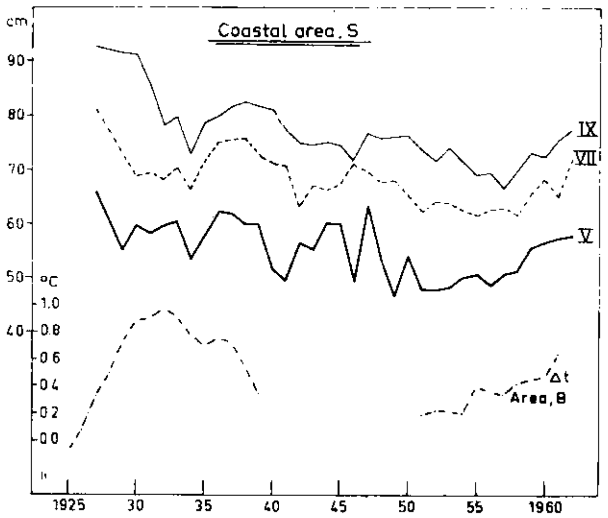

Fig. 1b. Variation in length of cod of age-groups V, VII and IX in the northern part of the West Greenland coastal area. Curves are for the southern coastal area of West Greenland.

the layers where the cod live.

In the following account, the length of each age-group is compared with the mean surface temperature anomaly during the life time of the year-classes in question. For the northwestern area and for the bank area, the anomalies of Smed's area A_1 are used; for the southwestern area, those of Smed's area B (Fig. 5). In all years considered, temperature anomalies are available for the months April to September in area A_1 and for the months April to October for area B. Only material from these months is used below.

In the calculations of the mean temperature anomalies the anomalies of the single years have been weighted according to the fraction of the year the cod group in question has existed. As the cod is spawned in April the temperature anomaly for its first year of life is weighted by 0.75 and as the cod on the average is caught in July the temperature anomaly for its last year of life is weighted by 0.5 and only the mean anomaly for the months April to June is used. Thus, the formula used for calculating the mean temperature corresponding to a cod group of year-class a and age-group n is as follows for area A_1:

$(0.75 \cdot \Delta t_{a,\ \text{Apr.-Sept.}} + \Delta t_{a+1,\ \text{Apr.-Sept.}} + \cdots \Delta t_{a+n-1,\ \text{Apr.-Sept.}} +$
$0.5 \cdot \Delta t_{a+n,\ \text{Apr.-June}}) \div (n+0.25)$, where $\Delta t_{a,\ \text{Apr.-Sept.}}$ means the mean temperature anomaly for the months April to September in the year a. In the formula for area B, the period April-October replaces April-September in the above formula.

In this way the mean temperature anomalies for the age-groups V to IX were calculated for each year-class in the three areas in question. As an example, the mean temperature anomalies corresponding to age-group V have been plotted in Fig. 1a and 1b.

CORRELATION BETWEEN LENGTH OF COD AND TEMPERATURE ANOMALIES

Figure 1 a and 1 b show that the mean temperature anomalies increased during the years from about 1924 to 1932 and then decreased. Unfortunately no temperature observations were made during the war, but in the post-war years there is a minimum around 1952 followed by an increase to 1961, the last year for which temperature observations are available.

The mean lengths of the cod and the variations in temperature thus show the same main features after 1932, but this was far from being the case in the 1920's.

The connection between temperature and average length of the single year-classes is further illustrated in Fig. 2a to 2e, 3a to 3e and 4a to 4e. Here the average length of a certain age-group of each year-class is plotted against the mean temperature anomaly during the life time of the year-class in question. The figures show that the average lengths for most of the year-classes previous to year-class 1923 are higher than the average lengths of year-classes following year-class 1924. Furthermore, the points of the year-classes between 1924 and 1956 group themselves around a straight line indicating increasing length with increasing temperature, but the year-classes previous to 1923 show no correlation with the temperature.

Because the numbers of cod in West Greenland waters increased rapidly in the first half of the 1920's and the lengths of the first year-classes which appeared in Greenland waters are nearly the same as those in the Icelandic cod stock, it seems reasonable to assume that the main part of the first year-classes which appeared at West Greenland had not grown up in these waters but had migrated from West Iceland waters to West Greenland as adult fish. In 1924 cod were spawning in West Greenland waters as Vedel Tåning found cod larvae there.

It is, therefore, reasonable to assume that the year-classes following the 1924 year-class consist mainly of cod which grew up in Greenland waters, while the 1921, 1922 and 1923 year-classes probably are a mixture of cod which were spawned in Greenland waters and which have immigrated from Iceland, and year-classes previous to the 1921 year-class are mainly cod which have immigrated from Iceland.

The correlation coefficients r between average length and mean temperature anomalies and the corresponding regression coefficients b have been calculated for age-groups V to IX for the three areas considered using the material for all the year-classes after the 1924 year-class for which temperature anomalies are available. The result as well as the number n of pairs of observations, and standard deviation, σ_b , on the regression coefficient are given in Table 1.

TABLE 1. CORRELATION BETWEEN AVERAGE LENGTH OF COD AND MEAN TEMPERATURE ANOMALIES.

	Coastal area north				Coastal area south				West Greenland Banks			
Age-group	n	r	b (cm/C°)	σ_b	n		b (cm/C°)	σ_b	n	r	b (cm/C°)	σ_b
V	22	0.845	20.6	5.3	22	0.767	15.2	4.3	19	0.725	16.9	5.5
VI	20	0.788	15.9	4.6	19	0.679	13.5	4.7	19	0.710	15.2	5.0
VII	18	0.682	12.5	4.4	18	0.673	14.1	5.1	17	0.689	14.8	5.4
VIII	16	0.652	11.7	4.6	16	0.716	17.1	6.1	15	0.680	15.4	6.1
IX	14	0.818	15.4	5.2	14	0.784	18.7	6.6	13	0.790	16.5	6.1

All the correlation coefficients are significant within the 0.02 probability limit. The regression coefficients show that the length of the cod increases by about 15 cm for an increase in temperature of one centigrade degree, and there are no significant differences in the regression coefficients of the different age-groups or from the different areas.

It is peculiar that the regression coefficients are not greater for the older age-groups than for the younger. Either the growth of cod is mainly influenced by the temperature during its first five years, or cod older than five years live mainly in water layers where the temperature variation does not follow the variation in surface temperature and therefore is not represented by the observations used in this paper.

The regression lines of cod lengths on mean surface temperature anomaly for the year-classes following the 1924 year-class, as well as the regression equations, are shown in Fig. 2a to 4e.

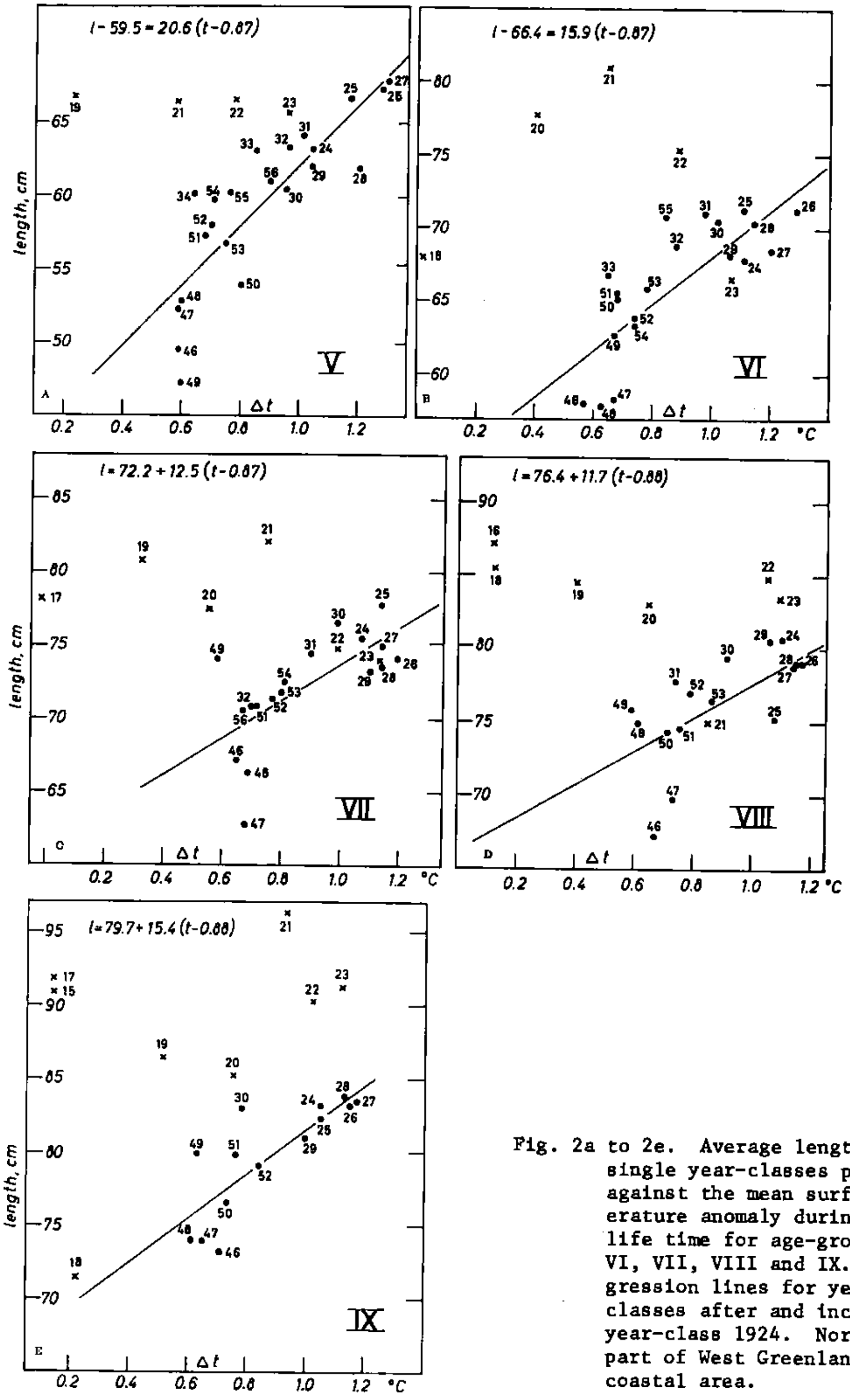

Fig. 2a to 2e. Average length of the single year-classes plotted against the mean surface temperature anomaly during their life time for age-groups V, VI, VII, VIII and IX. Regression lines for year-classes after and including year-class 1924. Northern part of West Greenland coastal area.

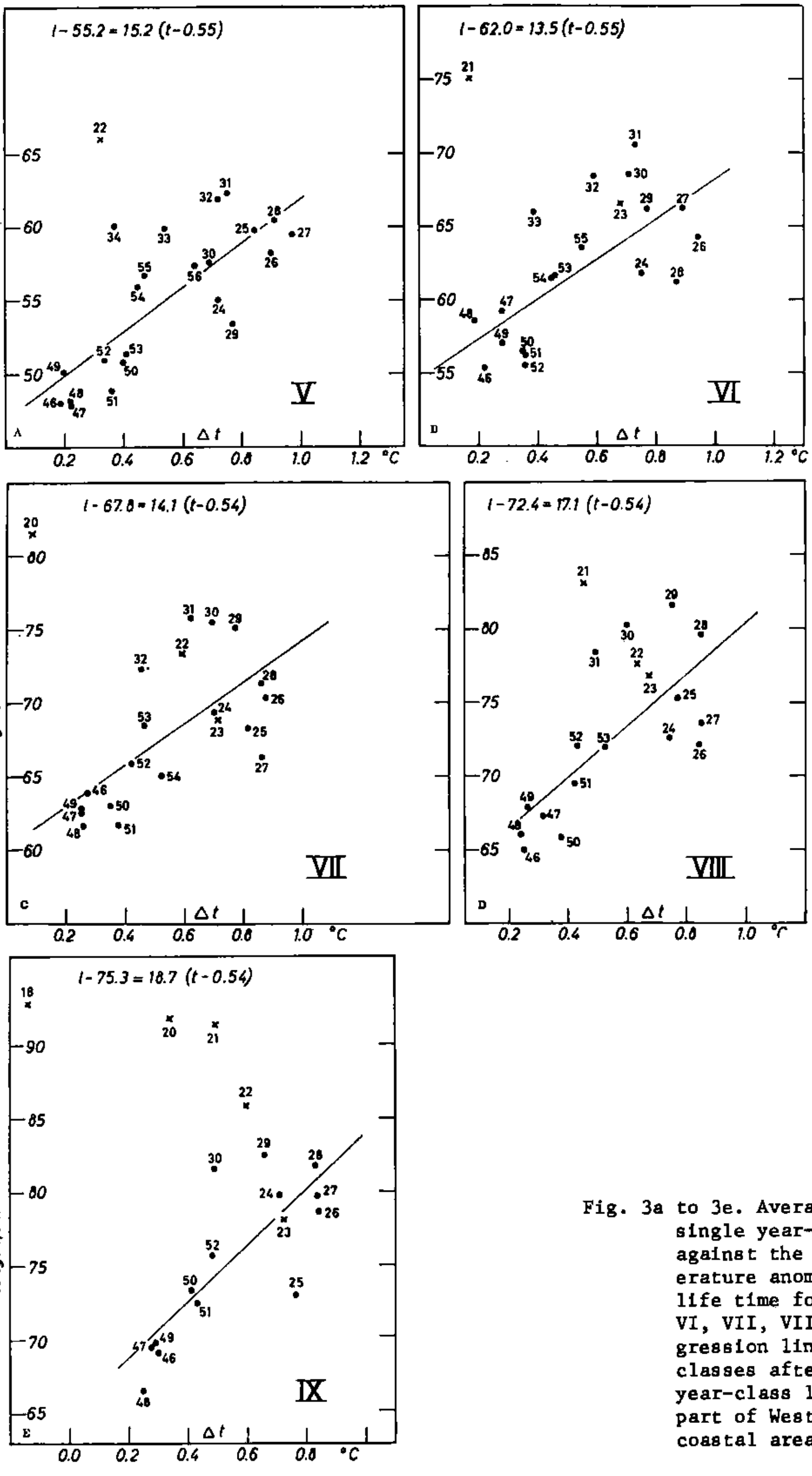

Fig. 3a to 3e. Average length of the single year-classes plotted against the mean surface temperature anomaly during their life time for age-groups V, VI, VII, VIII and IX. Regression lines for year-classes after and including year-class 1924. Southern part of West Greenland coastal area.

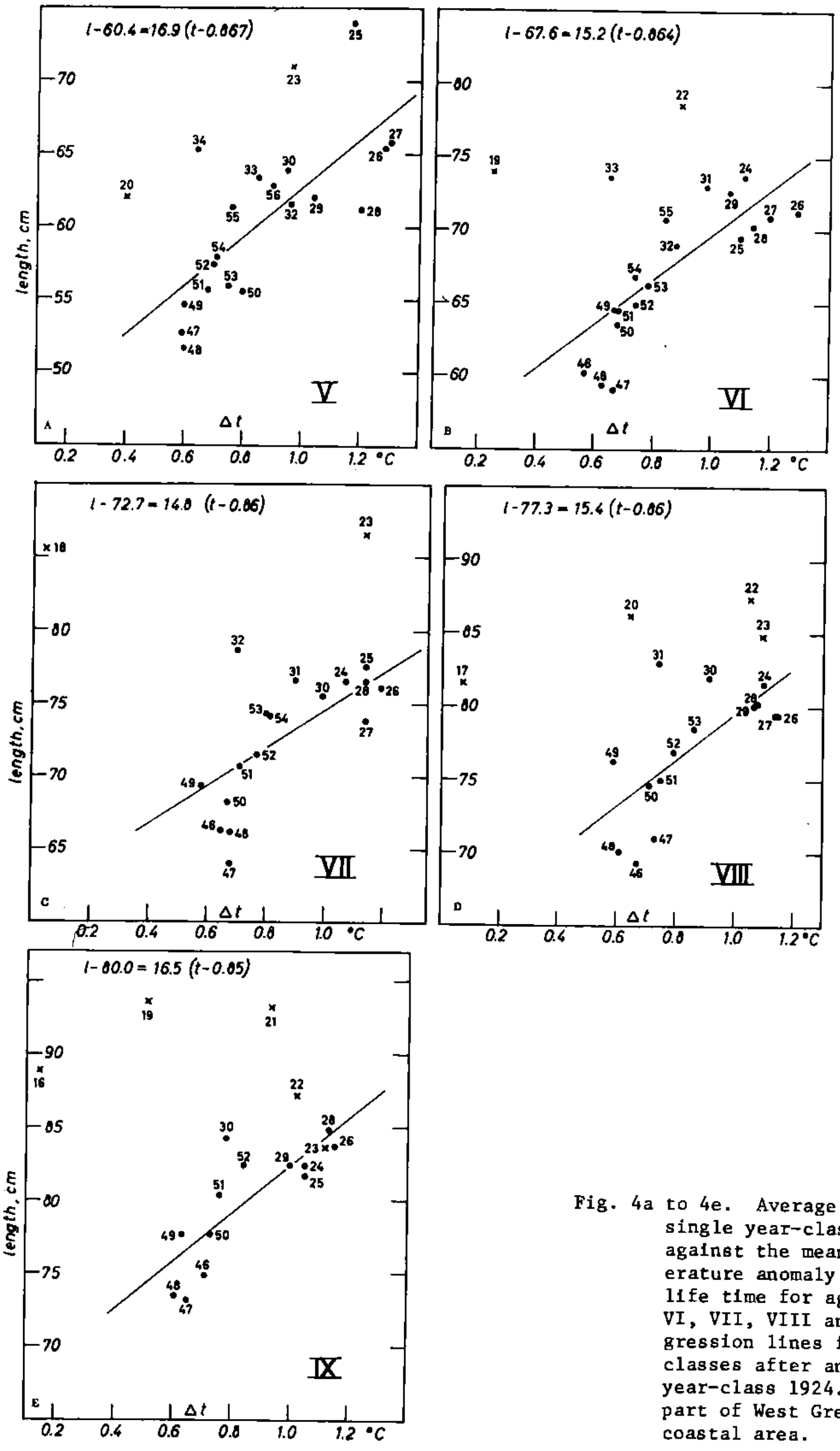

Fig. 4a to 4e. Average length of the single year-classes plotted against the mean surface temperature anomaly during their life time for age-groups V, VI, VII, VIII and IX. Regression lines for year-classes after and including year-class 1924. Western part of West Greenland coastal area.

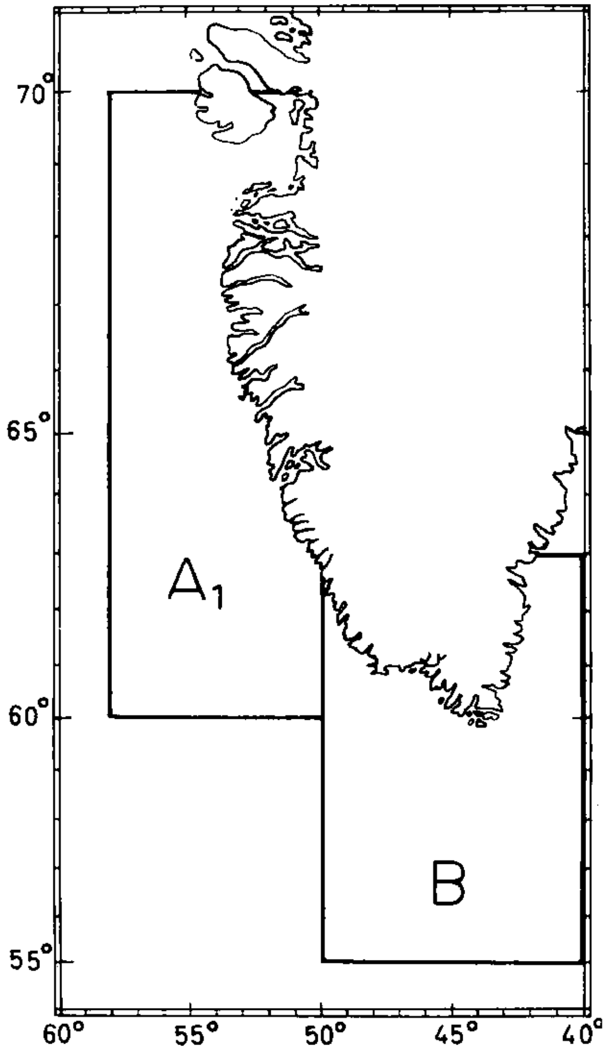

Fig. 5. Location of areas A_1 and B.

The fact that there is a significant correlation between the length of cod and the variation of sea temperature does not prove that the variation in length is caused by the variation in temperature. It only shows that the variations of cod lengths and of temperature have the same main features over a certain number of years.

Of factors other than sea temperature which could have influenced the growth rate of the cod, overpopulation is probably the most likely. The cod population could have increased in number from almost nothing about 1920 to a maximum in the early 1950's when the average lengths were a minimum. Owing to the strong development of the fishery on the West Greenland banks in the 1950's, the density of the population could decrease again with a consequent increase in growth rate.

Data on landings and effort show, however, that this overpopulation hypothesis is hardly correct. Hansen *et al.(this symposium)* found, from tagging experiments, that the fishing effort of the Greenlanders was 3.3 times greater in 1946-58 than in 1924-39. The average annual catch by the Greenlanders was 19,900 tons in 1924-39. The ratio between catches and the ratio between efforts are thus nearly the same in the two periods and consequently the average size of the cod population seems to have been roughly the same in the two periods.

The period 1924-39 represents the period when the growth rate was at its maximum and the period 1946-58, when the growth rate was at a minimum. Therefore, the decrease in average length from the beginning of the 1930's to the beginning of the 1950's can hardly be explained as an effect of overpopulation.

The increase in length of the latest year-classes, 1954 and 1955, seems in the correlation diagram to be somewhat greater than could be expected from the increase in temperature. The increase in growth rate found in the latest years may be a combined effect of rise in temperature and decreased density by fishing.

It seems improbable that a different degree of overpopulation is the main cause of the long term variations in the growth rate of the West Greenland cod. The authors are inclined to believe that these variations are mainly an effect of temperature variations. The effect of the temperature may be direct by affecting the activity of the cod, or indirect by affecting the abundance of food animals.

REFERENCES

HANSEN, P. 1949. Studies on the Biology of the Cod in Greenland Waters. *Rapp. Cons. Explor. Mer.*, CXXIII.

HANSEN, P., F. HERMANN, and S. HORSTED. 1964. The Effect of Temperature and Current on the Distribution and Survival of Cod Larvae at West Greenland. *This symposium, Contribution No. B-14.*

SMED, J. 1947-62. Monthly Anomalies of the Surface Temperatures in Areas of the Northern North Atlantic. *Ann. biol., Copenhague.* Vol. II-XVIII.

D-8

RELATIONSHIP BETWEEN THE GROWTH RATE AND POPULATION DENSITY OF HADDOCK IN THE BARENTS SEA

By

M. A. Sonina[1]

ABSTRACT

This contribution deals with the relationship between the rate of growth of haddock of individual year-classes, their abundance and the total abundance of haddock stock.

The Polar Research Institute (PINRO) has undertaken studies of growth rates (weight and length) of haddock of various sizes and age-groups, as well as of the individual year-classes, with the purpose of making more exact forecasts of the replenishment of the commercial stock.

The growth rate of haddock is influenced by many factors, including the abundance and availability of food, and the temperature conditions of the sea. Population density is also one of the factors determining the growth rate of the haddock. The present contribution deals with the relationship between the average length and weight, and the abundance of stock and of individual year-classes of haddock. The average length and weight of haddock of the same age vary from year to year. (Tables 1 and 2). In 1952, the average weight of 2- and 3-year-old specimens and the average length of 3-year-old individuals were somewhat below the long-term average estimated for 11 years. For the other age-groups, the average length and weight were found to be above the long-term average. In 1953 and 1954, the average weight and length observed in haddock under 5 years of age were below, but in older specimens, above or equal to the long-term average. From 1955 to 1958, the average weight and length of almost all age-groups were below the long-term average. In 1959, the average weight was somewhat greater, and specimens from 2 to 6 years old showed positive deviations. The rate of increase in length, however, remained slow and positive deviations were observed only in specimens from 1 to 3 years old. The average length of haddock of the other age-groups was below the long-term average. In 1960, the average weight and length were at the level of the long-term standard and in 1961-62 considerably above them. In these years, 3- to 8-year old haddock had especially high average weight and length.

Comparison of the rates of increase of weight and length growth with the relative abundance of the stock of haddock in the southern part of the Barents Sea for various years (Tables 1-3, Fig. 1) reveals that in the years when the stock of haddock was very abundant the rates of increase of weight and length growth were low, while in the years with a reduced or average abundance of the stock the rates were considerably higher. In 1952 and 1953, when small- and medium-size haddock of the 1950 and 1948 year-classes were very numerous, the rate of their growth was low. In the years characterized by a very abundant stock of haddock (1954 - 57) the rate of growth of all age-groups was declining; in the following years, characterized by a reduced and average abundance of the stock, the rate of growth was gradually rising, reaching a peak in 1961 and 1962.

An analysis of the rates of growth of various year-classes of haddock makes this relationship still more evident. Figure 1 shows deviations in growth of length and weight of the 1945 - 59 year-classes from the long-term average rate calculated for the period of 1945 - 62. The figure shows that the 1945 - 48 year-classes give mainly positive deviations of the growth rates whereas the 1949 - 53 year-classes are characterized by negative deviations. The lowest rate of growth is observed in the 1950 and 1949 year-classes. The rate of growth of the 1954 and 1955 year-classes is close to the long-term average for the first 6 years of their life, then it rises abruptly. The 1956 - 59 year-classes show high growth rates and positive deviations.

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TABLE 1. AVERAGE WEIGHT (KG) OF VARIOUS AGE-GROUPS OF HADDOCK IN THE SOUTHERN PART OF THE BARENTS SEA: NUMBER OF SPECIMENS IN PARENTHESIS

Age Group	Year					
	1952	1953	1954	1955	1956	1957
I	- (-)	0.09 (9)	0.18 (7)	- (-)	0.12 (3)	0.11 (65)
II	0.22 (130)	0.17 (187)	0.22 (5)	0.20 (1)	0.34 (103)	0.20 (19)
III	0.42 (36)	0.33 (1,225)	0.42 (75)	0.37 (2)	0.40 (537)	0.40 (108)
IV	0.74 (982)	0.53 (88)	0.62 (1,672)	0.50 (72)	0.55 (139)	0.60 (1,009)
V	1.13 (43)	1.01 (368)	1.05 (26)	0.77 (1,253)	0.76 (274)	0.79 (180)
VI	1.74 (26)	1.45 (30)	1.59 (263)	1.09 (43)	1.03 (2,250)	1.12 (243)
VII	2.18 (10)	1.92 (14)	1.67 (4)	1.98 (23)	1.58 (27)	1.32 (1,372)
VIII	2.97 (6)	3.20 (2)	2.47 (4)	- (-)	1.85 (15)	1.85 (23)
IX	3.12 (11)	- (-)	3.62 (2)	- (-)	- (-)	2.61 (17)
X	4.05 (2)	2.50 (1)	- (-)	- (-)	- (-)	- (-)
XI	4.90 (1)	3.95 (4)	- (-)	- (-)	4.75 (2)	- (-)

TABLE 1 (CONTINUED)

Age Group	Year						Average annual increment
	1958	1959	1960	1961	1962	1952-62	
I	0.08 (18)	0.10 (54)	0.09 (127)	0.09 (14)	0.17 (2)	0.11	0.11
II	0.24 (232)	0.31 (513)	0.25 (102)	0.30 (197)	0.26 (230)	0.25	0.14
III	0.39 (128)	0.59 (3,562)	0.57 (1,588)	0.65 (482)	0.56 (1,645)	0.46	0.21
IV	0.70 (317)	0.75 (545)	0.80 (2,361)	1.02 (1,442)	0.88 (936)	0.70	0.24
V	0.90 (1,436)	1.05 (415)	0.96 (224)	1.38 (1,171)	1.34 (1,403)	1.01	0.31
VI	1.21 (149)	1.43 (911)	1.49 (37)	1.76 (59)	1.84 (748)	1.43	0.42
VII	1.71 (173)	1.81 (66)	1.90 (36)	2.51 (16)	2.33 (45)	1.90	0.47
VIII	2.00 (504)	2.33 (67)	2.43 (8)	2.81 (34)	3.14 (22)	2.50	0.60
IX	2.91 (9)	2.77 (138)	3.39 (5)	3.93 (3)	3.26 (41)	3.20	0.70
X	3.85 (2)	3.49 (7)	3.40 (7)	3.71 (4)	3.15 (3)	3.45	0.25
XI	3.70 (1)	- (-)	- (-)	4.41 (15)	3.94 (7)	4.27	0.82

Comparison of rates of growth with the abundance of the various year-classes indicates that the rate of growth of each individual year-class is not closely related to its abundance.

In the following account, individual year-classes of haddock are defined as (1) poor; (2) medium; (3) rich; and (4) strong.

According to the results of the estimation of young fish (Baranenkova, 1957; Baranenkova and Baranova, 1962), the 1950 year-class of haddock is strong, the 1948, 1953, 1956 and 1959 year-classes are rich, the 1951 and 1957 year-classes are medium, and the rest are poor. The year-classes varying in abundance show both positive and negative deviations from the average rate of growth. The lowest rate of growth was observed for the strong 1950 year-class and for the poor 1949 year-class during almost the entire period of their life. Three of the rich year-classes (1948, 1956 and 1959) showed positive deviations, and the fourth one (1953) negative deviations. Of the two medium year-classes, one (1951) showed negative, and the other (1957) positive deviations. Of the poor year-classes, 1945 - 47 and 1958 are characterized by high, 1949 and 1952 by low, and 1954 and 1955 by medium growth rates.

A close correlation is, however, observed between the rate of growth of individual year-classes and the abundance of the entire stock of haddock. In the years with an abundant stock of haddock, a drop in the rates of growth of individuals of all year-classes was observed. On the other hand, when the stock of haddock was not abundant, all year-classes displayed a high growth rate. The existence of this relationship has already been mentioned by the author (Sonina, 1961).

TABLE 2. AVERAGE LENGTH (CM) OF VARIOUS AGE GROUPS OF HADDOCK IN THE SOUTHERN PART OF THE BARENTS SEA: NUMBER OF SPECIMENS IN PARENTHESIS

Age Group	Year					
	1952	1953	1954	1955	1956	1957
I	-	16.9 (9)	22.5 (37)	- (-)	21.4 (3)	22.9 (65)
II	29.2 (130)	25.4 (190)	26.4 (12)	25.1 (17)	32. (103)	26.5 (19)
III	34.5 (36)	33.0 (1,365)	33.6 (81)	30.8 (20)	34.5 (537)	34.6 (108)
IV	42.3 (982)	38.1 (109)	40.0 (2,247)	36.6 (156)	38.3 (139)	40.5 (1,009)
V	48.0 (44)	48.6 (601)	46.6 (32)	43.0 (2,424)	43.4 (274)	44.2 (180)
VI	55.3 (26)	54.4 (37)	52.7 (259)	47.7 (69)	48.0 (2,250)	49.2 (243)
VII	62.5 (10)	57.4 (17)	58.0 (2)	58.0 (38)	55.2 (27)	52.4 (1,372)
VIII	68.9 (6)	66.4 (3)	68.0 (2)	73.0 (1)	58.7 (15)	58.0 (23)
IX	69.4 (11)	- (-)	68.0 (2)	73.0 (1)	- (-)	66.0 (17)
X	75.5 (2)	68.0 (1)	- (-)	73.0 (1)	- (-)	- (-)
XI	78.0 (1)	75.5 (4)	- (-)	- (-)	80.5 (2)	- (-)

TABLE 2 (CONTINUED)

Age Group	Year						Average annual increment
	1958	1959	1960	1961	1962	1952-62	
I	20.8 (18)	21.7 (57)	20.6 (127)	19.5 (14)	20.5 (2)	20.8	20.8
II	29.6 (238)	30.0 (573)	28.4 (102)	29.4 (197)	28.4 (230)	28.2	7.4
III	34.5 (130)	37.1 (3,688)	37.8 (1,592)	38.5 (482)	37.0 (1,645)	35.1	6.9
IV	40.9 (336)	40.5 (570)	42.3 (2,367)	45.5 (1,442)	43.9 (936)	40.8	5.7
V	45.2 (1,603)	45.9 (424)	45.4 (226)	51.0 (1,171)	51.0 (1,403)	46.4	5.6
VI	49.3 (171)	51.1 (920)	51.4 (38)	55.7 (59)	57.5 (748)	52.0	5.6
VII	56.0 (178)	56.0 (67)	57.7 (44)	63.0 (16)	62.4 (45)	58.0	6.0
VIII	58.8 (533)	61.5 (67)	62.6 (11)	65.9 (35)	68.7 (22)	64.6	6.6
IX	67.6 (11)	64.7 (138)	68.9 (12)	73.0 (3)	70.3 (41)	69.0	4.4
X	75.5 (2)	69.4 (7)	70.7 (19)	14.5 (7)	73.0 (3)	73.1	4.1
XI	73.0 (1)	- (-)	78.0 (1)	76.1 (28)	75.2 (7)	76.8	3.7

The 1945-48 year-classes, characterized by positive deviations, were growing up when the stock of haddock in the southern part of the Barents Sea was not abundant. This is shown by the rather poor average catches of haddock in 1949-53 (Table 3) as well as by the number of haddock of different sizes caught per hour's trawling (Fig. 2). Figure 2 also shows the state of the stocks from 1945-62. The left side of the figure presents the numbers of haddock of different sizes in catches obtained per hour of trawling in 1945-62; the right side represents deviations from the long-term average. The figure shows that the period 1949-51 is characterized by a scarcity of fish of almost all sizes (except the small-sized fish in 1950) when compared with the long-term average. Haddock of the 1949-53 year-classes were growing up when the stock was abundant. Individuals of the 1954-55 year-classes during their early life were growing up,first,when the stock was abundant and, later, when the stock was reduced.

In 1958-62, when the abundance of the stock of haddock in the southern part of the Barents Sea became reduced, the rate of increase in weight and length observed in haddock of the 1956-59 year-classes increased and exceeded the average for the whole period of haddock life.

In haddock of the 1948 year-class a considerable drop in the rate of increase in weight and length was observed at the age of eight and nine years, *i.e.*, in 1956-57 when the stock of medium- and large-size haddock was more abundant than ever in the period under review. On the other hand, the rate of growth of the 1949-55 year-classes reached and exceeded the average in the period of

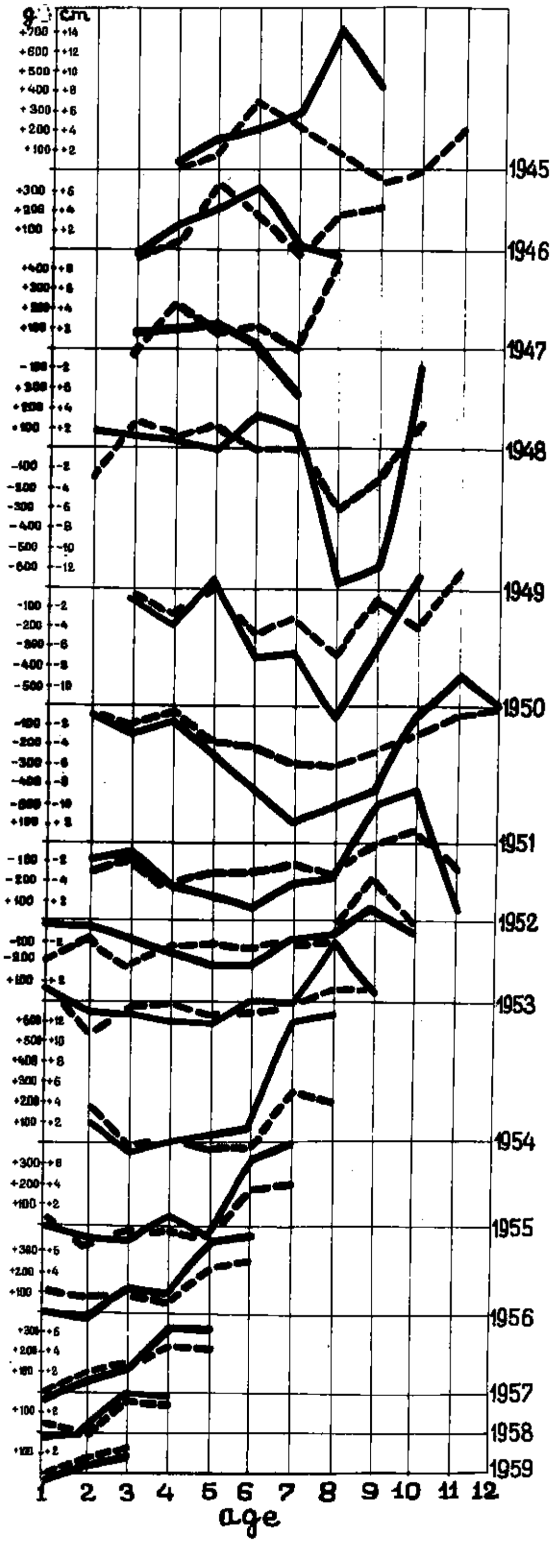

Fig. 1. Deviations in weight (——) and length (— — —) of 1945-59 year-classes of haddock from the long-term averages for 1945-62. Weight (g). Length (cm).

TABLE 3. AVERAGE CATCHES OF HADDOCK PER HOUR OF TRAWLING (CENTNERS) (1 CENTNER = 100 KG).

Year	1949	1950	1951	1952	1953	1954
Average catch per hour	0.5	0.8	0.6	1.0	1.1	1.6

Year	1955	1956	1957	1958	1959	1960
Average catch per hour	2.3	3.0	2.0	0.9	0.9	1.3

Year	1961	1962	1949-62
Average catch per hour	1.4	1.5	1.4

1958-62, *i.e.*, in the years characterized by a reduced abundance of the stock of haddock in the southern part of the Barents Sea.

It is, therefore, obvious that the growth rate of haddock of various year-classes depends on the abundance of the stock as a whole in the given years. When the stock is not abundant haddock grow fast and, on the other hand, an increase in the abundance of the stock results in a drop in the rate of growth of all year-classes living in the southern part of the Barents Sea at that time.

The growth rate of haddock, therefore, can be used to a certain degree as an indication of the abundance of the haddock stock.

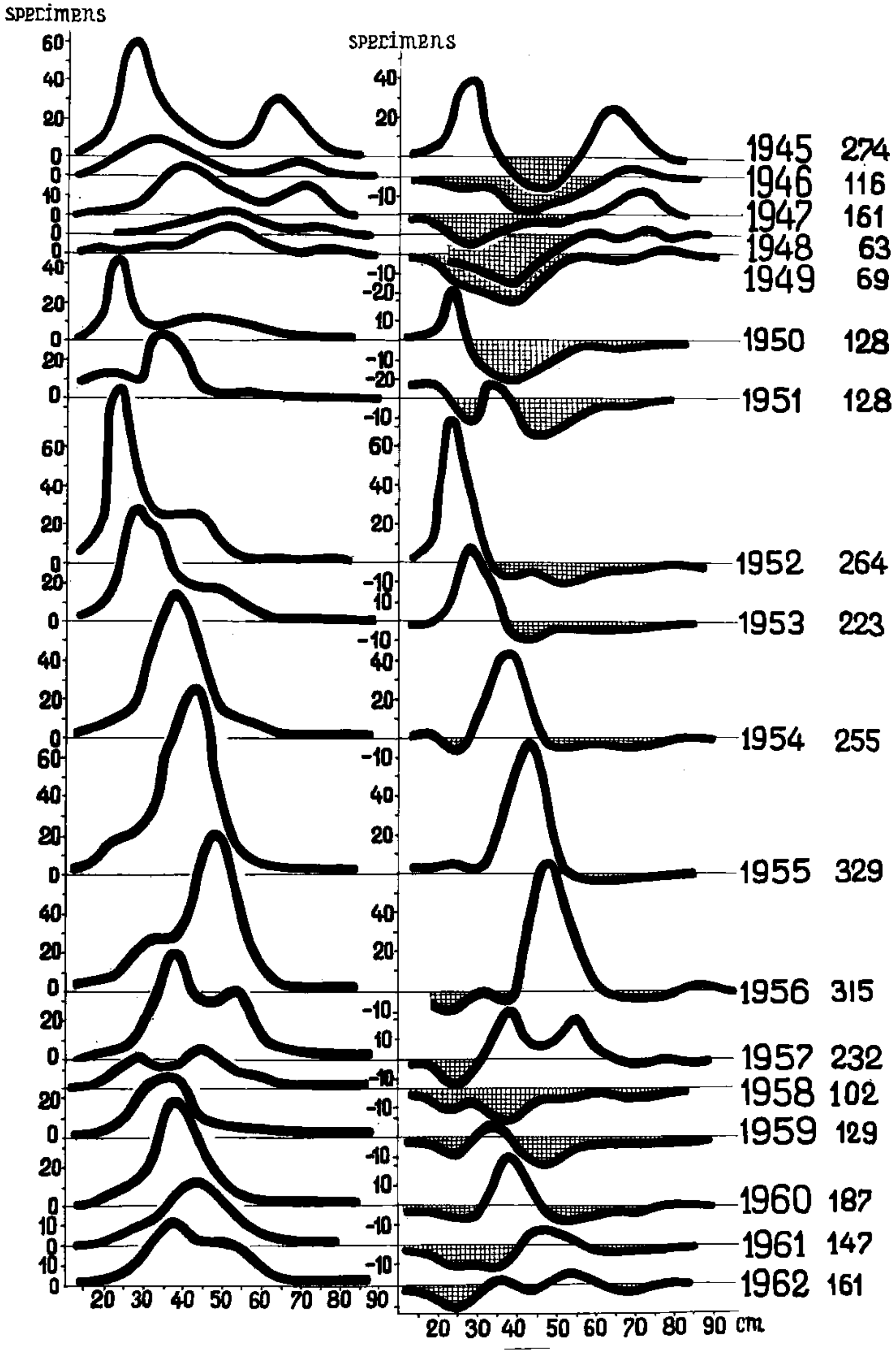

Fig. 2. Number of haddock of different sizes caught per hour's trawling (left) and their deviations from the long-term average (right), for the period 1945-1962. Figures on the right indicate average annual catches per hour of trawling (no. of specimens).

REFERENCES

BARANENKOVA, A.S. 1957. Comparative abundance of cod and haddock year-classes in the Barents Sea, based on the results of estimation of young fish and fisheries. Transactions of PINRO, vol. 10, p. 24, Fig. 10, Table 19. "Pischepromizdat".

BARANENKOVA, A.S., and Z.P. BARANOVA. 1962. Quantitative indices of the results of estimation of cod and haddock young in the Barents Sea in winter 1961-1962. *Scientific Bulletin of PINRO,* No. 4(22). p.5, Fig. 2, Table 7. Murmansk.

SONINA, M.A. 1961. Growth rate of haddock in the Barents Sea. *Scientific Bulletin of PINRO,* No. 2-3 (16-17). p.3, Fig. 2, Table 3. Murmansk.

D-9

CHANGES IN THE GROWTH RATE OF THE BARENTS SEA COD AS AFFECTED BY ENVIRONMENTAL FACTORS

By

T.F. Dementyeva[1] and E.M. Mankevich[2]

ABSTRACT

The growth rate of the cod in the Barents Sea continued to increase during the period from the end of the 1930's to the middle of the 1950's. It is suggested that this phenomenon was due to an increasing metabolic rate which was, in turn, caused by increased warming of the waters of the North Atlantic during the period. Such conclusions are based on analogic data on the growth in length of various fish species living in different environmental conditions and living on different food items over the same years and periods of life. Increase in growth rate is related to early maturity and mortality in cod.

Changes in the age of maturity of fish are known to be closely related to their growth rate as determined by the specific character of these fish. Vasnetsov (1934) demonstrated that maturation of fish was related to their length and not to their age.[3] This was later confirmed by Alm, 1959; Nümann, 1959; Monastyrski, 1952; Dementyeva, 1952; Tokareva, 1964, and others.

The relationship between growth and maturity is used to estimate future yields and, in particular, to calculate the amount of recruitment to the commercial stock (Monastyrski, 1952; Dementyeva, 1952 and others). Early maturation results in a shortening of the life-span of fish and, consequently, in a faster rate of exploitation of a given year-class by the fishery (Dementyeva, 1963; Tokareva, 1964).

It is, therefore, important to detect and explain changes in growth rate in order to determine the population dynamics of the fish and to make fishery forecasts.

This paper deals with the growth changes of the Barents Sea cod. Assumptions are made as to the causes and results of such changes on the basis of some long-term data.

Data include average lengths of the age-groups of cod in the catches made in 1934-37 (Maslov, 1944) and in 1946-60 (Mankevich, 1960).

Figure 1 presents the results of the analysis of the average lengths. Specimens four to nine years of age were used for comparison as they made up the most abundant age-groups in the Southern Barents Sea.

The data reveal, first, that, throughout the period, the average length of age groups, in general, increased gradually to 1937 and from the mid-1940's to 1958; second, that, along with this general increase in average length, some years had simultaneous increases in body length, while others had decreases; and, third, that growth of the younger age-groups varied more than that of the older age-groups.

It is quite evident that the rate of growth of fish and the factors affecting this rate should be estimated from the growth values obtained by means of back calculations. A comparison of the average sizes of fish by age-groups reveals only the general trend of the growth changes. Nevertheless, this trend is so pronounced (Fig. 1) that we may concentrate our attention on the changes

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[3] We do not consider here the problem of under-sized fish attaining maturity as a result of accelerated development.

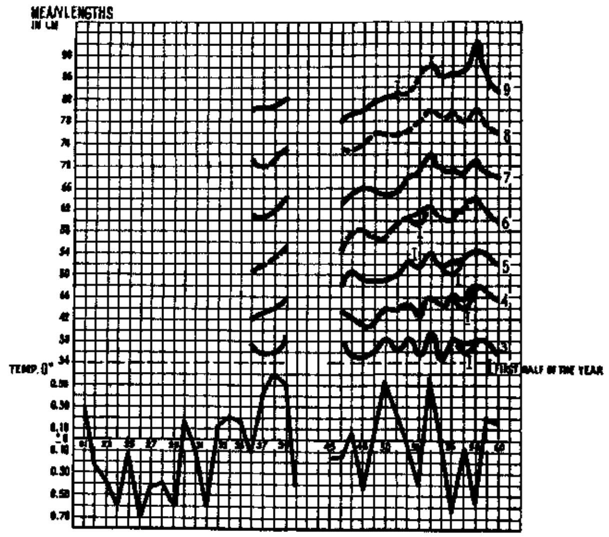

Fig. 1. Mean length of the age groups of the Barents Sea cod by years and the water temperature anomalies on the Kola meridian.

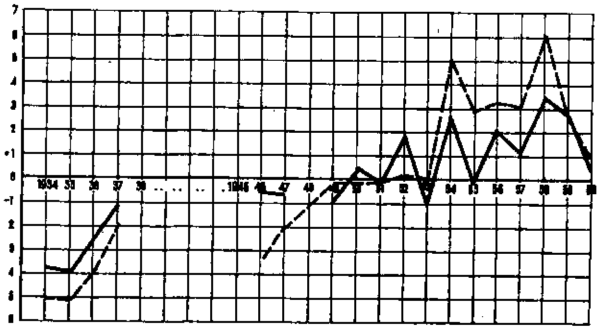

Fig. 2. Mean lengths of the older (——) and younger (— — —) age-groups shown as deviations from the long-term average for the period 1934-60.

that occur inside the population, despite the deficiency of data.

These changes are of greater importance than the general trend when the growth changes of cod have to be defined. For this purpose the annual deviations in growth rate from the long-term average were computed for the older and for the younger age-groups separately on account of the greater variability of the younger age-groups (Fig. 2). The mean lengths of the age-groups before 1952-53 were below the long-term average whereas those after 1952-53 were above. The growth of the younger specimens show the greatest deviations.

Maslov (1944) has pointed out that"the data obtained in 1937 revealed higher mean lengths for all age-groups of cod as compared to previous years. The reason for the increase in the mean length is yet to be ascertained". Earlier Rollefsen (1938) pointed out that fish of the same mean age were about 9 cm longer in 1936 than in 1932. The author suggested that the increase in the growth rate evidently was caused by changes in the hydro-meteorological conditions and that changes in the stock composition of cod results from the great sensitiveness of fish to environmental factors.

The following causes may be responsible for the above mentioned growth changes of the Barents Sea cod: 1) intensified growth in connection with poor yield[4] from year-classes; 2) changes in quantity and/or quality of food organisms; and 3) changes in metabolic activity and in availability and digestibility of food caused by fluctuations in the thermal regime.

Let us first consider the last of these three factors. It is, in our opinion, the most important because the simultaneous increase of growth of all the age-groups as shown in Fig. 1 forms a basis for the assumption that the cause of this increase may be the same for all the age-groups, *i.e.* metabolic changes may be caused by the general warming of the water. Figure 1 presents the variations of the mean temperature anomalies on the Kola meridian as deviations from the long-term temperature average. These data enable us to judge the changes in the hydrological conditions of the Northeast Atlantic. Comparison of these data with the increase of the growth rate of cod reveals that the best growth was observed mainly in the warmer years (1937, 1947, 1954, and 1957).

Analysis of the curve of temperature anomalies (Fig. 1) shows that the deviations during the period, 1922-32, were mainly negative, whereas after 1934 they were positive with the exception of those in the early 1940's and in the late 1950's. Thus 1945-55 is a period of warm years coinciding with the general increase in the growth rate of cod (Fig. 2). The low temperatures in 1939-42 and in the late 1950's resulted in lower values of fish length. The decrease in the growth of cod during 1939-46 is further confirmed by Rollefsen (1953) and from data on the mean length of "skrei" provided by G. Saetersdal (personal communication).

The dependence of the growth changes of cod on temperature is shown in Fig. 3 and 4. Figure 3 shows the fluctuations of the mean lengths of the three main age-groups, IV, V and VI, compared

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[4] the lower density of the stock caused by heavy fisheries

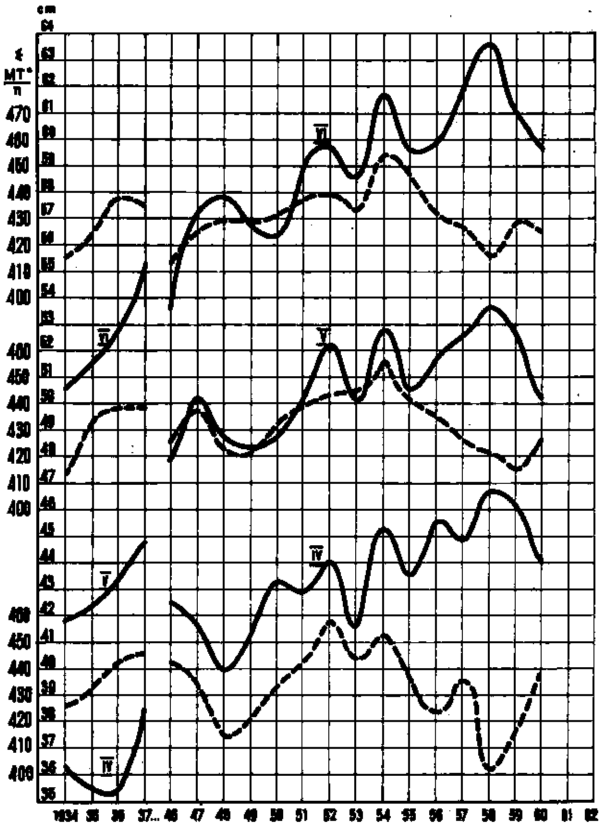

Fig. 3. Fluctuations of the mean lengths of cod (——) and the heat content of waters (– – –) during feeding periods throughout the life of specimens.

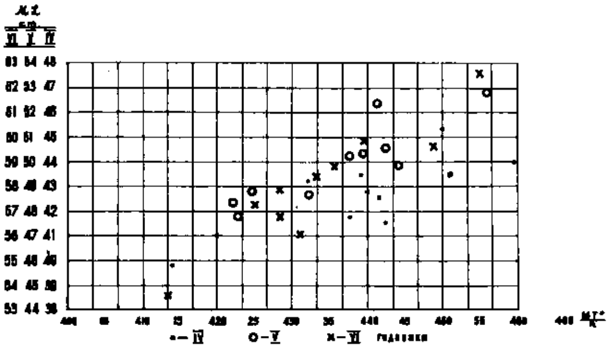

Fig. 4. Correlation between the mean lengths of the age groups of cod and the total average temperatures during feeding periods in 1946-56.

with the total average temperatures during the feeding period of the cod in the years, 1934-37 and 1946-62. To 1955-56 the trend in the heat content of the waters follows closely the trend in growth rate. With the onset of the cooler period, after 1955-56, the sizes of cod continued high to 1958 then decreased. Several reasons account for the large size of cod in 1958: first, the growth of these fish during their early years of life had taken place under higher temperatures; second, the sharp decline in numbers of cod during these years increased the growth rate; a fact which will be commented upon below. In Fig. 4 the mean lengths and temperature data for the period 1946-56 are plotted on the correlation grid. The correlation factor was found to be 0.71.

The variations in the growth rate of fish in relation to water temperature during the peak of the feeding period combined with the length of this period have been discussed by many authors. Nikolaev (1954) illustrates this by referring to studies (also experimental) on particular species of fish. Nikolski (1961) emphasizes the existence for each species of an optimum temperature which is the most suitable for metabolism and provides the fastest growth. One may assume that cod, like many other fish, grow faster in warmer than in colder years. In warmer years the feeding period is extended, the search for food is intensified, the digestion is improved so that food organisms are consumed in greater quantities which in turn causes an increase in the growth rate.

In their summary work on fishery hydrography, Hela and Laevastu (1961) formulate this problem as follows: "The rate of feeding, metabolism and growth is related not only to the availability of food, but also directly to water temperature. The feeding activity usually drops with the deviations from the optimum temperatures. The cod was found to cease feeding if the temperature went below 1°C. The growth is directly related to the intensity of metabolism, *i.e.* to the speed with which the food substances are transformed into the living matter. Hence the optimum growth corresponds to the optimum temperature and the intensity of metabolism of a given species depends to a considerable degree on the temperature". Taylor (1958) points to the susceptibility of cod to temperature fluctuations. He shows a linear relation between surface water temperature and the growth rate of certain North Atlantic populations of cod and warns against possible errors in evaluating the significance and effect of the fishery.

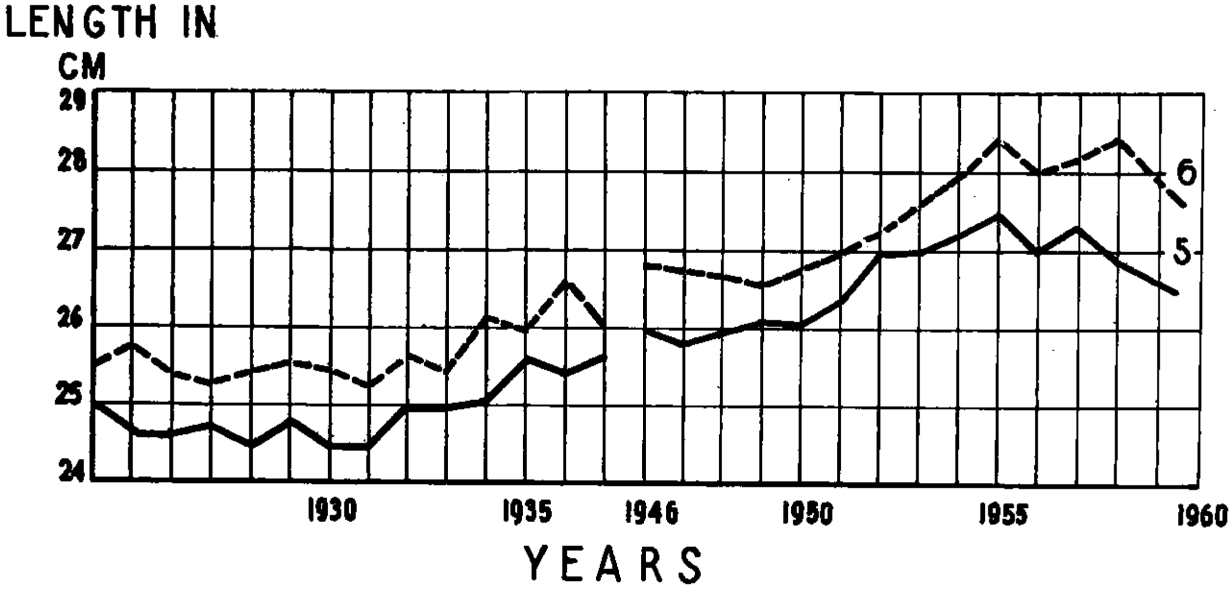

Fig. 5. Changes in the mean lengths of herring in 1932-59 (after Cushing, 1961).

The observed relation between growth rate of cod and temperature conditions was further supported by the fact that during the same years North Sea herring have also increased their growth rate. Cushing (1962) noted that herring have increased their growth rate since 1951. Figure 5, borrowed from his work, shows that the trend and the rate of increase of the mean length of herring are similar to those of the Barents Sea cod. Since 1958 both species have slowed down their rate of growth which is probably related to the onset of the colder period. Ancellin (1960) also showed that for 7 to 8 years, to 1955, the sizes of fish of one and the same age have considerably increased. However, in 1955-59 sizes decreased to normal as seen from the following table:

The mean length of herring by age groups

(after Ancellin)

Age	Years of catch		
	1945	1955	1959
3	22.56	26.41	23.0
4	22.47	26.12	25.17
5	25.73	27.42	26.82
6	26.59	28.13	27.76

The similarity in the growth changes in different North Atlantic species both in respect of food and fishing mortality suggest that the main cause of these changes is the intensity of metabolic processes, probably connected with changes in the general hydrological conditions of the North Atlantic waters including the habitat of the species under consideration.

This indicates the close relation between the processes in the physical medium and their influence on the productivity of the sea. This was discussed by Izhevski (1961) who also pointed out on page 19, the common nature of the water dynamics not only of each of the North Atlantic seas but also of all north European seas collectively.

Changes in the hydrological regime also affect the availability and accessibility of the food organisms themselves, plankton in particular, which, in turn, results in changes in the growth rate of plankton-eaters in certain years (Burd, 1962). Izhevski develops this idea pointing out that the growth rate of fish exclusively depends on the availability of the food, which is more abundant in the warmer years.

Unfortunately, we have no information on the year-to-year abundance of food organisms and we cannot follow this relationship with respect to cod on a long-term basis. We can, however, refer to sporadic data available in literature on the feeding of cod.

The feeding habits of the Barents Sea cod were studied by Zatsepin and Petrova (1939) and later by Grinkevich (1957). The authors conclude that annual changes in the feeding habits of cod follow the seasonal pattern, but are influenced by the biological peculiarities and the changes in the abundance of food organisms.

For example, in warm years, cod begin feeding on euphausiids as their main food item, earlier than in the cold years when the spawning of euphausiids is delayed and the euphausiids reach the near-bottom layers later than usual. In cold years, the habitat of the cod coincides closer with that of their food item - Polar cod (*Boreogadus saida*). During these colder years, capelin became the most sifnificant cod food item because their northeast migration is slower and they, therefore, remain in the area of cod fisheries much longer.

The feeding of cod on herring also depends on the availability of red *Calanus*. Intense production of the latter in June-July accounts for the high fat content of herring and facilitates the formation of their near-bottom concentrations, thus providing better feeding conditions for cod.

These data enable us to conclude that even in years with different hydrological conditions cod can be satisfactorily supplied with food. Thus changes in the growth rate of cod, though being to a certain degree related to the availability and accessibility of food (Mankevich, 1960), are much more dependent on the metabolic intensity of the consumers.

In warm years the production of plankton organisms serving as food for herring, increases. However,this is not the case with such cod food items as capelin, polar cod, bottom crustaceans, etc. whose abundance is affected by conditions for reproduction in the previous year or years.

In a number of cases the growth rate of fish is influenced by the density of the population, especially when there is a sharp increase of cod produced by rich year-classes. Under such circumstances the growth rate of fish becomes slower even with a fairly good food supply. Also, the growth rate becomes faster when the stock is thinned out by fisheries and when the stock is composed of a number of poor year-classes.

The intensified rate of growth of the Barents Sea cod was observed both in 1950-55 when the rich 1950 year-class was dominant and in the years 1957-58 when there was a sharp decline in abundance of fish. In the latter years (Fig. 3) the decline of the density factor may have played a considerable role along with the increased heat content of the water, in causing the greater growth of cod.

Saetersdal and Cadima (1960) concluded that body length tended to decrease with increasing density of the "skrei" population. However, if their data are analysed from the point of view of the time of sampling (excluding samples made in 1925-30), it will be seen that the lowest lengths were observed in samples from 1931-37 and the highest lengths in samples from 1940-47, *i.e.* the changes in the body length of the "skrei" fit into the pattern shown in Fig. 2. We suggest that the changes observed in this particular case are due more to environmental factors than to insufficient amounts of food during the growth period of the rich year-classes.

GROWTH RATE AND MATURITY

As mentioned in the beginning of this paper, there is a direct relationship between growth rate and age of maturity. This relationship can be used to calculate the composition of the stock under formation and the fishing mortality. Mean lengths of cod in each age-group have been shown to vary as much as 11 to 15 cm over the years (Fig. 1). This greatly influences the rate of maturity of cod.

It must be noted that during the period under consideration, there was an intensive development of the trawl fishery. This has resulted in a lower mean age of the stock as evident from the following table of data taken from the ICES Working Group on the Arctic cod (1959), from Rollefsen (1953) and from Saetersdal (1959):

Relation of fishing intensity to the rate of exploitation of cod generations by fisheries:

Years	Hours of trawling (in thousands) in the Southern Barents Sea	Prevailing age	
		in the Barents Sea stock	in the "skrei" stock (acc. to Norwegian data)
1932-38		6-7-8	
1945-50	75-131	6-7	10-11
1950-55	162-267	4-5-6	9-10
1955-59	186-333	4-5-6	8-9

These data show that mean age of the commercial stock decreases with the growing fishing intensity and that regulation measures are rèquired. It may be supposed, however, that the decrease in mean age of the stock is not only caused by the development of fisheries; but may also be caused, to a certain degree, by the earlier maturation of cod due to more rapid growth, especially in the early 1950's, when the fishery had not yet reached full intensity.

Saetersdal suggests that, in addition to the influence of fishing, changes in the age af maturity of the Arctic cod caused the decrease in mean age of the spawning stock of cod in Norwegian waters. He notes, however, that investigators lacked opportunities to distinguish changes from those inflicted by the fisheries.

Still earlier Rollefsen (1938) indicated that the early age of maturity may conceivably result from increased growth rate of cod. He believed that even if there was no direct causal connection, the same circumstance which conditioned the faster growth rate may have also influenced the course of sexual maturation. "Furthermore," says G. Rollefsen, "the earlier age of maturity and the increased mortality in the mature stock should be looked upon as the cause responsible for the reduction of the average age of the stock". We support this author's opinion, and believe that the above data serve to clarify, to some extent, the causes which are responsible for the changes in the composition of the stock of cod, though these causes do not fully determine the actual ranges of the changes. It appears from our observations that these causes were valid not only for the Barents Sea but also for the whole North Atlantic area, including the North Sea.

SUMMARY

The above data on cod provide the basis for the following recommendation:

When analysing the changes in the composition of the total and the commercial stocks of a fish, it is necessary to determine all the causes inflicting these changes, including the changes in the maturity rate in relation to the growth rate. Changes in the age at maturity may be caused by the feeding conditions and intensified by the influence of the hydrological factors (thermal regime affecting the intensity of the metabolic exchange resulting in the consumption of food organisms in greater amounts than usual). The rate of exploitation of the year-classes which, in its turn, sometimes is intensified by extensive fisheries, increases with early maturation.

REFERENCES

ALM, G. 1959. Connection between Maturity, Size and Age. *Inst. of Freshw. Res.* Drottningholm, Report No.40, p. 5-145.

ANCELLIN, J. 1960. Observation sur le hareng du Sud de la Mer du Nord et de La Manche Orientale. Comité du Hareng, No.26, R.d.ICES.

BURD, A.C. 1962. Growth a. Recruitement in the Herring of the Southern North Sea. *Fish. Invest., Lond.(1)*, vol. XXIII, No. 5, p. 1-43.

CUSHING, D.N. 1962. Recruitement to the North Sea Herring Stocks. *Ibid.* p. 45-71.

DEMENTYEVA, T.F. 1952. The growth of fish in relation to the problem of population dynamics. *Zoological journal*, vol. XXXI, No. 4, p. 634-637.

1963. The methods of assessment of the relative abundance of a population, formation of a commercial stock and the rate of its exploitation by fisheries (in press). *Trudy VNIRO*, vol. 50.

GRINKEVICH, N.S. 1957. Annual changes in feeding of the Barents Sea Cod. *Trudy PINRO*, No. X, p. 88-105.

HELA, I. and J. LAEVASTU. Fisheries Hydrography. Fishing News (Books) Ltd., London.

IZHEVSKI, G.K. 1961. Oceanological foundations of the formation of commercial productivity of the sea. Pishchepromizdat (Food Industry Publishers) p. 3-215.

MANKEVICH, E.M. 1960. Biological pecularities of certain groups of the Barents Sea cod. Collection of papers *VNIRO-PINRO*, p.253-266.

MASLOV, N.A. 1944. Bottom fishes and bottom fish fisheries of the Barents Sea. *Trudy PINRO*, No. 8, p. 3-187.

MONASTYRSKI, G.N. 1952. Population dynamics of commercial fishes. *Trudy VNIRO*, vol. XXI, p. 3-162.

NIKOLAEV, I.I. 1954. Meteorology and fisheries. Problems of ichthyology. No. 2. Publ. Ac. of Sc. of the USSR, p. 46-57.

NIKOLSKI, G.V. 1961. The Ecology of Fish. Vyshaya Shkola, p. 7-336.

NÜMANN, W. 1959. Arch. Fischereiwiss., X, 1/2, Braunschweig, Okt., p. 5-20.

ICES Working Group on the Arctic Cod. 1959. Collection "Scientific Information", *VNIRO*, No. 14.

ROLLEFSEN, G. 1938. Changes in mean age and growth-rate of the year-classes in the Arctic-Norwegian stock of cod. *Rapp. Cons. Explor. Mer*, vol. CVIII, p. 37-44.

1953. Observations on the cod and the cod fisheries of Lofoten. *Rapp. Cons. Explor. Mer*, vol. CXXXVI, p. 40-47.

SAETERSDAL, G.S. and E.L. CADIMA. 1960. A Note on the Growth of the Arctic Cod and Haddock. ICES, No. 90.

SAETERSDAL, G.S. 1959. Norwegian Investigations into the Arctic Cod. *"Rybnoe Khozyaistvo"*, I, p. 13-21.

TAYLOR, G. 1958. Cod Growth and Temperature. *J. Cons.*, vol. XXIII, No. 3, p. 366-370.

TOKAREVA, G.I. 1963. Some data on the pecularities of the growth rate of the Baltic cod. *Trudy AtlantNIRO*, (in press).

VASNETSOV, V.V. 1934. An attempt of comparative analysis of the linear growth of Cyprinidae family. *Zoological journal*, vol. XIII, No. 3, p. 540-583.

ZATSEPIN, V.G. and N.S. PETROVA. 1939. Feeding of sea shoals of cod in the Southern Barents Sea. *Trudy PINRO*, No. 5, p. 3-169.

SECTION
E

E-1

EFFECT OF LIGHT ON MOVEMENTS OF HERRING IN THE BAY OF FUNDY

By

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ABSTRACT

Crude laboratory experiments indicate that young herring (*Clupea harengus* L.) 10-15 cm long are attracted to the surface by incident light intensities which do not exceed 15-16 m-c and that the speed of attraction varies inversely with the light intensity. Sonic-sounder recordings in depths of 7-22 m show that "sardine" herring lie on or very close to the bottom on sunny, winter afternoons. At twilight they rise from the bottom in dense shoals and after dark become widely dispersed in the upper water layers.

INTRODUCTION

It is well known that herring make vertical migrations which are associated with changes in light intensity. Larval herring are caught within the upper 20 m of water under all light conditions but are taken in greatest numbers in the top metre of water at night (Tibbo and Legaré, 1960). Similarly shoals of adult herring are comparatively rare at the surface during the day but are caught in enormous quantities in the upper water layers at night (Johansen, 1925). Brawn (1960) has shown from echo-sounder records that herring are closer to the surface by night than by day during every month of the year. Because of this diurnal vertical movement drift-nets and purse seines are usually operated at the surface at night, whereas, bottom trawls are used chiefly during the daylight hours.

It is also known that herring near the surface at night are attracted to lights. Torching (*i.e.*, attracting herring with a light and dipping them into a boat) is an effective method of cap- in some areas (Scattergood and Tibbo, 1959). Weir fishermen in the Passamaquoddy region of the Bay of Fundy are aware of relationships between availability of young herring (sardines) and light intensity. For example, some weirs are most effective in the morning and others in the evening (Johnson, 1940) and catches are better at some phases of the moon than at others (personal communication with fishermen).

In spite of this general awareness of the response of herring to light there has been little effort to measure the light intensities which attract or repel herring or of changes in light intensity which may induce vertical migrations. To obtain some information on these subjeacts crude laboratory experiments were carried out at the St. Andrews Station of the Fisheries Research Board of Canada and a field experiment was carried out in Maces Bay, New Brunswick.

LABORATORY EXPERIMENTS

For the laboratory experiments approximately 100 herring (10 to 15 cm total length) were kept in an outdoor, covered tank (ca. 4 m × 6 m × 1 m deep) for several months and subsequently exposed to artificial light, the intensity of which could be varied within certain limits.

The experiments were carried out at various times of day during the winter of 1948-49. They were done at irregular intervals with a minimum of 1 hr between successive tests to allow the fish time to adjust to darkness. The tank cover (ca. 1.5 m high at the centre) kept the fish in darkness except when artificial lights were turned on. An electrical outlet was attached to the under side of the tank cover. The distance between the lamps and the surface of the water was 142 cm. A reflector directed the light downward to the surface of the water. Light intensities were measured with a Weston incident light meter.

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TABLE 1. SOURCE OF LIGHT, INCIDENT LIGHT INTENSITY AND RESPONSE OF HERRING TO LIGHT.

Lamp	Filter	Incident light intensity	Phototropism
w		*m-c*	
7 1/2	None	4.3	+
7 1/2	Yellow	3.2	+
7 1/2	Red	1.1	+
7 1/2	Blue	0.3	+
15	None	15.1	-
15	Yellow	8.6	+
15	Red	4.3	+
15	Blue	1.1	+
40	None	26.9	-
40	Yellow	16.1	+
40	Red	7.5	+
40	Blue	2.2	+
60	None	48.4	-
60	Yellow	36.6	-
60	Red	15.1	-
60	Blue	5.4	+

Table 1 shows that herring were attracted to and stayed within the influence of a faint light but were repelled by strong light. Attraction was determined by measuring the time from the turning on of the lamp until 50% of the fish came within the circle of light shed by it.

A 7.5 w, 110 v lamp with a blue glass filter (0.3 m-c) exerted the greatest attraction. It took twice as long to attract the fish with the 7.5 w lamp using red (1.1 m-c) and yellow (3.2 m-c) filters. The herring were attracted but still more slowly by the 7.5 w lamp with no filter (4.3 m-c). Lamps of 15, 40 and 60 w with and without filters were used to produce light intensities varying from 1.1 to 48.4 m-c. From the results it was concluded that herring are attracted to incident light intensities which do not exceed 15 to 16 m-c and that the speed of attraction varies inversely with the light intensity.

FIELD EXPERIMENT

For the field experiment echo-sounder recordings were made from the research vessel *Gulf Explorer* using a Bendix DR1 model echo-sounder. During the daytime on a bright, sunny afternoon recordings were made directly in front of a bottom trawl that was being towed by another vessel, the *Li'l Abner*. At twilight and during the night on the same date (8 February, 1952) recordings were made as close to a fleet of purse seiners as it was possible to go without interfering with their operations.

Figure 1 gives four typical echo-sounder recordings showing the distribution of herring under different light conditions. Figure 1A is typical of the daytime recordings. There was nothing on these recordings to indicate the presence of herring except, possibly, the wide bottom trace at 72 ft (22 m) which is characteristic of soft, muddy bottoms. In Maces Bay much of the bottom is hard packed sand which gives a sharper narrower trace, *e.g.*, Figure 1C. The fishing vessel *Li'l Abner* operated a bottom trawl in this area and made catches from 0.7 to 3.6 metric tons per hour's towing. To obtain the record shown in Fig. 1A the *Gulf Explorer* cruised in all directions ahead of, alongside and over the trawl being towed by the *Li'l Abner*. The trawl and trawl warps were recorded (not included in the Fig.) whenever we passed over them but there was never any more indication of fish than is shown in Fig. 1A which was for areas directly in front of the trawl during one tow. The catch during this tow was 0.9 metric tons.

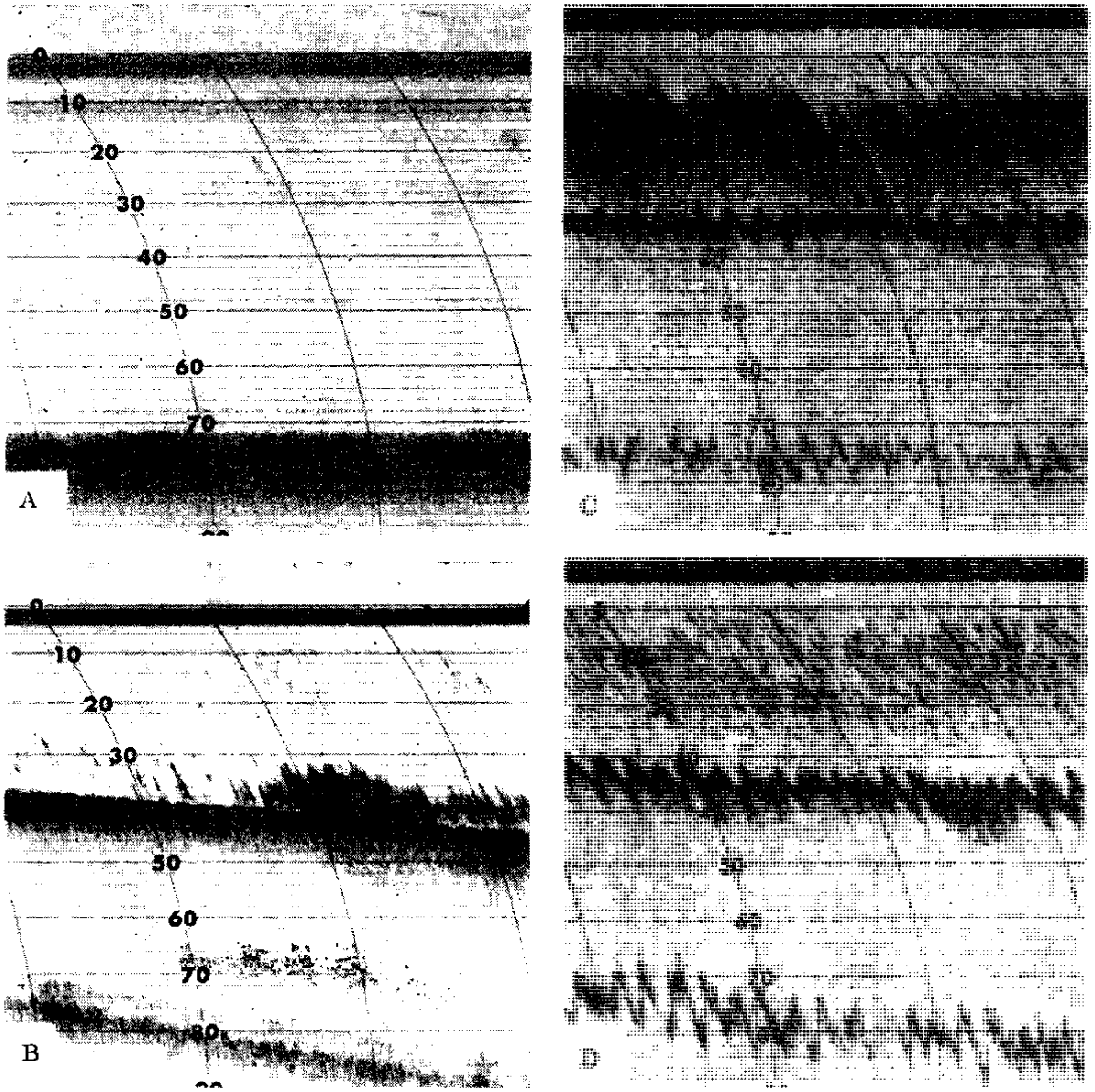

Fig. 1. Echo-sounder recordings from Maces Bay, New Brunswick.
- A. Typical daytime recording with herring on or close to bottom.
- B. Typical twilight recording showing herring off bottom.
- C. Typical dusk recording showing dense shoals of herring in mid-water.
- D. Typical night recording showing herring scattered in mid-water.

Figure 1B and 1C illustrate the type of recordings made just after sunset in the same general area of Maces Bay. In these recordings dense shoals of herring can be seen just off bottom and at mid-depths. The movement away from the bottom was quite rapid as evidenced by the fact that the recording shown in Fig. 1C was made less than 15 min after the recording shown in Fig. 1B. It is during the twilight period that the purse seiners are active and catches from 14 to 36 metric tons were made at the same time and in the same area as these recordings were being made.

Figure 1D typifies recordings made at night in showing how the herring have dispersed. Attempts to purse seine these dispersed shoals have yielded small catches (0.9 to 1.3 metric tons) which are not worth the effort.

DISCUSSION

From the pattern of commercial fishing operations it appears that the behaviour of herring illustrated by the echo-sounder recordings from the field experiment is typical of the behaviour of "sardine" herring in the Bay of Fundy. Tentatively this behaviour is explained as a strong, positive attraction to light of low intensity as indicated by our crude laboratory experiment.

Obviously present information is inadequate for an understanding of light-induced movements of herring but from the point of view of the fisheries this understanding may be important. It would be useful to know the depths to which herring will go to avoid light of high intensity.

The recordings shown here indicate that in winter sardine-size herring will descend to the bottom (about 21 m). However, Brawn (1960) showed that some fish of this size were off bottom and that the median depth during the day from May to December varied from 9.1 to 13.4 m. From January to April it varied from 25.3 to 38.4 m. Furthermore, Leim *et al.* (1957) observed that "sardine" herring were distributed at mid-depths after several hours of bright sunlight in areas where the depth of water was about 27 m and concluded that herring do not react to daylight in the same way at all times.

It is obvious that the effect of light on herring is poorly understood and merits serious study.

REFERENCES

BRAWN, VIVIEN M. 1960. Seasonal and diurnal vertical distribution of herring (*Clupea harengus* L.) in Passamaquoddy Bay, N.B. *J. Fish. Res. Bd. Canada,* 17 (5): 699-711.

JOHANSEN, A.C. 1925. On the diurnal vertical movements of young of some fishes in Danish waters. *Medd. Komm. Danm. Fisk. Havundersøg. Bd.* VIII, Nr. 2, 27 p.

JOHNSON, W.H. 1940. Effects of light on movements of herring. *J. Fish. Res. Bd. Canada,* 4 (5): 349-354.

LEIM, A.H., S.N. TIBBO and L.R. DAY. 1957. Explorations for herring in Canadian Átlantic waters, 1945-1950. *Bull. Fish. Res. Bd. Canada,* No. 111, p. 35-83.

SCATTERGOOD, L.W., and S.N. TIBBO. 1959. The herring fishery of the Northwest Atlantic. *Bull. Fish. Res. Bd. Canada,* No. 121, 42 p.

TIBBO, S.N., and J.E. HENRI LEGARE. 1960. Further study of larval herring (*Clupea harengus* L.) in the Bay of Fundy and the Gulf of Maine. *J. Fish. Res. Bd. Canada,* 15 (6): 1451-1469.

E-2

DISTRIBUTION OF PLANKTON AND SUMMER FEEDING OF HERRING IN THE NORWEGIAN SEA AND ON GEORGES BANK

By

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ABSTRACT

Comparison of the conditions for the spring-summer feeding of herring in the Norwegian Sea and on Georges Bank (the Gulf of Maine) shows that herring prefer the areas where the biomass of *Calanus finmarchicus* amounts to 200-500 mg/m^3. In search of such concentrations of *Calanus finmarchicus* the Atlanto-Scandian herring of the Norwegian Sea migrate over great distances from the coastal waters into the waters of Atlantic origin and then into the mixed and polar waters where biological spring starts.

On Georges Bank several generations of *Calanus finmarchicus* develop during one season, so herring are provided with food and do not undertake extensive migrations.

An increase in the water temperature in the Norwegian Sea and on Georges Bank results in the change of plankton composition: Medusae and Tunicata occur in great numbers, thus providing the unfavourable conditions for herring.

Soviet plankton investigations were conducted in the Norwegian and Greenland Seas to study the role of plankton in the feeding migrations of herring. The first observations in the Greenland Sea were made in the region of Spitsbergen in June-July, 1947, by an expedition organized by Ju. Ju. Marty and B.P. Manteifel. Subsequently with the extension of the Soviet herring fisheries in the Greenland and Norwegian Seas, the region of plankton investigations also extended over a greater area. As a result of the investigations carried out in the Norwegian Sea, it was established (Marty, 1956; Pavshtics, 1956 and 1960; Rudakova, 1956) that the life cycle of Atlanto-Scandian herring is most closely related to the dynamics of the development of plankton.

The herring developed the habit of feeding migrations during the historical development of the species. The habit allows the fish to take full advantage of the vernal outburst of plankton on which they feed intensely in coastal, Atlantic, mixed and polar waters. Herring adapt easily to considerable changes of environmental conditions. Repeated observations have shown that changes in hydrometeorological conditions in the Norwegian Sea were accompanied by considerable (up to a month) variations in the time of development of plankton and that a corresponding change was also observed in the duration of the herring feeding period.

In the Norwegian Sea in cold years (1958 and 1962) and in years approaching normal conditions (1951, 1953, 1955) (Alekseev and Istoshin, 1960; Istoshin and Alekseev, 1959; Alekseev, Istoshin and Shmarina, 1962) herring usually began to feed in March-April on the spring concentrations of breeding Euphausiacea and *Calanus finmarchicus* near the continental slope of the coast of Norway.

By June the herring migrated from the southern part of the Norwegian Sea to the west (Grusov, 1960 and 1961) and from the coasts of north Norway - to the north-west, to the regions of the Polar Front, where the biological spring (spawning of *Calanus*) begins later (Pavshtics, 1956 and 1960; Pavshtics, 1958). Usually the feeding period of the herring ended in August-September in the mixed waters in the region of the Mohn Ridge and Jan Mayen. In the warm year 1960 and partly in 1959 (Grusov and Pavshtics, 1961) due to a considerable warming of the mixed waters in the south-western region of the Norwegian Sea near the Faroes, the breeding and development of *C. finmarchicus* occurred

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earlier than in 1951-1958. Accordingly in 1960 the herring reached its highest fat content earlier than in the preceding years - by June-July instead of August-September. In 1960 the feeding period started in an unusual way. The herring, migrating in April 1960 from the coast of Norway to the Faroes, did not encounter the concentrations of breeding *Calanus* which are present at that time of the year. Here the spawning of *Calanus* was already over and the bulk of plankton was composed of small young *Calanus*. Therefore, by the end of May and in early June 1960, in contrast to other years, the herring in the mixed waters, at the Faroes and on the boundaries of the East Iceland current fed on fat red *Calanus* (*Calanus finmarchicus*, III-IV-V stages). The biomass of plankton in the feeding regions was extremely high, two times higher than in previous years (Pavshtics, 1962; Pavshtics and Rudakova, 1962). Due to the early development of red *Calanus* in the western region of the Norwegian Sea in the warm year 1960 not only the young (21-28 cm) but the older herring fed on red *Calanus*.

Earlier detailed field observations on the feeding of young and old herring were made in the Norwegian Sea in the summer 1955 (Pavshtics, 1956). At that time a quite different picture was observed. In June 1955, characterized by a retarded development of plankton, young herring (21-28 cm) were feeding in the central regions of the Norwegian Sea; but red *Calanus* was scarce so that *Oikopleura* sp. and *Themisto abyssorum* were the main items of the diet in June 1955. Older herring stayed in the region of the Polar Front near Jan Mayen, where the biological spring was just beginning, feeding on *Calanus hyperboreus* and *Calanus finmarchicus* in VI copepod stage. In 1955 the red *Calanus* (*Calanus finmarchicus* of the III-IV-V stages) developed in August-September near Jan Mayen and in the region of Mohn Ridge. By that time both old and young herring migrated to this area.

The 1955 observations convinced us that during periods of feeble and slow development of *Calanus*, herring can feed on other plankton organisms, such as *Themisto* juv. and *Oikopleura labradoriensis*, though *Calanus finmarchicus* and various species of Euphausidae still remain their favourite food (Rudakova, 1956; Pavshtics and Rudakova, 1962). In 1960 the highest fat content of herring was already reached in June. In 1955 and 1958, years of retarded development of *Calanus*, the highest fat content was observed only in August-September (Pavshtics, 1962; Pavshtics and Rudakova, 1962). In 1960 and 1959, characterized by an early development of *Calanus*, the feeding period of the herring was short, and at the end of this period the herring was not as fat as in moderate and cold years. The feeding of herring is at times unfavourably affected by an early development of medusa *Aglantha digitale* in the waters of the Norwegian Current.

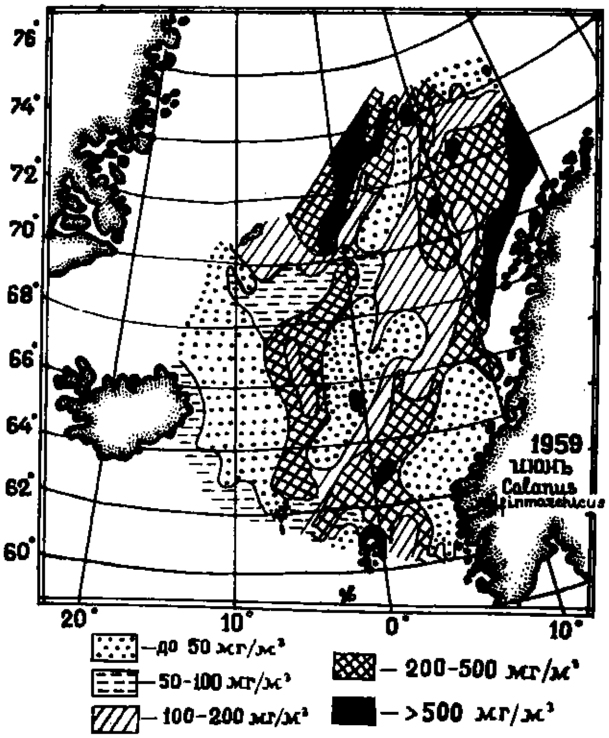

Fig. 1. Quantitative distribution of *Calanus finmarchicus* in June 1959 in the Norwegian Sea (biomass in mg/m^3).

In warm years (1954, 1959, 1960) *Aglantha digitale* appeared in the central and southern regions of the Norwegian Sea as early as June, whereas in colder years a mass development of *Aglantha digitale* was observed in July-August and even in September. The medusae are greatly reducing the quantity of *Calanus* in the upper water layers, thus affecting the feeding of herring. Most often herring moved from the southern and central regions in June-July westwards or northwards, into colder waters, where no medusae are found at that season. At the edge of the East Icelandic Current, where herring feed in June, the biomass of *Calanus* rarely exceeds 200-500 mg/m^3 (Fig. 1). A typical situation was observed in June 1959, when the feeding area of the herring was limited on the west by a zone of *Aglantha digitale*, where the biomass of *Calanus* was less than 50 mg/m^3 (Grusov, 1961). During this period the herring did not move farther west because in June the cold waters of the East Icelandic Current still contain the poor plankton concentrations in winter (Grusov and Pavshtics, 1961). The herring feeding in the mixed waters gradually moved north along the margin of the cold East Icelandic Current.

In 1961 and 1962 material was collected on plankton and feeding of herring in the region of Georges Bank (the Gulf of Maine). A comparison of these materials with observations on the feeding of herring (Benko and

Vilson, 1962) showed that on Georges Bank, like in the Norwegian Sea, the herring feed mainly on *Calanus* (*Calanus finmarchicus* III-IV stages) and *Euphausiacea*. The most intensive feeding on *Calanus* is observed here in May-June. On Georges Bank, like in the Norwegian Sea, herring during the feeding period keep to the mixed waters of the frontal zone and easily tolerate even sharp variations of water temperature.

On the slopes of Georges Bank, Atlantic waters, cold waters of the Nova Scotia Current and moderately warm, low salinity waters of the Gulf of Maine are encountered (Bigelow, 1926). Each water mass carries to the Bank its own plankton. Herring feed mainly on boreal plankton: *C. finmarchicus, Pseudocalanus minutus, Metridia lucens, Thysanoessa inermis, Meganyctiphanes norv., T. compressa f. compressa* and others. This plankton community inhabits the northern and northwestern slopes of the Bank washed by the waters of the Gulf of Maine. Here in the summer months of 1962 were observed the most abundant concentrations of *Calanus finmarchicus* (Table 1). At Station 44 *Calanus finmarchicus* accounted for 94% of the total plankton (by number of specimens). The least amount of food plankton was observed in the central part of the Bank with a rich development of phytoplankton. On the south-eastern slope of the Bank washed by Atlantic waters, the quantity of *Calanus finmarchicus* decreases to 62 specimens per m^3, as compared with 880 specimens per m^3 on the northern slope of the Bank. Here, as in the Norwegian Sea, herring fed mainly where the biomass of *Calanus* reached 200-500 mg/m^3 (Fig. 2).

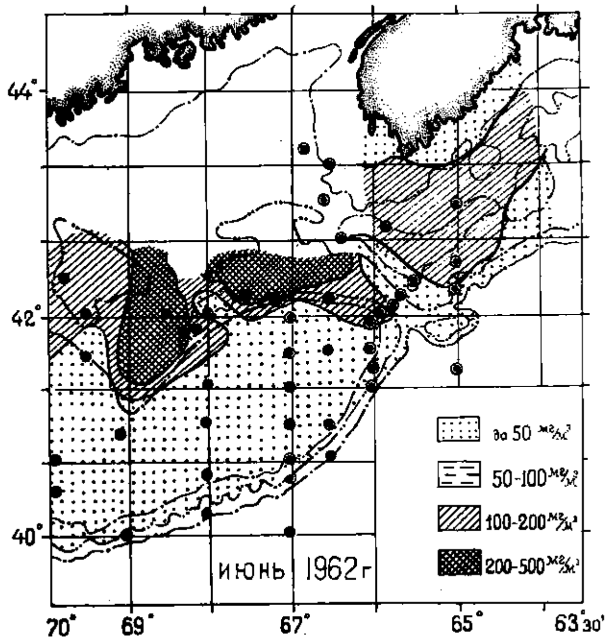

Fig. 2. Quantitative distribution of *Calanus finmarchicus* in June 1962 on Georges Bank (Gulf of Maine) (biomass in mg/m^3).

The importance of the most common Copepoda in the plankton of Georges Bank, is shown in Table 1 (percentage of the total number of plankton organisms). Comparison of the composition of plankton on Georges Bank and in the Norwegian Sea, shows regular phenomena common to both regions. In the waters of the continental slope, where Atlantic waters mix with coastal waters, *Calanus finmarchicus* predominates (Pavshtics, 1960, p. 166). Regions where Atlantic waters mix with cold waters from the north, are characterized both in the Norwegian Sea and on Georges Bank, by a predominance (in number of specimens) of *Oithona similis*.

In the Norwegian Sea, for instance, in the region of Jan Mayen, where waters of the western branch of the Norwegian Current meet a branch of the cold East Greenlandic Current, *Oithona similis*, in June 1959, made up 69% of the plankton in numbers of specimens (not in the biomass). A similar picture was observed in the region of Georges and Browns Banks where Atlantic waters mix with the Nova Scotia Current. Here *Oithona similis* composed about 37% of the plankton.

There are, however, some differences between the feeding conditions of the Norwegian Sea and those of Georges Bank. According to Fish (1936*a* and *b*) the high water temperature - up to 18-20°C - in the Gulf of Maine favours the development of several generations of *Calanus finmarchicus* and *Pseudocalanus minutus* during a single season. The breeding period of Euphausiacea and of Hyperiidae is prolonged too which ensures a prolonged stay of their young in the mid water layers. As a result, the herring is provided with food almost all year and, in contrast to the herring of the Norwegian Sea, can feed without undertaking any distant migrations. Some data on the feeding of herring in the regions investigated are given in Table 2. When comparing the feeding intensity of herring on Georges Bank with that of herring in the Norwegian Sea, it must be remembered that the herring feeding on Georges Bank are summer spawners, whereas in the Norwegian Sea spring spawners were predominant. The lower average indexes of stomach fullness in herring from Georges Bank in the summer months seem to be determined by a more rapid food digestion owing to higher water temperatures as compared with the Norwegian Sea.

TABLE 1. THE IMPORTANCE OF THE MOST COMMON COPEPODA IN PLANKTON ON THE SLOPES OF GEORGES BANK (IN PERCENT OF TOTAL NUMBER OF PLANKTON ORGANISMS).

Stations, Date, Positions	*Calanus finmarchicus*			*Pseudocalanus minutus (elongatus)*			*Metridia lucens + longa*			*Temora longicornis*		
	Spec/m³	%	Weight	Spec/m³	%	Weight	Spec/m³	%	Weight	Spec/m³	%	Weight
South-eastern slope 3 June, 1962 Depth 85 m Temp. 7.5°C Layer 80-0 m	62.5	9.3	27.6	17.5	2.6	1.4	1	0.1	1.1	0.5	0.05	0.028
Eastern slope 4 June, 1962 Depth 100 m Temp. 8.6°C Layer 100-0 m	280	16	117.3	234	13.3	13.9	27.7	1.5	25.2	11.6	0.7	0.65
Northern slope 8 June, 1962 Depth 200 m Temp. 10.9°C Layer 50-0 m	728	16	299	180	4	11.3	68	1.5	61.9	-	-	-
Northern slope 7 June, 1962 Depth 210 m Temp. 1.1°C Layer 50-0 m	880	34.2	497	480	18.7	41.3	280	10.9	255	-	-	-
North-western slope 7 June, 1962 Depth 100 m Temp. 11.9°C Layer 60-0 m	690	94	401	23	3.3	1.8	1	0.1	1.67	-	-	-

TABLE 1 (CONT'D).

Stations, Date, Positions	*Centropages hamatus*			*Oithona similis*			*Nauplii calanoida*			Weight of Common Species mg/m^3	Total Quantity of Plankton ml/m^3
	Spec/m^3	%	Weight	Spec/m^3	%	Weight	Spec/m^3	%	Weight		
South-eastern slope 3 June, 1962 Depth 85 m Temp. 7.5°C Layer 80-0 m	0.5	0.05	0.06	105	15.7	0.53	420	62.8	3.4	34	0.75 "Blooming"
Eastern slope 4 June, 1962 Depth 100 m Temp. 8.6°C Layer 100-0 m	-	-	-	634	36.2	3.2	400	22.8	3.2	163	0.3
Northern slope 8 June, 1962 Depth 200 m Temp. 10.9°C Layer 50-0 m	-	-	-	1016	22.1	5.1	2000	43.6	16	393	0.6
Northern slope 7 June, 1962 Depth 210 m Temp. 1.1°C Layer 50-0 m	-	-	-	440	17.1	2.2	392	15.2	3.1	799	1.8
North-western slope 7 June, 1962 Depth 100 m Temp. 11.9°C Layer 60-0 m	-	-	-	1	0.1	0.0005	17	2.4	0.14	405	1

TABLE 2. SOME DATA ON THE FEEDING OF HERRING ON GEORGES BANK AND IN THE NORWEGIAN SEA IN 1961. BASED ON DATA COLLECTED BY BENKO, VILSON (1962) AND RUDAKOVA'S PERSONAL COMMUNICATION.

	April	May	June	August	October	November	December
Georges Bank Average index of stomach fullness	0.58	1.14	0.54	0.30	0.29	0.37	0.68
Norwegian Sea Average index of stomach fullness	0.87	1.33	1.47	0.95	0.32	0.15	0.09
Georges Bank Average index of fat content	0.84	1.40	1.77	0.76	0.67	0.44	0.83
Norwegian Sea Average index of fat content	0.35	0.58	1.65	1.80	1.16	1.17	1.56

The low index of stomach fullness in herring of the Norwegian Sea during November-December is caused by a sharp decrease in the quantity of plankton during the autumn-winter seasons. In the Gulf of Maine and on Georges Bank the herring is winter fed on Euphausiacea. From November to February no *Calanus finmarchicus* occur on Georges Bank. Their place in the plankton is occupied by small tropical copepods and tunicates. Occasionally Euphausiacea, *Nematoscelis megalops* and *Meganyctiphanes norvegica* appear on the Bank. Due to the earlier development of plankton on the Bank, the herring reach their maximum fat content somewhat earlier than in the Norwegian Sea. In 1961 the fat content of the herring on Georges Bank increased by May-June as compared with June-July in the Norwegian herring. In December, in the Gulf of Maine and on Georges Bank, the feeding of the herring was irregular, though occasionally their stomachs were found to be filled with Euphausiacea (Benko and Vilson, 1962). Perhaps, due to this, the fat content of herring was somewhat higher in December. The increase in the average index of fat content of the Norwegian herring in December 1961 is apparently due to the presence in the catch of young fatter herring of the 1959 year-class (materials from the Herring Laboratory of PINRO).

CONCLUSIONS

1. In the Norwegian Sea and on Georges Bank (Gulf of Maine) the herring feed mainly in frontal zone: The most favourable feeding conditions occur most often in May-June near the continental slope and around islands, where Atlantic waters meet coastal waters. In these regions *Calanus finmarchicus* and Euphausiacea, the favourite food of herring, are often predominant in the plankton.

2. With an increased inflow of Atlantic waters into the Norwegian Sea and on Georges Bank the temperature of the water rises; this is followed by an increase in percentage of jelly fish (*Aglantha digitale* in the Norwegian Sea) and Tunicata (*Salpa fusiformis*, *Doliolum* sp. - in the plankton on Georges Bank). In these cases the quantity of plankton suitable for herring food is reduced sharply.

3. Surveys of summer concentrations of herring should not be conducted in regions rich in jelly fish and tunicates. In the summer herring are found mainly in moderately warm waters (5-8°C), where the biomass of *Calanus* reaches 200-500 mg/m^3 (Fig. 1 and 2). The intensive feeding of herring may greatl reduce the biomass of *Calanus*. By contrast, in northern and eastern regions of the Norwegian Sea whe no herring occur in June, the biomass of plankton is usually very high (more than 500 mg/m^3).

4. Regular observations on seasonal variations in plankton make it possible to predict feeding conditions and to determine with greater accuracy the routes of the migrating herring in different parts of the sea.

REFERENCES

ALEKSEEV, A.P. and B.V. ISTOSHIN. 1960. Some results of oceanographical investigations in the Norwegian and Greenland Seas. *In* Soviet Fisheries Investigations in North European Seas. Moscow.

ALEKSEEV, A.P., B.V. ISTOSHIN and L.R. SHMARINA. 1962. Hydrological conditions in the Norwegian and Greenland Seas in 1961. *Scientific-technical bulletin of PINRO* No. 2-3 (20-21).

BENKO, Ju. K., and A.P. VILSON. 1962. The feeding and physiological condition of herring of the Georges Bank in 1961. *In* "Herring of the North European basin and adjacent seas". *Trudy PINRO,* XIV.

BIGELOW, H.B. 1926. Plankton of the offshore waters of the Gulf of Maine. *Fish. Bull., U.S.* (1924) 40.

FISH, C. 1936*a*. The biology of *Calanus finmarchicus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull.,* LXX, (1).

1936*b*. The biology of *Pseudocalanus minutus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull.,* LXX, (2).

GRUSOV, L.N. 1960. Development of water "blooming" and *Calanus finmarchicus* in the southern regions of the Norwegian Sea in 1958. *Trudy BALTNIRO,* VI.

1961. Influence of plankton on the feeding migrations of herring in the Norwegian Sea in 1959. *Trudy BALTNIRO,* VII.

GRUSOV, L.M. and E.A. PAVSHTICS. 1961. Soviet plankton investigations in the Norwegian Sea. *Ann. biol., Copenhague,* XVI.

ISTOSHIN, B.V. and A.P. ALEKSEEV. 1959. Long termed variations of water temperature in the Norwegian and Greenland Seas during the summer period. *Scientific technical bulletin of PINRO,* No. 2 (10).

MARTY, JU. JU. 1956. Major stages of the life cycle of Atlanto-Scandian herring. *In* "Seldy Severo-Evropeiskogo basseina i smejnykj morey." (Herring of the North-European basin and adjacent seas). *Trudy PINRO,* IX.

PAVSHTICS, E.A. 1956. Seasonal changes in the plankton and the feeding migrations of herring. *Trudy PINRO,* IX.

1958. Plankton survey of the Norwegian Sea in 1956. *Ann. biol., Copenhague,* XIII.

1960. Basic regularities in the development of plankton in the Norwegian and Greenland Seas. *In* Soviet Fisheries Investigations in North European Seas. Moscow.

1962. Soviet plankton investigations in the Norwegian Sea, 1960. *Ann. biol., Copenhague,* XVIII.

PAVSHTICS, E.A. and V.A. RUDAKOVA. 1962. To the problem of long-termed changes in the development of plankton and conditions of the feeding of herring in the Norwegian Sea. *Trudy PINRO,* XIV.

RUDAKOVA, V.A. 1962. Materials on the feeding of Atlanto-Scandian herring. *Trudy PINRO,* IX.

E-3

WATER TEMPERATURE AND THE HERRING FISHERY OF MAGDALEN ISLANDS, QUEBEC

By

L.M.Lauzier[1] and S.N.Tibbo[1]

ABSTRACT

At Magdalen Islands there is a direct relationship between water temperatures during the latter part of April and the "relative" catch of herring during April. The start of the fishery is usually preceded by a rapid warming of the waters to 2.1°C. Air temperatures and ice conditions during the previous winter provide a basis for forecasting the starting date and relative size of the herring fishery in April. A selective and intermittent movement of herring into the spawning area is suggested.

INTRODUCTION

The Magdalen Islands area lends itself to a study of the effects of the physical environment on a fishery. It is located in the centre of the outflow of the Gulf of St. Lawrence and is isolated from other inshore fishing areas (Fig.1). Surrounding waters have a large annual amplitude of temperature. After the disappearance of ice, vernal warming is rapid and during this period there is an intensive herring fishery with landings varying greatly from year to year. This fishery is carried on mainly with trap nets set close to shore. Within the last 30 years, landings have been as low as 4,121 metric tons (1933) and as high as 22,482 metric tons (1955). Generally, the fishery lasts 6 to 8 weeks, beginning in April in some years and in May in others.

Day (1957, *a, b*) described the herring fishery of the Magdalen Islands and showed a relationship between vertebral numbers and water temperatures. Lauzier (1952) drew attention to the unusually high water temperatures of April 1951 which were associated with large landings of herring during that month. This paper presents additional data to show that there is a relationship between herring landings and water temperatures and describes other features of the herring fishery in the Magdalen Islands area.

HERRING LANDINGS AND WATER TEMPERATURES

Figure 2 shows annual herring landings, herring landings in April and surface water temperatures during the latter half of April for the years 1942-63. Landings were obtained from publications of the Bureau des Statistiques, Ministère de L'Industrie et du Commerce, Quebec. Average temperatures (April 16-30 inclusive) were calculated from observations made twice daily at Entry Island. There is some evidence of a direct relationship between herring landings and water temperatures. Total landings, landings in April and water temperatures were all higher in the 1950's than in the 1940's. The decrease in landings after 1955 is probably due to an epidemic disease of herring that caused widespread mortalities in the Gulf of St. Lawrence in 1954-56 (Sinderman, 1958). The increase in landings after 1960 probably reflects recovery from the effects of the disease (Tibbo and Graham, 1963).

From 1942 to 1963, the landings of herring in April varied between 0 and 82% of the total annual landings. These are shown in Figure 3 as "relative" landings in April and plotted against the average water temperature during the second half of April. The correlation coefficient between "relative" landing and the temperature was calculated to be + 0.71 ($P_{0.01} = 0.54$) and the coefficient between the actual landings and the temperatures for the same years was + 0.61. Within the last 22 years, there are a number of years for which data on landings, date of arrival of herring and temperatures are all available. Representative cold and warm year data are given in Table I and, except for 1949 and 1960, show that the warmer the waters, the earlier fishing starts and the greater the percentage landings in April.

Over this 22-year period from 1942 to 1963, the start of the herring fishery was recorded for 13 years. The earliest first catch was made on April 4 in 1951 and the latest on May 6 in 1943. The average date of the first catch was April 25.

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[1] Fisheries Research Board of Canada, Biological Station, St. Andrews, N.B.

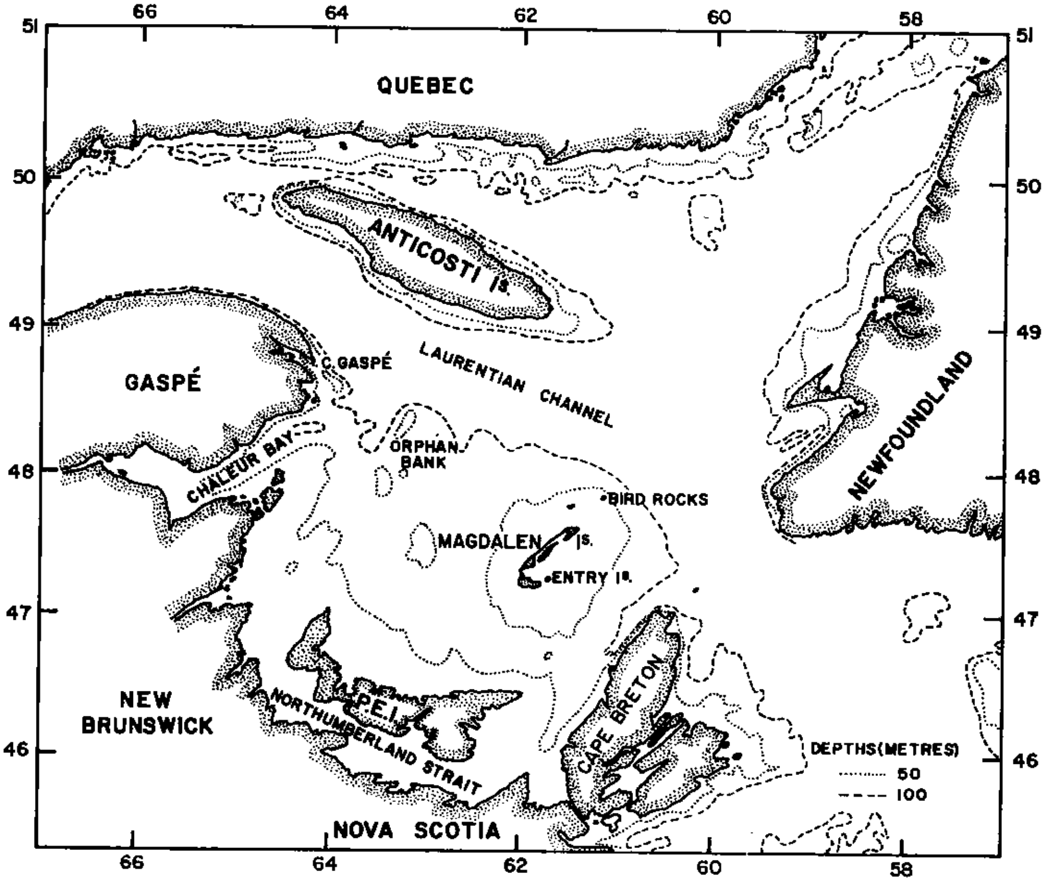


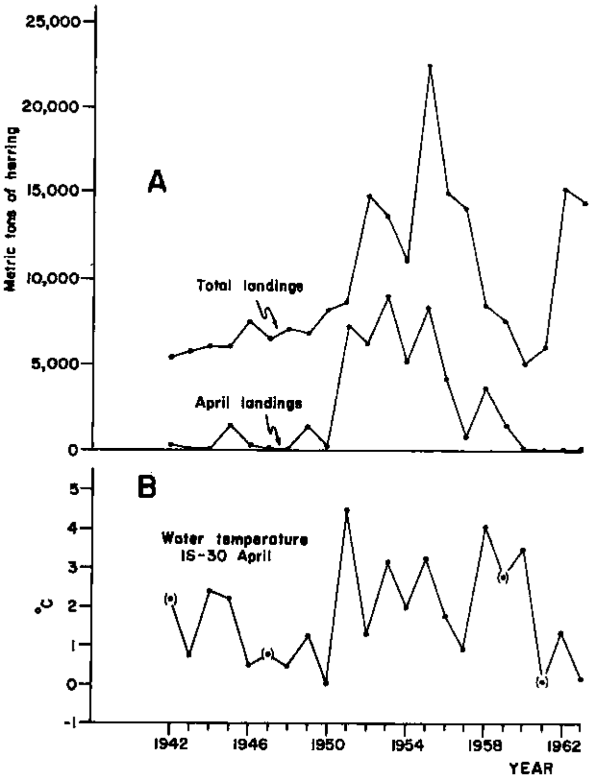
Fig. 1. Chart of the Gulf of St. Lawrence

BEGINNING OF THE FISHERY AND WATER TEMPERATURES

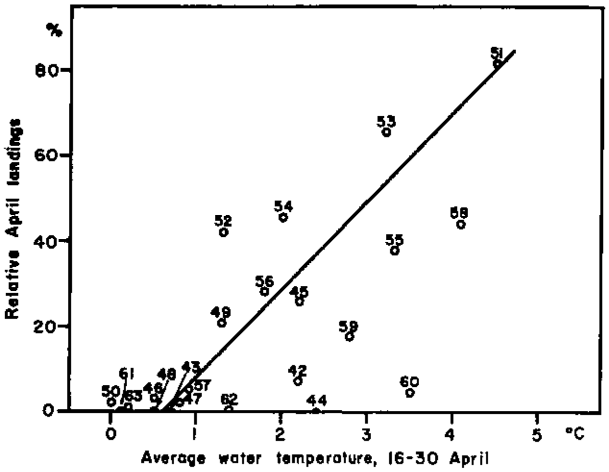
For 13 years, between 1942 and 1963, the date of the first catch of herring and the daily water temperatures before and after that date were compiled to show temperature conditions at the beginning of the fishery. Figure 4 shows that up to 6 days before the first catch of herring the average temperature increased rather slowly and erratically but remained below 1.0°C. This is followed by a more rapid and regular increase in temperature. The first catches were made when water temperatures were increasing rapidly and the average temperature on the day of the first catch of herring was 2.1°C with a standard deviation of 0.9°C.

For each day, before and after the start of the fishery, the temperatures indicated in Fig. 3 are averages based on 5 to 13 observations with a standard deviation varying between 0.9° and 1.6°C. The increase in temperature from one day to the next is not large enough, with such standard deviations, to show the temperature on one day as significantly different from the temperature on the following day. The important feature, however, is the trend in the temperatures, *i.e.*, the average increase with time, and the peculiarities which occur at the beginning of the fishery.

Figure 3 also shows that for the 20-day period after the start of the fishery there is a succession of increases in temperature to about 5.0°C. This rapid increase in temperature is undoubtedly due to advection of warmer waters from another area and not to warming *in situ*. The movement of ice during April on the Magdalen Shallows suggests that warmer waters are located to the northwest of Magdalen Islands. Present surface temperature charts produced three times a week by the Oceanographic Services of the Department of Mines and Technical Surveys support this suggestion. It seems then that the succession of temperature increases is brought about by intermittent drift of warmer waters into the Magdalen Islands area from the northwest. The few wind observations that we have



ig. 2. Herring landings (A) and average water temperature during the second half of April (B) from 1942 to 1963 in the Magdalen Islands area.



ig. 3. Relationship between relative April landings and the average water temperature during the second half of April for twenty years between 1942 and 1963. (42 means 1942)

from the area (these were taken twice a day at the same time the water temperatures were recorded) are inadequate to establish any relationship between wind direction and the succession of temperature increases.

Herring catch statistics are recorded on a monthly basis and hence do not show day to day variations in catch. However, it is a common occurrence and well known especially by fishermen, that within a fishing season several days of good fishing are followed by an equally long period of poor fishing. Biological studies show that the size and age of spawning herring decreases as the season advances. Day (1957*a*) described this phenomenon for spawning runs in Northumberland Strait, on the North Shore of Prince Edward Island and at Magdalen Islands. At Magdalen Islands, for example, the length and age of herring decreases from 30.0 cm and 5.7 years respectively in May to 26.8 cm and 3.8 years in June of the same season. This suggests a selective movement of herring into the spawning area. It is quite possible that this movement is not only selective but intermittent and that such a selective intermittent movement coincides with successive increases in temperature or with successive advection of warmer water. However, this must be considered only as a working hypothesis to explain the prespawning behaviour of herring in the Magdalen Islands.

The location of herring stocks in the Gulf of St. Lawrence during the late winter and early spring is poorly understood. No surveys for herring have been carried out during the January to April period. However, fishing for groundfish species (mainly cod) from the research vessel C.G.S. *A.T. Cameron* was carried on from 1960 to 1962 along the western edge of the Laurentian Channel, near Cape Gaspé at the entrance to Chaleur Bay, between Orphan Bank and Magdalen Islands, near Bird Rocks, and off Cape Breton. Although mesh sizes of the bottom trawls used were unsuitable for catching small fish, some herring were taken in more than half of the sets made. The best catches were made in depths of 48-66 fathoms, at temperatures around -0.7°C. The largest catches were made to the west and northwest of Magdalen Islands at the entrance of Chaleur Bay and this could presumably be the late winter habitat of herring which spawn either in Chaleur Bay area or in the Magdalen Islands in the spring

BEGINNING OF THE FISHERY AND ICE CONDITIONS

Observations made over several years at Entry Island show that, on the average, the first catches of herring are made 10 days after the disappearance of ice, when water temperatures are increasing rapidly. Water

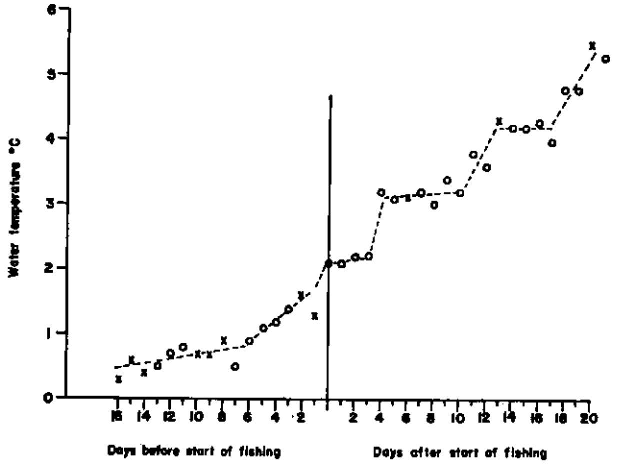


Fig. 4. Average surface temperature before and after the start of herring fishery. (x = temperatures for 5 years or less, o = temperatures for 6 years or more)

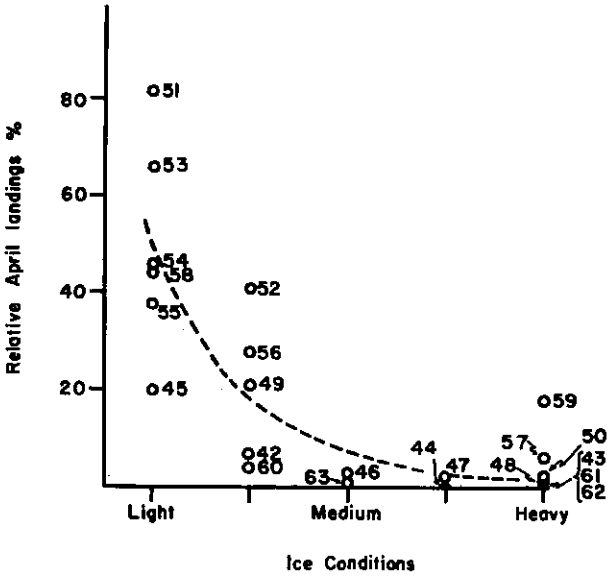


Fig. 5. Relationship of relative April landings of herring and ice conditions during the previous winters (51 means 1951). Ice conditions: "light" indicates that the quantity and extent of ice was smaller than usual with ice concentrated along the coasts and in bays, very little ice in the central Gulf; "heavy" represents a nearly complete coverage of ice in the central Gulf.

temperatures may increase rapidly, as in 1935, after the late disappearance of ice, or they may increase slowly, as in 1955, after the early disappearance of ice. The presence of ice, however, does not seem to prevent herring fishing, since in 1934, 1938 and 1940, the fishery started 1 to 3 days before the disappearance of ice. The average water temperature for those three years on the day of the first catch was 0.3°C as compared to the overall average of 2.0°C. In some years the fast ice disappears from the area but other ice fields drift into the area and prevent warming.

FORECASTING THE FISHERY FROM ICE CONDITIONS

Forward (1954, 1958) made a study of the distribution and movement of ice in the Gulf of St. Lawrence during March, April and May for the period 1940-57. For 1958 to 1962 inclusive the distribution of ice throughout the ice season was reported in Circulars issued by the Meteorological Branch of the Canadian Department of Transport (Anon., 1959; Archibald *et al.*, 1960, 1961 and 1962*a* and *b*). Figure 5 shows that the "relative" landings of herring in April are inversely related to severity of ice conditions during the previous winter. Total landings over the whole fishing season are not related to ice conditions.

During the winter, if air temperatures are below average, there are heavy ice conditions and a late spring break-up. However, the prevailing winds in the spring influence the break-up pattern. The presence of ice until late spring slows the warming of the waters and the herring fishery commences late in April or early in May as it did in 1943, 1944, 1947, 1948, 1950, 1957, 1959, 1961 to 1963. Light ice conditions are the result of above average air temperatures for the winter months. In this case, there is an early disappearance of ice, allowing an early warming of the waters in spring and a consequent early beginning of the herring fishery as in 1945, 1949, 1951, 1952, 1953, 1954, 1955, 1956 and 1958.

It is possible, therefore, by following air temperatures or ice conditions or both during the winter to make a reliable forecast of the starting date and of the "relative" catch of herring in April in the Magdalen Islands area.

SUMMARY

1. Variations in annual herring landings, herring landings in April and surface temperature conditions at Magdalen Islands, Quebec, were examined and showed that "relative" April landings were directly related to water temperatures during the second half of April.

TABLE 1. HERRING FISHERY AND WATER TEMPERATURES AT THE MAGDALEN ISLANDS

	Year	Water temp. 16-30 April	Date of arrival of herring	Landings Metric tons Total	April	Relative landings in April[a]
Cold	1946	0.5°C	29 April	7,648	210	3
	1948	0.5	30 April	7,066	1	0
	1949	1.3	24 April	6,798	1,415	21
	1950	0.0	30 April	8,230	136	2
	1962	1.4	30 April	15,443	13	0
	1963	0.2	29 April	14,590	106	1
Warm	1951	4.5	4 April	8,696	7,104	82
	1955	3.3	18 April	22,482	8,388	37
	1958	4.1	7 April	8,595	3,714	43
	1960	3.5	8 April	5,057	211	4

[a] Relative landings in April = $\frac{\text{April landings}}{\text{Total landings}} \times 100$

2. The arrival of herring or start of the herring fishery is preceded by an increase in water temperature to an average of 2.1°C on the day of arrival.

3. At the beginning of the fishery, the water temperature increases intermittently, suggesting that warmer waters drift into the area in "waves".

4. The intermittent pattern of movement of herring to the spawning area seems to coincide with the intermittent pattern of temperature increases.

5. From air temperatures and ice conditions during the previous winter it is possible to forecast the starting date of the Magdalen Islands herring fishery and the relative size of the landings in April.

REFERENCES

ANON. 1959. Aerial sea ice observing and reconnaissance program in the St. Lawrence River, the Gulf of St. Lawrence and the Strait of Belle Isle, 1958. Meteorological Branch, Department of Transport, Canada, Circular No.3273.

ARCHIBALD, D.C., M.N.MONSINGER and T.B.KILPATRICK. 1960. Aerial ice observing and reconnaissance St. Lawrence River, the Gulf of St. Lawrence and coastal waters of Newfoundland - 1959. Meteorological Branch, Department of Transport, Canada, Circular No.3417.

1961. Aerial sea ice observing and reconnaissance St. Lawrence River, the Gulf of St. Lawrence and coastal waters of Newfoundland, 1960. *Ibid.*, Circular No.3465.

1962*a*. Aerial sea ice observing and reconnaissance, St. Lawrence River, the Gulf of St. Lawrence, and coastal waters of Newfoundland - 1961. *Ibid.*, Circular No.3591.

1962*b*. Aerial ice observing and reconnaissance, Eastern Canadian Seaboard, 1962. *Ibid.*, Circular No.3768.

DAY, L.R. 1957*a*. Populations of herring in the southern Gulf of St. Lawrence. *Bull. Fish. Res. Bd. Canada*, No.111, p.121-137.

1957*b*. Vertebral numbers and first-year growth of herring (*Clupea harengus* L.) in relation to water temperature. *Ibid.*, p.165-176.

FORWARD, C.N. 1954. Ice distribution in the Gulf of St. Lawrence during the break-up season. Geographical Bulletin 6, p.45-84, Ottawa.

1958. Ice conditions in the Gulf of St. Lawrence during the spring seasons 1953-1957. Geographical Branch, Department of Mines and Technical Surveys, Canada, Geographical Paper No.16, 13 p.

LAUZIER, L. 1952. Recent water temperatures along the Canadian Atlantic coast. *Fish. Res. Bd. Canada, Atlantic Prog. Rept.*, No.53, p.5-7.

SINDERMAN, C.J. 1958. An epizootic in Gulf of St. Lawrence fishes. Transactions 23rd North American Wildlife Conference (March 1958), p.349-360.

TIBBO, S.N. and T.R.GRAHAM. 1963. Biological changes in herring stocks following an epizootic. *J. Fish. Res. Bd. Canada,* 20(2): 435-449.

E-4

THE INFLUENCE OF WATER MASSES OF THE NEW ENGLAND AND NOVA SCOTIA SHELF ON THE FORMATION OF COMMERCIAL CONCENTRATIONS OF HERRING

By

V.A. Bryantsev[1]

ABSTRACT

Three water masses govern the distribution and spatial changes of T-S characteristics of the shelf waters. Their peculiarities were ascertained by the analysis of the data collected during the 1960-1962 research cruises organized by ATLANTNIRO.

The most fish-abundant shelf areas of herring fisheries are situated in the regions of the outflow of Labrador waters on the bank slopes, in particular those of Georges and Banquereau Banks. The greatest values of food biomass are observed on the bank slopes in the zone of double border along the 50-100 m isobaths where the borders of Labrador and coastal waters lie in close proximity on the one side and Gulf Stream bottom waters on the other. The reduction of the zone of two borders resulting from the summer transformation consequently effects the reduction of food migration routes of herring in the Georges Bank area. Wind conditions, by shifting the borders of water masses, substantially influence the efficiency of fishing operations. By estimating the value of projection of wind on the SW-NE line it is possible to forecast the relative changes of catches 24 hr in advance.

1. The surface layer within the shelf is occupied by the coastal water mass. It is characterized by a relatively low salinity (the extreme value is assumed to be 30.00 ‰) and rather wide changeability of temperature, from 4°C in winter to 16°C in summer.

2. Outside the shelf the coastal waters border upon the waters of the Gulf Stream. The extreme values of the latter are as follows: salinity (maximum in the shelf area) is 36.00 ‰; temperature (also maximum in the area) is 15°C in winter and 25°C in summer. Besides, the waters of the Gulf Stream that extend within the shelf along the deep-water valleys at 150-200 m are characterized by the temperature 7 to 8°C and salinity from 33.50 to 35 ‰. These characteristics result from mixing of Gulf Stream waters with Labrador waters situated immediately above. We call this water mass a bottom modification of the Gulf Stream waters.

3. By "Labrador waters" we refer to an intermediate cold layer of the water mass that extends along the shelf from Newfoundland to Georges Bank and is formed by the Polar waters flown into this area with the branches of the Labrador Current. On the shelf these waters are situated beneath the coastal waters and above the bottom modification of the Gulf Stream waters within the depth range of 50-75 to 150-200 m. The extreme values of this water mass are as follows: temperature, (minimum for the shelf), -1°C, salinity, 33.00 ‰.

Of the three water masses the Labrador water mass presents the greatest interest. It was defined by the analysis of the results of the hydrological observations carried out by ATLANTNIRO expeditions during December 1960 - February 1961. The data were treated in accordance with a general analysis method suggested by V.T. Timofeev. The following extremes were used:

Coastal water mass	T°C	S ‰
Coastal water mass	4	30.00
Labrador water mass	-1	33.00
Gulf Stream waters	15	36.00

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[1] Atlantic Research Institute of Marine Fisheries and Oceanography (ATLANTNIRO), Kaliningrad, USSR.

These values were used for the construction of T-S nomograms on which the tabulations of all hydrological stations at 0.50, and 100 m layers were plotted. Then, the per cent volume of each water mass was indicated on the map of the area near each station for each of the above layers, and isolines of these values were drawn.

The isolines of 50% volume of Labrador water (the edge of the water mass according to the terms of the method) showed that this water mass was flowing continuously at the 100 m layer, from Newfoundland along the whole shelf area far to the southwest. Judging by the patterns of the 0 and 50 m layers in the Banquereau and Georges Bank areas on the map, there should be an outlet of these waters on the slopes of the above banks. It is in these areas that the Soviet fishing fleet is engaged in an intensive herring fishery.

In summer 1962, more detailed studies of the distribution of water masses were initiated in the Georges Bank fishing area. An attempt was also made to evaluate the degree of changeability in the distribution of waters affected by various factors. The investigations have revealed that the coastal waters occupy the depth ranging from 0 to 50-75 m; the cold Labrador waters occupy the layer from 50-75 m to 150-200 m, and in the Bay of Fundy below 150-200 m the bottom modification of the Gulf Stream waters is observed.

Due to the peculiarities of the bottom relief, the upper edge of the intermediate cold layer over the bottom at the depth of 50-75 m, should wedge out and form a demersal border with the adjacent coastal waters; another demersal border is formed with bottom waters of the Gulf Stream at 150-200 m. The data of observations have supported such delimitation of Labrador waters (Fig. 1). So, in the demersal layer along the slopes of Georges Bank there is something like a narrow inflow of cold waters, bordering upon the coastal waters on the shallower side (50-75 m), and upon the bottom modification on the side of greater depths (150-200 m). However, this cold inflow is not traced at these depths on the southern slopes of the bank. This is explained by the fact that the coastal waters, warm in summer, and the surface warm waters of the Gulf Stream actively transform the cold bottom layer. The degree of such transformation increases with the intensification of the summer heating. Thus, if in May the cold tongue occupies all the slopes, including part of the southern slope, then in late August it is not observed even on the eastern slope.

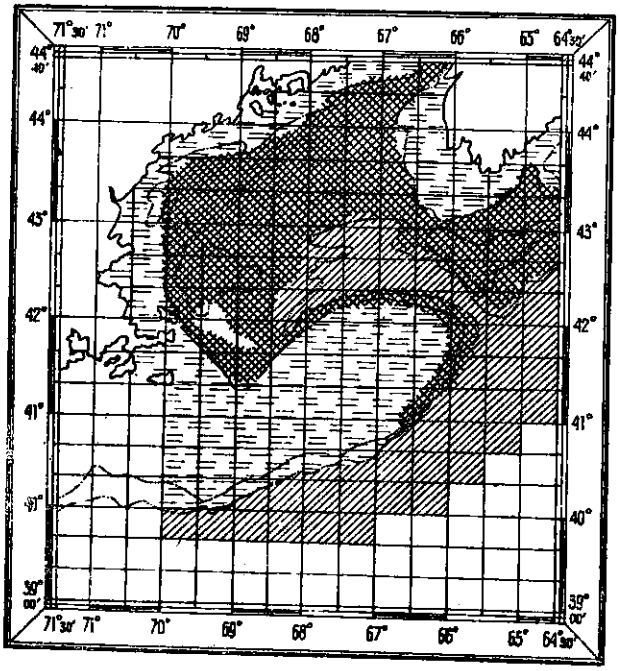

Fig. 1. Near-bottom distribution of water masses. Survey, 5-25 June, 1962.

////	Gulf Stream waters
▩	Labrador waters
═	Coastal waters

Such a specific area of two bottom borders is normally characterized by considerable temperature gradients. And it is in this area that, according to the planktonic surveys, the greatest quantities of food plankton gather (Fig. 2). It follows from a comparison of the maps of distribution of water masses and the statistical chart of fishery in 1962 (Fig. 3) that through the whole period of food migrations (March - August) herring form concentrations mainly in the zone of the two bottom borders. Periodically, moving along this zone, herring reduce their route as the cold water flow that forms this zone is getting shorter with the season. In May, herring concentrations may be observed on all the slopes, including part of the southern and the whole southeast slopes, whereas in June-July herring do not move beyond the southeast slope. In

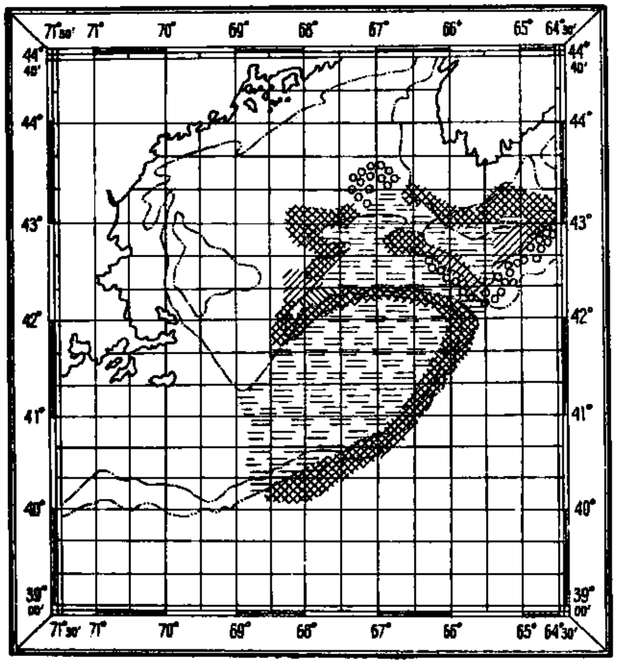

Fig. 2. Distribution of plankton, 29 June - 3 July 1962.

▨ *Calanus* from 100 to 250 mg/m^3

oooo *Calanus* to 500 mg/m^3 (phytoplankton in small numbers)

=== Phytoplankton (*Calanus* in small numbers)

//// *Calanus*, Euphausiidae, *Themisto*.

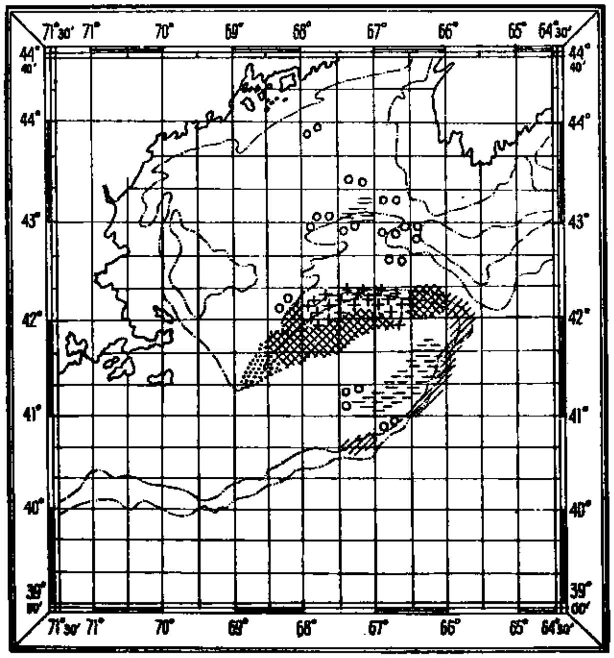

Fig. 3. Operations of fishing fleet in May-August 1962.

++++ Areas of continued fishing operations (92-50% of time)

▨ Areas of periodic fishing operations (50-40% of time)

Areas of seasonal fishing operations. === May-June;

//// June-July; :::: August.

oooo Occasional fishing operations (>5% of time)

August they can, but rarely, be encountered on the eastern slope and continue their migrations along the northern and north-west slopes only. So, the data on the degree of summer transformation of the cold tongue on the eastern and southeast slopes are absolutely indispensible for making forecasts for the fishing fleet.

Apart from the seasonal changeability, the variations of the Labrador water borders were found to be caused by wind. The lack of many days' observations did not permit establishment of the quantitative relationships between the changes of the velocity and direction of wind and the location of the water mass border. Therefore, in order to determine the influence of wind, we had to apply an indirect method of the analysis. The direct changes in a day's catch per net were analysed together with the changes of wind. The former value was taken for March in the Georges Bank area and for April in the Banquereau area. During these months, herring in both areas remained within a limited area, thus making the catch data most indicative.

In order to evaluate wind effects we assumed as a working hypothesis the theory of coastal wind-induced tidal phenomena. In accordance with this theory the water movement in the northern hemisphere is directed to the right of the wind direction. Taking into consideration the fact that the shoreline in the shelf area lies in SW-NE direction, the SW wind will drive waters in the seaward direction and the NE wind will drive them shoreward. This will be accompanied by the changes of the borders of water masses on the slopes of the banks.

It was repeatedly observed during fishing operations that the catches increased in the time of SW winds and decreased in the time of NE winds. This allows us to assume the positive effect of the former and the negative effect of the latter. Taking the SW- NE direction for the 0° to 180° line and by reducing this line, and by means of projecting, the directions of wind of all bearings, we shall obtain the expression of wind effect:

$$P = T \times V \times \text{Cos}\ (\alpha + 135°),\ \text{where}$$

P - projection of wind on the line
T - time
V - velocity of wind
α - direction of wind

Then, the total "P" value for a given space would be

$$P = \frac{\Sigma\ T \times V \times \text{Cos}\ (\alpha + 135°)}{n}$$

where n - number of observations at individual points.

To simplify computations the P values were tabulated (in conventional units).

TABLE 1.

Direction of wind		Cos	Value of V × Cos (α + 135°) for units of Beaufort scale							
Bearings	Degrees :	(α + 135°) :	0	1	2	3	4	5	6	7
N	0	-0.71	0	-0.71	-1.4	-2.1	-2.8	-3.6	-4.3	-5.1
NNE	22.5	-0.92	0	-0.92	-1.8	-2.8	-3.7	-4.6	-5.5	-6.4
NE	45	-1.00	0	-1.00	-2.0	-3.0	-4.0	-5.0	-6.0	-7.0
ENE	67.5	-0.92	0	-0.92	-1.8	-2.8	-3.7	-4.6	-5.5	-6.4
E	90	-0.71	0	-0.71	-1.4	-2.1	-2.8	-3.6	-4.3	-5.0
ESE	112.5	-0.38	0	-0.38	-0.8	-1.1	-1.5	-1.9	-2.3	-2.7
SE	135	0.00	0	0.00	0.0	0.0	0.0	0.0	0.0	0.0
SSE	157.5	0.38	0	0.38	-0.8	1.1	1.5	1.9	2.3	2.7
S	180	0.71	0	0.71	1.4	2.1	2.8	3.6	4.3	5.0
SSW	202.5	0.92	0	0.92	1.8	2.8	3.7	4.6	5.5	6.4
SW	225	1.00	0	1.00	2.0	3.0	4.0	5.0	6.0	7.0
WSW	247.5	0.92	0	0.92	1.8	2.8	3.7	4.6	5.5	6.4
W	270	0.71	0	0.71	1.4	2.1	2.9	3.6	4.3	5.0
WNW	292.5	0.38	0	0.38	0.8	1.1	1.5	1.9	2.3	2.7
NW	315	0.00	0	0.00	0.00	0.0	0.0	0.0	0.0	0.0
NNW	337.5	-0.38	0	-0.38	-0.8	-1.1	-1.5	-1.9	-2.3	-2.7

The values of wind strength in the table range from 0 to 7 (Beaufort scale) because if the wind is stronger the fishing operations are discontinued. The wind values were taken for the given periods (March and April) from the daily weather maps; then the mean wind values were computed for the points Boston, Halifax and Sable Island. The computed P values for each day and average catches in kilograms per net were then tabulated for both areas (Table 2). In this latter table the increased values of P and catches are marked by (+) and the decreased values by (-). A comparison of the trends of both characteristics makes it possible to infer that they coincide (in the table the coincidence is marked by C and the lack of coincidence by N) in 15 cases out of 21 for the Georges Bank area and in 17 cases out of 21 for the Banquereau area. Thus it follows that the percentage of coincidence is 71% in the first case and 81% in the second.

Since the wind values were registered at 3 pm Moscow time, *i.e.* at 20 hr local time of the day before, the P value should be considered as shifted 24 hr ahead.

TABLE 2.

Georges Bank (March 1962)							Banquereau Bank (April 1962)						
Date	P	Avg. catches in kg per net	P trend	Trend of catches	Comparative trend	Percentage coincidence	Date	P	Avg. catches in kg per net	P trend	Trend of catches	Comparative trend	Percentage of coincidence
1	-2.4	8.0					1	1.8					
2	-1.1	8.0	+	0			2	-1.4		-			
3.	-0.7	-	+				3	1.0		+			
4	-1.6	-	-				4	0.0	62.5	-			
5.	-2.3	14.5	-				5	2.0	100.0	+	+	C	
6	-3.7	10.0	-	-	C		6	1.1	17.6	-	-	C	
7	-2.1	0.0	+	-	N		7	1.4	44.5	+	+	C	
8	-3.4	-	-				8	2.3		+			
9	-1.8	83.5	+				9	1.4		-			
10.	-0.8	86.9	+	+	C		10	2.5	37.5	+			
11	-1.8	29.8	-	-	C	71%	11	1.4	47.2	-	+	N	81%
12	-2.8	17.8	-	-	C		12	0.1	13.3	-	-	C	
13.	1.4	26.1	+	+	C		13	-1.8	25.0	-	+	N	
14	-3.7	42.1	-	+	N		14	-2.1	22.3	-	-	C	
15	-2.1	12.1	+	-	N		15	2.4	-	+			
16	1.9	25.1	+	+	C		16	3.0	148.7	+	+	C	
17	1.8	9.0	-	-	C		17	0.0	-	-			
18	0.0	15.3	-	+	N		18	-0.7	98.4	-	-	C	
19	-0.8	0.7	-	-	C		19	0.9	66.5	+	-	N	
20	1.0	0.7	+	0			20	-1.0	42.2	-	-	C	
21	-0.6	0.0	-	-	C		21	-0.9	49.2	+	+	C	
22	-1.8	0.0	-	0			22	1.8	84.4	+	+	C	
23	-3.0	0.0	-	0			23	1.4	68.5	-	-	C	
24	-2.7	4.2	+	+	C		24	0.0	15.6	-	-	C	
25	-2.3	0.0	+	-	N		25	-0.5	9.1	-	-	C	
26	-1.4	7.4	+	+	C		26	-0.4	18.8	+	+	C	
27	-2.8	1.6	-	-	C		27	0.4	21.8	+	+	C	
28	-2.1	9.9	+	+	C		28	1.4	34.1	+	+	C	
29	0.0	12.8	+	+	C		29	1.3	15.8	-	-	C	
30	1.6	56.0	+	+	C		30	-0.2	17.2	-	+	N	
31	2.0	39.7	+	-	N								

In this way the wind, by changing the borders of water masses, influences the behaviour of herring and, consequently, the efficiency of the herring fishery. By estimating, on the basis of wind data, the values of projection on the SW-NE line, one may forecast the expected relative decrease or increase in catches for the next 24 hr.

CONCLUSIONS

1. The most fish-abundant shelf areas of herring fisheries are situated in the regions of the outflow of Labrador waters on the bank slopes, in particular those of Georges Bank and the Bánquereau area.

2. The greatest values of food biomass are observed on the bank slopes, in the zone of double border along the 50-100 m isobaths, where the borders of Labrador and coastal waters on the one side lie in close proximity to the Gulf Stream bottom waters on the other.

3. The reduction of the zone of two borders resulting from the summer transformation consequently effects the reduction of food migration routes of herring in the Georges Bank area.

4. Wind conditions, by shifting the borders of water masses, substantially influence the efficiency of fishing operations. By estimating the value of projection of wind on the SW-NE line it is possible to forecast the relative changes of catches 24 hr in advance.

REFERENCES

DOBROVOLSKY, A.D. 1961. On the definition of water masses. *Oceanology*, No. 1, Moscow.

KHANAICHENKO, N.K. 1947. On the types of water masses transformation, *Meteorology and Hydrology*, No. 1.

MARTY, JU. JU. 1961. Fishery and some problems of oceanology. *Oceanology*, No. 5, Moscow.

TIMOFEEV, V.T. 1948. The method of isopycnic analysis of mixing and transport of water masses. *Trudy ANII*, vol. 196, Glavsevmorput.

E-5

EFFECTS OF ENVIRONMENT ON SEVERAL DISEASES OF HERRING FROM THE WESTERN NORTH ATLANTIC

By

Carl J. Sindermann[1]

ABSTRACT

Several diseases and parasites of herring (*Clupea harengus harengus*) from the western North Atlantic have been investigated during the past eight years. Two important parasites of immature herring, a myxosporidian (*Kudoa clupeidae*) and a larval trematode (*Cryptocotyle lingua*) were found to be distributed discontinuously in the Gulf of Maine, occurring with greatest abundance in the western coastal area. The occurrence of both parasites seems directly related to summer sea water temperature. Study of a systemic disease of herring caused by the fungus *Ichthyosporidium hoferi* has disclosed apparent periodicity of epizootics and has provided experimental evidence for the importance of high spore concentrations in the environment to abundance and severity of the disease in herring. Since parasites and their abundance are often characteristic of particular age groups of geographic areas, information about herring stocks and their movements has been obtained.

INTRODUCTION

Among the biological features of the environment that affect the abundance of marine species, disease is of great significance. This can be best demonstrated in inshore sedentary species, but applies to pelagic or demersal species as well. Few pelagic species have been adequately examined for diseases, but during the past decade the U.S. Bureau of Commercial Fisheries Biological Laboratory, Boothbay Harbor, Maine, USA, has carried on a continuing study of diseases and parasites of Atlantic herring, *Clupea harengus harengus*. Attention was first directed to disease in this species because of recurring epizootics of a systemic fungus pathogen (*Ichthyosporidium hoferi*), the most recent of which occurred in the Gulf of Saint Lawrence in 1954-55 and the Gulf of Maine in 1947. The fungus disease has been studied continuously at the Boothbay Harbor Laboratory since 1947 and other diseases and parasites of herring have also been examined.

Many extrinsic and intrinsic factors combine to determine the incidence, distribution, and effect of disease on herring populations. Extrinsic factors include such environmental influences as temperature, salinity, availability of vectors or alternate hosts, and infection pressure (the relative numbers of infective organisms present in the environment at a given time). Intrinsic factors are those which determine susceptibility to disease, including individual and population levels of natural or acquired resistance, and nutritional state of the fish.

The isolation of specific factors in one or the other category is difficult, since many have aspects that fall in both -- for example, immune responses in poikilothermic animals are intrinsic, but are clearly influenced by environmental temperature. Despite some overlap, an attempt has been made to confine this paper to examples of extrinsic or environmental factors that affect certain diseases and parasites of herring in the western North Atlantic. Only three diseases, "pigment spot" caused by metacercariae of the trematode *Cryptocotyle lingua*, myxosporidian disease caused by *Kudoa clupeidae*, and fungus disease caused by *Ichthyosporidium hoferi*, will be considered here, and of these only those aspects pertinent to environmental influences will be included.

PIGMENT SPOT DISEASE

Ecological information is available for the larval trematode *Cryptocotyle lingua*, an important parasite of western North Atlantic herring. The worm occurs as a metacercaria in the skin and flesh. It's life cycle in the Gulf of Maine (Fig. 1) includes the common periwinkle *Littorina littorea* as a first intermediate host and the gull *Larus argentatus* as the definitive host. Herring are

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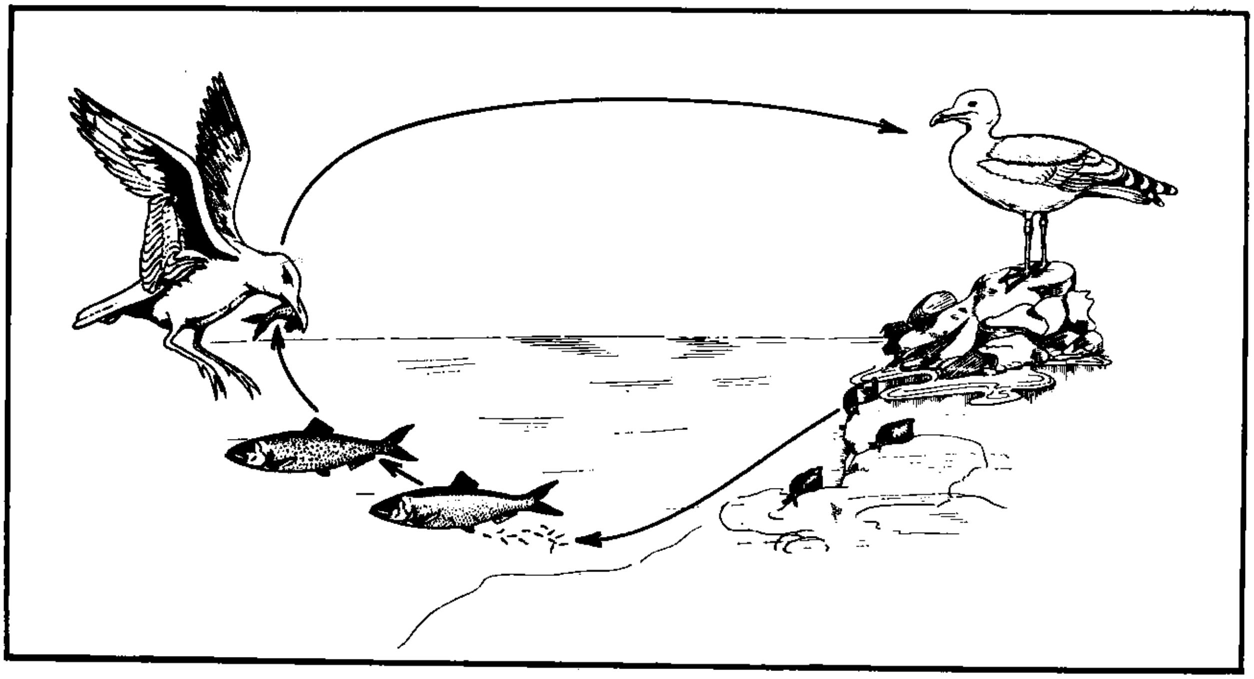


Fig. 1. Life cycle of *Cryptocotyle lingua* in northern New England.

important second intermediate hosts in this region of the western Atlantic. Examination of immature herring from coastal waters of the Gulf of Maine in 1961, 1962 and 1963 disclosed marked geographic variation in intensity of parasitization by *Cryptocotyle* metacercariae. Degree of parasitization was determined according to the following criteria: uninfected; lightly infected (1-5 metacercariae); moderately infected (6-50 metacercariae); heavily infected (over 50 metacercariae). A parasite concentration index (Sindermann 1953) was obtained for each sample by ranking each individual according to the following scale: uninfected (0), lightly infected (1), moderately infected (2), and heavily infected (3). Summation of ranks for each sample of 50 fish provided a concentration index for the sample. Numbers of samples examined were 20 in 1961, 26 in 1962 and 30 in 1963. The northern New England coast was divided into major areas with the following boundaries: (A) Isles of Shoals eastward to Cape Small; (B) Cape Small to Matinicus Island, (C) Matinicus Island to Mount Desert Island; (D) Mount Desert Island to West Quoddy Head; (E) West Quoddy Head to the Saint John estuary. Concentration indices for all samples in each area were averaged in each year to obtain a single index for the area and year (Fig. 2). Parasite concentration indices decreased sharply from west to east in each year.

Since parasitization of herring depends on availability of infective cercariae, a study was made in the summer and early autumn of 1963 of incidences of *Cryptocotyle* larvae in *Littorina*, the first intermediate host. Samples of 50 snails each were collected in the high tide zone from as many locations as possible. Infection was determined by crushing the snail and examining the digestive gland. Results grouped by major coastal areas are presented in Fig. 3. Wide variations in incidences within areas were noted, but no major variations on a coastwide basis were found. This was quite different from the geographic change in abundance of metacercariae in herring just mentioned and suggested that other environmental factors were important for completion of the parasite life cycle. Earlier studies (Sindermann and Rosenfield 1954*b*; Sindermann and Farrin 1962) demonstrated a direct relationship between temperature and cercarial emergence. Emergence declined with lowered sea water temperatures and ceased when temperatures fell below 10°C. Examination of coastal temperatures in July, 1963 (Fig. 4) suggests that the northern New England coast may be a critical zone for the parasite. Easternmost areas, with colder summer sea temperatures, were characterized by much lower parasite indices in herring. Factors other than temperature may be operative, since earlier experimental studies demonstrated that cercarial emergence was also inhibited by salinities below 18 $^{o}/oo$ (Sindermann and Farrin, *op. cit.*). However, no east-west change in salinity was observed in hydrographic data for 1963 that would be great enough to account

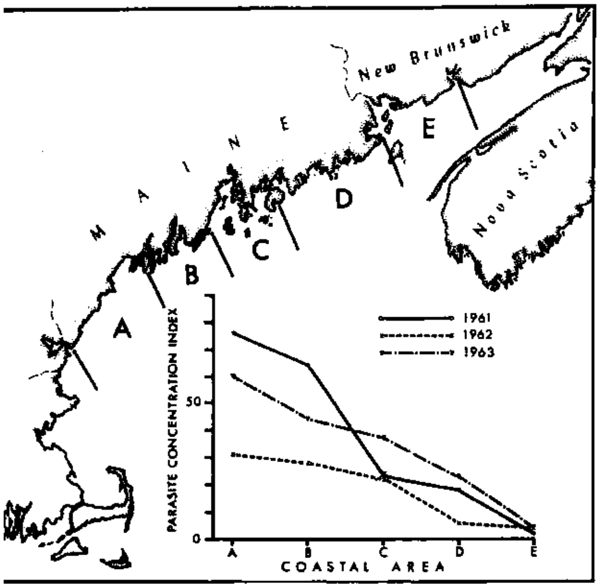
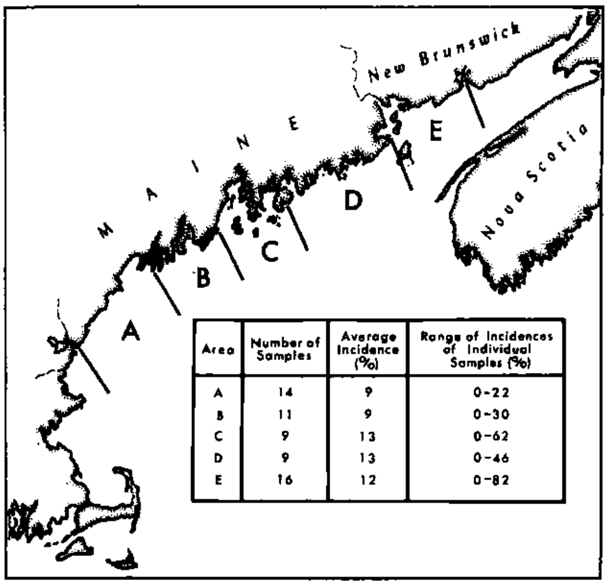


Fig. 2. Coastal sampling areas and concentration indices of *Cryptocotyle lingua* metacercariae in immature herring 1961-63.



Area	Number of Samples	Average Incidence (%)	Range of Incidences of Individual Samples (%)
A	14	9	0-22
B	11	9	0-30
C	9	13	0-62
D	9	13	0-46
E	16	12	0-82

Fig. 3. Incidences of *Cryptocotyle* larvae in *Littorina littorea* from the high tide zone along the northern New England coast, 1963.

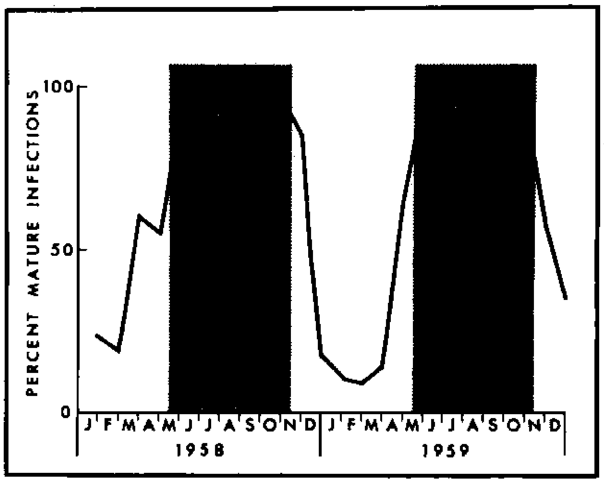


Fig. 4. Periods of the year when immature herring are most abundant in inshore waters (shaded zones) and average monthly maturity of snail infections (line graph). Mature infections are diagnosed by findings of fully-formed active cercariae in crushed snails.

for observed geographic changes in parasite incidences. Based on experimental findings, however, it would be possible for local changes in salinity to enhance or reduce effects of temperature on cercarial emergence.

The evidence suggests a relationship between environmental temperature in summer and degree of parasitization of herring by *Cryptocotyle*. There are of course still many questions to be answered. No information is available on possible geographic variations in degree of parasitization of the definitive host (the gull). Also, local variations in temperatures occur that could produce local anomalies in parasite abundance. For example 1963 hydrographic stations in the upper Penobscot Bay have disclosed July temperatures above 15°C, even though the general coastal area is described as a 10° to 15°C zone.

Comparisons of herring movements and availability of infective cercariae are striking. Immature fish are most abundant in inshore waters from May to November. This is the period when most snail infections are mature and producing cercariae, and maximum opportunity for parasite transfer exists. Results of a two-year study on one island off the central Maine coast are presented in Fig. 5. When cercariae are present in greatest numbers in inshore waters the susceptible second intermediate hosts are also present in abundance.

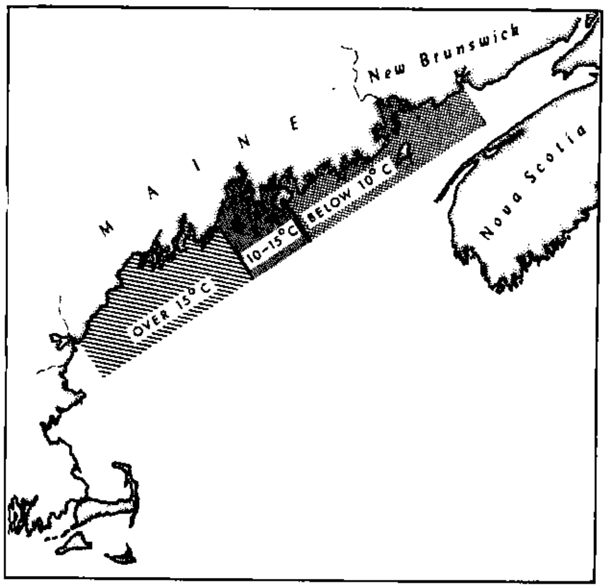


Fig. 5. Average distribution of summer sea water temperatures along the northern New England coast in 1963.

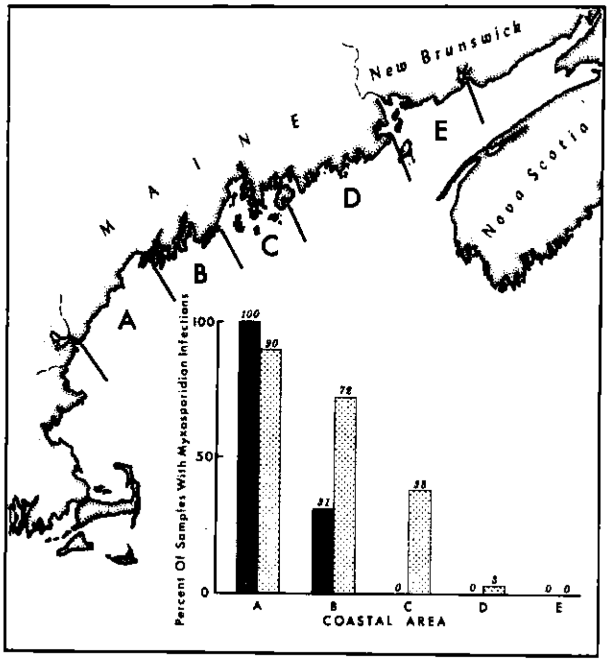


Fig. 6. Percent of samples of one-year-old (horizontal bar) and two-year-old (stippled bar) herring in which myxosporidia (*Kudoa clupeidae*) were present during the period 1955-63. Each sample consisted of 50 fish, and total samples of one-year-old fish were 112, and of two-year-old fish 242. Equal numbers of samples were not obtained in each year or for each area.

MYXOSPORIDIAN DISEASE

Another important parasite of western North Atlantic herring is the myxosporidian *Kudoa clupeidae*. This protozoan occurs in intramuscular cysts in immature herring. Infections are acquired in the early months of life and have been shown to persist in aquarium-held herring for two years, but were rarely found in adult fish (Sindermann and Rosenfield, 1954*a*; Sindermann, 1961). The geographic distribution of the parasite in Gulf of Maine herring has been studied since 1955. Infected fish were common along the western Maine coast, but were almost non-existent on the eastern Maine coast. Average incidences in the major coastal areas already described are presented in Fig. 6. Infections have not been found in one-year-old fish east of Matinicus Island. Infected two-year-old fish, with a single exception (one fish in a sample from Grand Manan Island in 1963) have not been found east of Mount Desert Island. The fect that infections were carried annually as far east as Mount Desert Island by eastward movement of infected two-year-old fish, while the disease organism did not occur east of Matinicus Island in one-year-old fish, indicates that some limiting influence on the disease is operative. While other environmental factors may be important in determining the discontinuous distribution of *Kudoa*, temperature may exert a critical influence. Decreasing summer sea water temperatures from west to east along the coast (Fig. 4) correlate positively with parasite incidences, with Matinicus Island the general eastern limit of temperatures in excess of 15°C and the eastern boundary of infections in one-year-old fish.

Another indication of possible influence of temperature on the distribution of *Kudoa* is seen in the larger picture of its occurrence in herring of the western North Atlantic. Herring occur from Virginia northward to Labrador, with centers of abundance in the Gulf of Maine and the Gulf of Saint Lawrence. Although sampling has been concentrated in the Gulf of Maine, herring from the Rhode Island and New Jersey coasts, the Nova Scotia coast and the Gulf of Saint Lawrence have been examined since 1955. Infections were common in herring from Rhode Island and New Jersey, were absent on the Nova Scotia coast, but reappeared in the southern Gulf of Saint Lawrence where, because of shallow water, summer temperatures often reach 20°C. The parasite occurred in waters that characteristically exceed 15°C in summer and did not occur in waters with lower summer maximum temperatures (Fig. 7).

It is possible, of course, that factors other than environmental temperature may be important in determining the geographic distribution of *Kudoa clupeidae* in herring, or that temperature may act indirectly by influencing the distribution

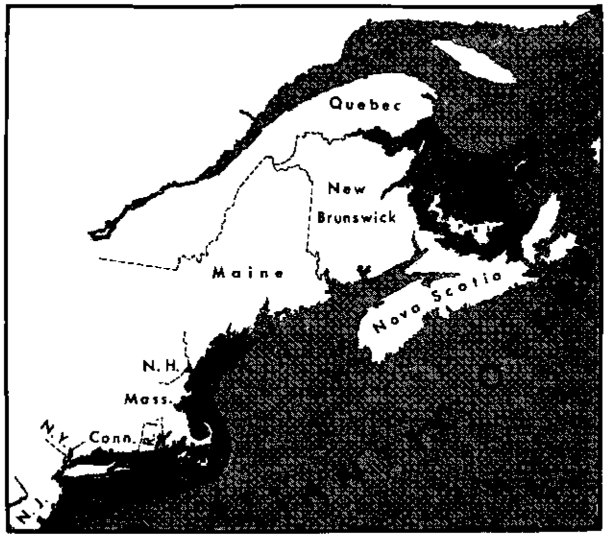


Fig. 7. Coastal areas of the western North Atlantic (heavy shading) where summer sea water temperatures usually exceed 15°C and where *Kudoa clupeidae* occurs in immature herring.

of transfer or other hosts. The Myxosporidia are usually considered one-host parasites, but the possibility of an invertebrate intermediate host needs further exploration. If another marine species plays a role in determining abundance or distribution of *Kudoa* in herring, temperature may operate indirectly.

FUNGUS DISEASE

Another disease of Atlantic herring with interesting environmental relationships is that caused by a systemic fungus pathogen *Ichthyosporidium hoferi*. At least six epizootics of this disease have occurred in herring during the past 70 years, resulting in widespread mortalities and affecting abundance of the species in the western North Atlantic (Sindermann, 1963). Individual variations in susceptibility to the pathogen have been demonstrated (Sindermann, 1958) and an explanation of changes in disease abundance based on intrinsic factors such as changes in population susceptibility and extrinsic factors such as infection pressure has been proposed.

Infection pressure appears to be an ecological factor of significance in determining outbreaks of *Ichthyosporidium*. Transmission from fish to fish is effected by heavy-walled spores which have been found to survive in sea water cultures for over six months with no loss of viability. Spores have been demonstrated in inshore bottom sediments during an epizootic. Since during an outbreak peak an average of one-fourth of the population is infected, and since most infected fish die either from acute or chronic infections, the spore load in mortality areas can be very high.

Knowledge about the effects of increasing infection pressure on occurrence of the fungus disease in susceptible hosts has been obtained by experimental exposures and experimental epizootics created in aquarium populations of immature herring. Massive and repeated exposures were necessary to achieve infection in two-year-old fish (Table 1). Beyond a critical dosage level, acute as well as subacute or chronic infections resulted. With experimental demonstration of the effect of increasing spore dosage or infection pressure on prevalence and severity of the disease, a large scale experimental epizootic was created in a laboratory population of 2,000 one-year-old herring. Spore dosage of 2×10^5 spores on each of four consecutive days resulted in infection of 23% of the population--8% acute and 15% subacute. The disease was terminal in all acute cases within 30 days. Chronic or subacute infections resulted in death of all but very light cases within six months. As with most aquarium studies of this kind, occasional deaths due to causes other than fungus disease occurred in experimental and control groups during the 18 month observation period, but these were infrequent enough so that they would not materially alter the findings. At the termination of the experiment (18 months after initial exposure) all surviving individuals were examined; only three lightly infected fish were found.

Experimental results agree with findings during the last outbreak in Gulf of Saint Lawrence herring (Sindermann, 1958). Twenty-seven percent of all fish sampled in that Gulf during the epizootic peak were infected, the ratio of acute to subacute being approximately one to two. Disease incidence was very low when spawning fish first appeared on the coast in late April, but mortalities due to acute infections began about one month after inshore migration. Deaths continued at a low level throughout the summer, due to subacute infections. A related observation of the effect of infection pressure concerned the alewife, *Alosa pseudoharengus*. This species has been reported, principally on the basis of histological evidence, to be less susceptible to *Ichthyosporidium*, by Sindermann and Scattergood (1954). During the recent epizootic in herring, alewives present in inshore waters also became infected, in sufficient numbers so that mortalities were observed and reported.

TABLE 1. SPORE DOSAGE AND EXPERIMENTAL INFECTION RATE IN TWO-YEAR-OLD HERRING. (Experimental groups of 50 fish each, from a laboratory population previously found to be free of fungus disease, were maintained in 250 gallon sea water tanks. Spores were obtained from naturally infected fish and tested for viability by culturing in Sabouraud-serum agar. Spore suspensions were added to food just before the fish were fed. The experiment was terminated at 90 days, and surviving fish examined for gross or histological evidence of disease).

Exposure and Dosage Schedule	Observations
2×10^5 spores in single exposure	No gross or histological evidence of disease after 90 days.
2×10^5 spores on each of 3 consecutive days	After 90 days, 4 of 50 fish had subacute or chronic infections; spores few and encapsulated; other fish uninfected.
2×10^5 spores on each of 5 consecutive days	After 20 days, 1 fish dead with massive acute infection; extensive tissue necrosis; little host response. After 90 days, 10 of remaining 49 fish exhibited subacute or chronic infections of varying severity; 39 fish uninfected.
2×10^5 spores on each of 7 consecutive days	After 15 to 30 days, 5 fish dead with massive acute infections. After 90 days, 12 with subacute infections of varying severity; 33 fish uninfected.
Control (no spore exposure)	No gross or histological evidence of disease.

DISCUSSION AND SUMMARY

The distribution and abundance of many parasites of herring vary geographically to such an extent that several have been used as "natural tags" in migration and population studies. Incidences of encysted larval cestodes (Trypanorhyncha) and nematodes (Anisakinae) have been examined over much of the range of herring in the western North Atlantic (Sindermann, 1961), and have been found during eight years of sampling to occur with characteristic frequencies in different geographic areas. Undoubtedly the presence and abundance of infected first intermediate and definitive hosts for these worms plays a role in determining parasitization of herring, although environmental variables might also be of importance.

Age of the herring is related to the kinds and numbers of parasites found. Certain parasites are characteristic of only very young fish, others only of older fish, while still others occur in herring of all ages. Adult cestodes (Pseudophyllidea) and a sporozoan (*Plistophora* sp.) occur only in herring younger than six months; the myxosporidian *Kudoa clupeidae* occurs only in immature fish; larval cestodes (*Trypanorhyncha*) occur only in fish older than one year; while the fungus *Ichthyosporidium hoferi* may occur in fish of any age. Diet, proximity to other hosts in the life cycle, segregation by size in schooling, and increasing immunity with age may all be of importance to the changing spectrum of disease with age. Research in the USSR that can best be described as ecological parasitology of fishes has been admirably summarized by Dogiel *et al.* (1958). Changes in parasite fauna of marine fishes with age and geography have been documented for a number of European species, including White Sea and Baltic herring.

Other diseases of herring, particularly those of bacterial etiology, deserve intensive ecological and laboratory study. Systemic bacterial infections are not uncommon in immature herring, and have been responsible for mass mortalities in experimental tanks. Artificially high temperatures, near the upper limit of tolerance of herring, were accompanied by extensive mortalities of experimental fish exhibiting characteristic symptoms of bacterial disease described by Sindermann and Rosenfield (1954*a*) as "bacterial tail rot". Snieszko (1962) has demonstrated that furunculosis and other bacterial diseases of fresh-water fishes can be influenced to a marked degree by temperature, and that even slight increases in temperature can increase mortality rates significantly.

Diseases in marine species result from a complex and constantly changing relationship between factors extrinsic and intrinsic to the individual and the population. Extrinsic or environmental influences on occurrence and effects of diseases may in some instances be marked, but have been inadequately studied, particularly in pelagic species. A continuing investigation of disease in Atlantic herring, *Clupea harengus, harengus*, has provided some information about environmental effects on three diseases: "pigment spot" disease caused by a larval trematode (*Cryptocotyle lingua*); myxosporidian disease caused by *Kudoa clupeidae*, and fungus disease caused by *Ichthyosporidium hoferi*.

Larval trematode abundance was found to decrease markedly from west to east along the northern New England coast. Fewer parasites occurred in herring from eastern Maine and New Brunswick than in herring from western Maine. Incidences of the larval trematode in *Littorina littorea*, the snail first intermediate host, did not have a corresponding geographic distribution. Experimental studies demonstrated a critical role of temperature in determining emergence of infective cercariae from the snail, and a relationship of abundance of the parasite in herring and environmental temperatures has been proposed.

Myxosporidian distribution and abundance followed a trend much like that of the larval trematode, with fewer infections in eastern regions of the Gulf of Maine than in western. The parasite did not occur in one-year-old fish taken on the eastern coast during eight years of sampling, but was abundant in fish of the same age taken on the western coast. The larger picture of occurrence of this parasite in the western North Atlantic provides further indication of a direct relationship of parasitism with environmental temperature, although other factors may be involved.

Epizootics of the fungus disease have occurred repeatedly in western North Atlantic herring. While knowledge about the possible influence of environmental conditions on prevalence of the disease is incomplete, it has been demonstrated experimentally that increasing infection pressure (increased dosage of spores) results in increased abundance and severity of the disease in herring. Intrinsic factors such as individual and population resistance are undoubtedly important also, and individual variations in susceptibility have been demonstrated.

Other instances of changes in occurrence of disease with locality and age of the fish have been observed during the course of this research. Surveys of disease incidence, life cycle studies, experimental studies of the role of environmental variables; all should prove to be fruitful areas for future investigations. Concurrent studies of immune responses and variability in resistance should provide a broad basis for understanding the role of disease in herring populations.

REFERENCES

CHRISTENSEN, N. and H. ROTH. 1949. Investigations on internal parasites of dogs. *K. Vet Højsk. Aarsskr.* (Copenhagen) 1949: 1-73.

DOGIEL, V.A., G.K. PETRUSHEVSKI and Y.I. POLYANSKI. 1958. Parasitology of fishes. Leningrad Univ. Press (Translation by Z. Kabata, English edition published by Oliver and Boyd Ltd. Edinburgh.)

DOLLFUS, R. 1956. Liste des parasites animaux du hareng de l'Atlantique Nord et de la Baltique. *J. Cons.* 22: 58-65.

SHULMAN, S.S. 1956. (Parasite fauna of *Clupea harengus, Osmerus eperlanus*, and *Eleginus navaga* in the White Sea.) Tr. Karelo-Finsk. fil. AN SSSR. 4 (cited by Dogiel *et al.* 1958 -- original not seen).

SINDERMANN, C. 1953. Parasites of fishes of North Central Massachusetts. Mass. Div. Fish and Game, Fishery Rept. for North Central Massachusetts, 1950: 4-28.

1958. An epizootic in Gulf of St. Lawrence fishes. *Trans. N. Amer. Wildl. Conf.* 23: 349-360.

1961. Parasite tags for marine fish. *J. Wildlife Mgmt,* 25: 41-47.

1963. Disease in marine populations. *Trans. N. Amer. Wildl. Conf.* 28: 221-245.

SINDERMANN, C. and A.E. FARRIN. 1962. Ecological studies of *Cryptocotyle lingua* (Trematoda: Heterophyidae) whose larvae cause "pigment spots" of marine fish. *Ecology* 43: 69-75.

SINDERMANN, C. and A. ROSENFIELD. 1954*a*. Diseases of fishes of the western North Atlantic. I. Diseases of the sea herring (*Clupea harengus*). *Maine Dept. Sea and Shore Fish., Res. Bull.* No. 18: 1-23.

1954*b*. Diseases of fishes of the western North Atlantic. III. Mortalities of sea herring (*Clupea harengus*) caused by larval trematode invasion. *Maine Dept. Sea and Shore Fish., Res. Bull.* No. 21: 1-16.

SINDERMANN, C. and L.W. SCATTERGOOD. 1954. Diseases of fishes of the western North Atlantic. II. *Ichthyosporidium* disease of the sea herring (*Clupea harengus*). *Maine Dept. Sea and Shore Fish., Res. Bull.* No. 19: 1-40.

SNIESZKO, S.F. 1962. Predisposing factors in the occurrence of diseases in fish. *Proc. First Internat. Conf. on Wildl. Dis.* 1962: 56-58.

STUNKARD, H.W. 1940. The life history of *Cryptocotyle lingua* (Creplin) with notes on the physiology of the metacercariae. *J. Morph.* 50: 143-191.

E-6

SEASONAL AND AREAL DISTRIBUTION OF GULF OF MAINE COASTAL ZOOPLANKTON, 1963

By

Kenneth Sherman[1]

ABSTRACT

Gulf of Maine coastal waters were sampled for zooplankton on single cruises during the winter, spring, summer and fall, 1963. Areal and seasonal variations were found in zooplankton volumes, major group occurrences and species composition. Three areas - the western, central and eastern Gulf - showed differing patterns of relative zooplankton abundance, with highest volumes occurring in the western sector, moderate volumes in the central area and lowest volumes in the eastern area.

Major zooplankton groups were more numerous in the western Gulf during winter, spring and fall. In summer, zooplankton groups were found in a variable pattern throughout each of the sampling areas. Larval forms were most numerous during spring and summer, indicating widespread breeding during these periods.

Copepods were the most numerous group of zooplankters encountered. Twenty-two species were present of which eight - *Calanus finmarchicus, Centropages typicus, Metridia lucens, Pseudocalanus minutus, Acartia longiremis, Oithona similis, Temora longicornis,* and *Tortanus discaudatus* - were most numerous. Six species were more abundant in the western area then in the eastern sector during all seasons. *Calanus finmarchicus* was more abundant in the east than the west in spring and *P. minutus* reached maximum numbers in the central area during summer. The fluctuations in seasonal and areal distribution of zooplankton volumes, major groups, and species are discussed in relation to previous studies and possible causes of variation.

INTRODUCTION

As part of a research program on the relation between environmental factors and availability of immature herring, *Clupea harengus* L., the Bureau of Commercial Fisheries Biological Laboratory, Boothbay Harbor, Maine, initiated a study of the Gulf of Maine coastal zooplankton. Research has provided information regarding seasonal and annual changes in zooplankton distribution and abundance.

In his classic work, Bigelow (1926) was first to describe the Gulf of Maine zooplankton. He characterized the dominant forms as the "Calanus Community" and showed that this endemic assemblage of zooplankters underwent seasonal pulsations in standing crop, progressing from a winter minimum to a spring-summer maximum, and was augmented annually by intrusions of northern and southern immigrant forms. Subsequent studies of Fish and Johnson (1937) and Redfield (1941) acknowledged the permanence of Bigelow's calanoid community, and the occurrence of immigrant species. Reports on endemic copepod species have been published by Fish (1936*a*, *Calanus finmarchicus;* 1936*b* *Pseudocalanus minutus;* 1936*c* *Oithona similis;* 1955 *Microstella norvegica*) and Redfield (1941, Calanoid species). Information regarding immigrant zooplankters was presented by Redfield (1939) for populations of the pteropod *Limacina retroversa* and by Redfield and Beale (1940) for several chaetognath species. Recently, Colton, *et al.* (1962) reported on the periodic intrusions of oceanic copepods into the inner reaches of the Gulf.

In the earlier works of Bigelow (1926) and Fish and Johnson (1937), lower mean-annual-volumes of zooplankton were reported east of the centrally located Penobscot Bay area than to the west of this region. Recent information, provided by staff members of the Boothbay Harbor Laboratory, suggests that this difference in areal distribution along the Maine coast is not limited to zooplankton. During 1962, it was observed that mean length of two-year-old herring was greater in the area west of Penobscot Bay than to the eastward (Watson, J.E., unpublished data). Erythrocyte antigen frequencies

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of young herring were found to differ east and west of Penobscot Bay (Sindermann, 1962). A discontinuity of the myxosporidian parasite, *Kudoa clupeidae*, was observed in small herring with infestations occurring west of Penobscot Bay but not to the eastward (Sindermann, 1961). Also, differences in spawning time of herring occur east and west of Penobscot Bay, as evidenced by the occurrence of larvae (≤ 9 mm standard length) east of Penobscot Bay two to three weeks earlier than larvae of the same size found to the westward (Graham, J.J., personal communication). In view of these findings, sampling was undertaken to determine whether differences in the composition and relative abundance of zooplankters occurred along the Maine coast.

METHODS

This report is based on the examination of 71 zooplankton samples collected from Gulf of Maine coastal waters during four seasonal cruises of the research vessel, *Rorqual*. Station locations and periods of collection are given in Table 1. Zooplankton samples were collected with a Gulf III sampler

TABLE 1. STATION LOCATIONS AND PERIODS OF COASTAL ZOOPLANKTON COLLECTIONS, *Rorqual* CRUISES 1, 4, 5 AND 7, 1963.

Station number	Position		Sampling periods, 1963			
	Lat.	Long.	*Rorqual* 1 5-16 Jan.	*Rorqual* 4 25 May- 2 June	*Rorqual* 5 10-22 July	*Rorqual* 7 11-20 Oct.
1.	42°43'	70°30'	X	X	X	X
2.	42°51'	70°43'	X	X	X	X
3.	42°56'	70°41'		X	X	X
4.	43°08'	70°23'		X	X	X
5.	43°17'	70°30'	X	X	X	X
6.	43°24'	70°12'		X	X	X
7.	43°39'	70°09'		X	X	X
8.	43°35'	69°52'	X	X	X	X
9.	43°42'	69°42'			X	X
10.	43°48'	69°29'	X	X	X	X
11.	43°51'	69°26'		X	X	X
12.	43°46'	69°06'	X	X	X	X
13.	43°48'	68°47'		X	X	X
14.	43°57'	68°93'	X	X	X	X
15.	44°02'	68°14'	X	X	X	X
16.	44°17'	68°07'	X	X	X	X
17.	44°10'	67°53'	X	X	X	X
18.	44°27'	67°50'		X	X	X
19.	44°27'	67°18'	X	X	X	X
21.	44°34'	67°19'	X	X	X	X
Number of stations sampled			12	19	20	20

Gehringer, 1962), fitted with an eight-inch nose cone and monel netting (aperture width 0.37 mm). All tows were of 30-min duration, taken during daylight hours, from 20 m to the surface in an oblique manner, with 10 min of towing at the surface and at depths of 10 and 20 m. A calibrated flow meter, affixed to the tail section of the Gulf III, was used to determine the amount of water strained. In addition, a U.S. Navy Electromagnetic Underwater Log, mounted on the keel of the *Rorqual*, measured the distance traversed during each tow. Analyses of the variation in the amount of water strained as determined by meter readings and Electromagnetic Log values indicated no significant differences in amount of water strained (Graham, J.J., unpublished data). For cruises 1 and 7, meter readings were used to calculate the amount of water strained, and for cruises 4 and 5, Electromagnetic Log readings were used. The average 30-min tow covered a distance of three nautical miles and filtered approximately 200 m^3 of water. Towing speed was maintained at approximately 6 knots.

In the laboratory, displacement volumes of all samples were taken. Ctenophores, large coelentrate remains (>2 cm long), and all fish larvae were removed from the samples and not included in the final volume determinations. Samples containing large quantities of ctenophores and medusae were not included in the analyses, due to the filtration error introduced by mesh clogging. Zooplankton samples were split into aliquots ranging from a half to a sixty-fourth, depending on the mass of the sample, and sorted into major taxonomic groups. Copepods were identified to species and the numbers of copepods and other zooplankters, per 100 m^3 of water strained were calculated.

RESULTS

Zooplankton Volumes

Seasonal and areal distributions of zooplankton volumes were compared. Abundance estimates are considered to be minimal, as use of a 0.37 mm mesh aperture limited sampling to the larger zooplankters. Also, tows were limited to the upper 20 m, and were taken only during daylight hours. To examine differences in areal distribution, the coastal region was divided into three areas, a central area located in the vicinity of Penobscot Bay, an eastern area extending from Mt. Desert Island to Grand Manan Island, and a western area from Casco Bay to Cape Ann. The areas, station locations, and sampling periods are shown in Fig. 1.

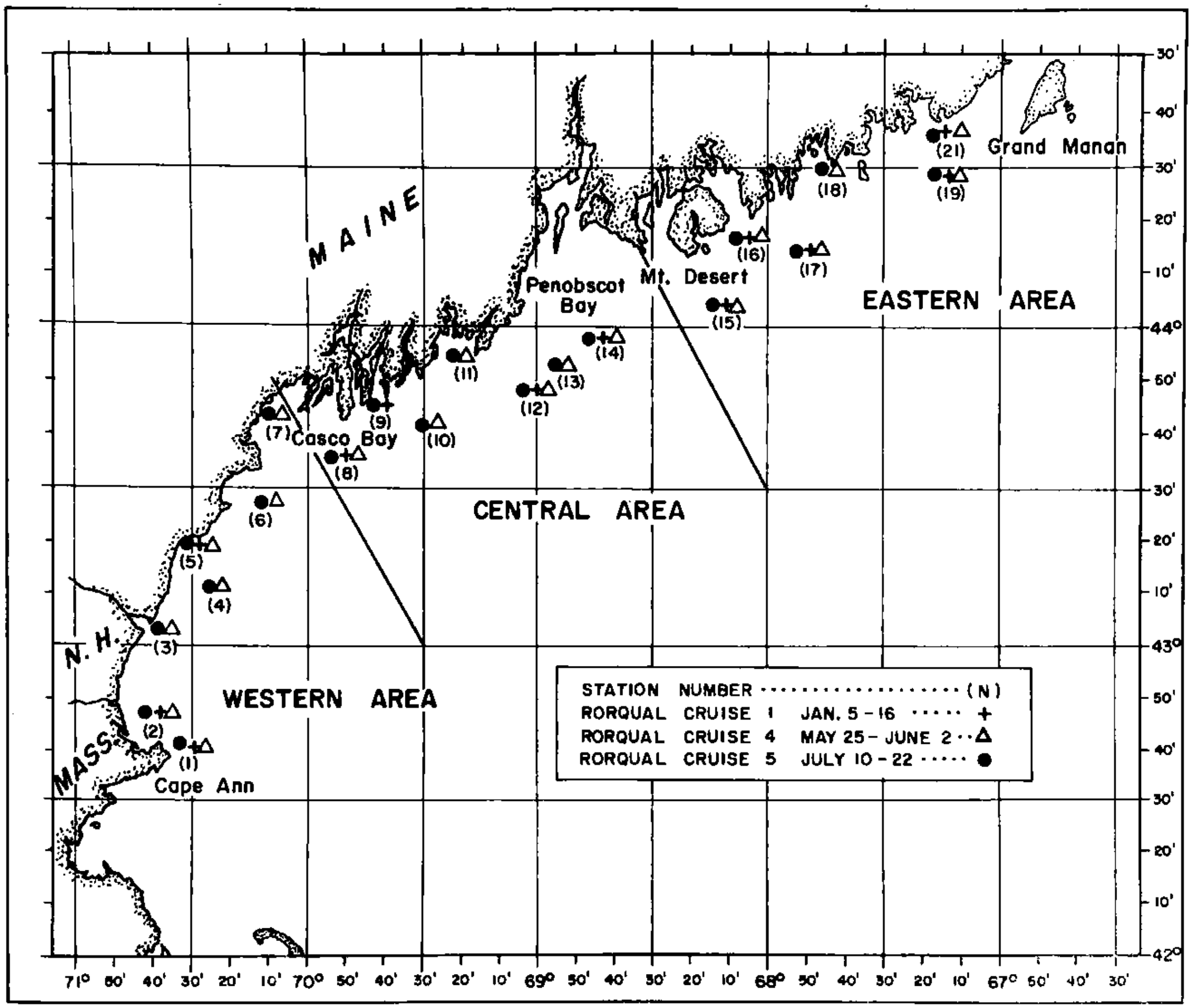

Fig. 1. Zooplankton sampling areas, station locations and periods of collections.

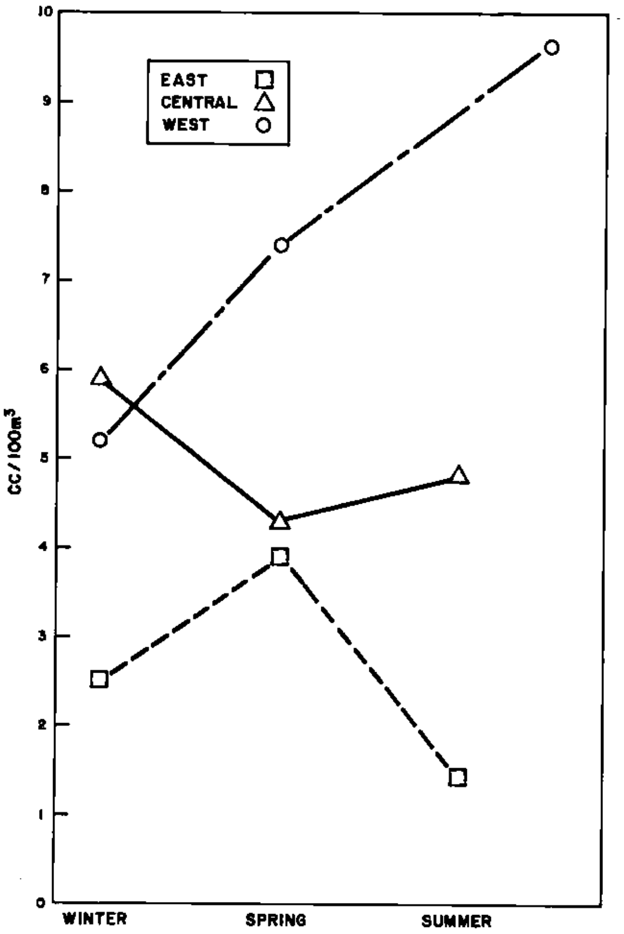

Fig. 2. A comparison of average zooplankton volumes per 100 m^3 of water strained among seasons for each of the three areas.

A comparison of average zooplankton volumes among areas for each of the four seasons is given in Fig. 2. Significant differences among areas ($H=19.159$, $P < .01$) were found using the Kruskal-Wallis analysis of variance (Siegel, 1956). In the eastern area the displacement volumes were the lowest encountered, ranging from a spring high of 3.9 cc/100 m^3 to a summer low of 1.4 cc/100 m^3. An intermediate range of values was found in the central area, ranging from a winter high of 5.9 cc/100 m^3, to a fall low of 3.2 cc/100 m^3. The greatest seasonal change in mean volumes occurred in the western area with values progressing from a winter low of 5.2 cc/100 m^3 to a summer high of 9.6 cc/100 m^3.

Zooplankton Groups

The percentage composition of the zooplankton groups encountered on each of the seasonal cruises is presented in Fig. 3. Copepods were the dominant zooplankters during each of the seasons, reaching a fall and winter high of 91% of the total zooplankton and declining to 45% in summer. Of the other planktonic forms found, nine-pteropods, chaetognaths, decapod larvae, cladocerans, brachyuran larvae, tunicates (appendicularians), cirripeds, and fish and crustacean eggs--constituted greater than 1% of the total zooplankton. The spring and summer decline in percentage composition of copepods was associated with the increase of other abundant (> 1% of the total zooplankton) groups; from two in winter to five in spring and seven in summer (Fig. 3). The breeding period of many species during warmer months was evidenced by the abrupt rise in decapod larvae in spring, and fish eggs and crustacean eggs during summer. Cirripeds occurred in swarms during spring, but diminished in summer with the onset of substrate attachment. Brachyuran and pelecypod larvae occurred during the summer and fall periods only. The fall decrease in the number of abundant zooplankton groups present indicated that the zooplankton population was approaching the winter minimum.

To examine the areal distribution of the dominant zooplankton groups, the mean number of zooplankters per 100 m^3 of water was determined for each of the three areas and for each of the seasonal cruises. Differences in areal distribution were plotted for major groups only (>100/100 m^3). During the winter period, copepods were the dominant zooplankters in all areas (Fig. 4A), but were more numerous in the western than in the eastern area.

In spring as in winter, copepods were the dominant zooplankters, increasing in numbers from a group mean of 645/100 m^3 in winter to 5,575/100 m^3 in spring (Fig. 4B). The spring rise in copepods was accompanied by increases in numbers of other major groups - decapod larvae, cladocerans, pteropods, cirriped larvae and tunicates. All major groups, with the exception of cirriped larvae, decreased in numbers from west to east (Fig. 4B).

An increase in the number of major groups was evident during the summer period (Fig. 4C). As in the preceding two seasons, copepods were the dominant zooplankters, with the grestest number (9,853/100 m^3) present in the western sector. Decapod and brachyuran larvae were also more numerous in the western area than in the east. The central area was characterized by a number of dominant

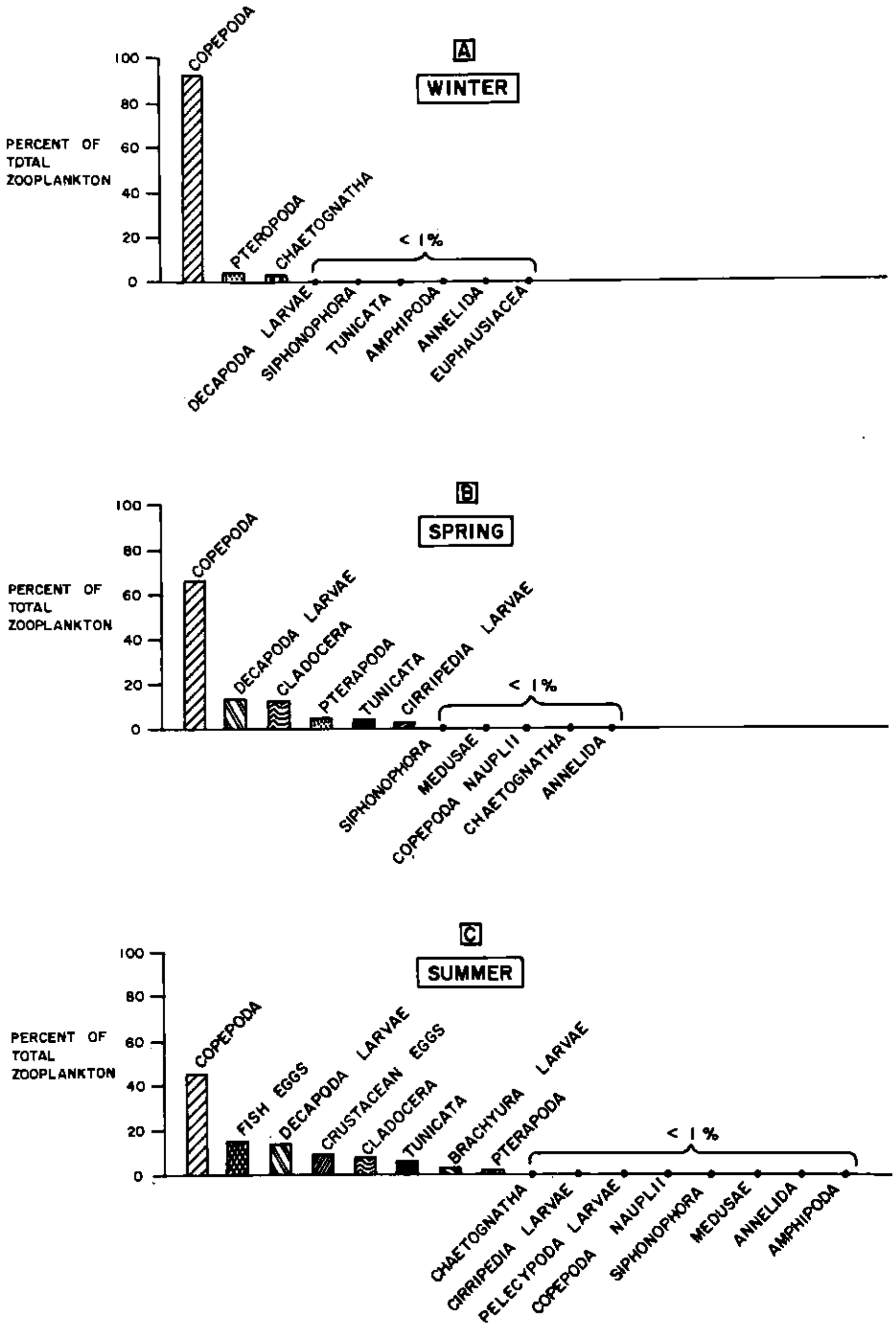

Fig. 3. Percentage composition of the zooplankton groups encountered on each of the seasonal cruises.

forms; cladocerans, pteropods, chaetognaths and fish eggs. Tunicates and crustacean eggs were more numerous in the eastern area.

During fall, fewer major groups of zooplankters were found than in summer, with a reduction from nine to four (Fig. 4D). Fish and crustacean eggs were also markedly reduced in numbers, from a summer high of 4,625/100 m^3 and 2,721/100 m^3, respectively, to less than 100/100 m^3. As in the preceding seasons, copepods were the dominant zooplankters in all areas, with the greatest number

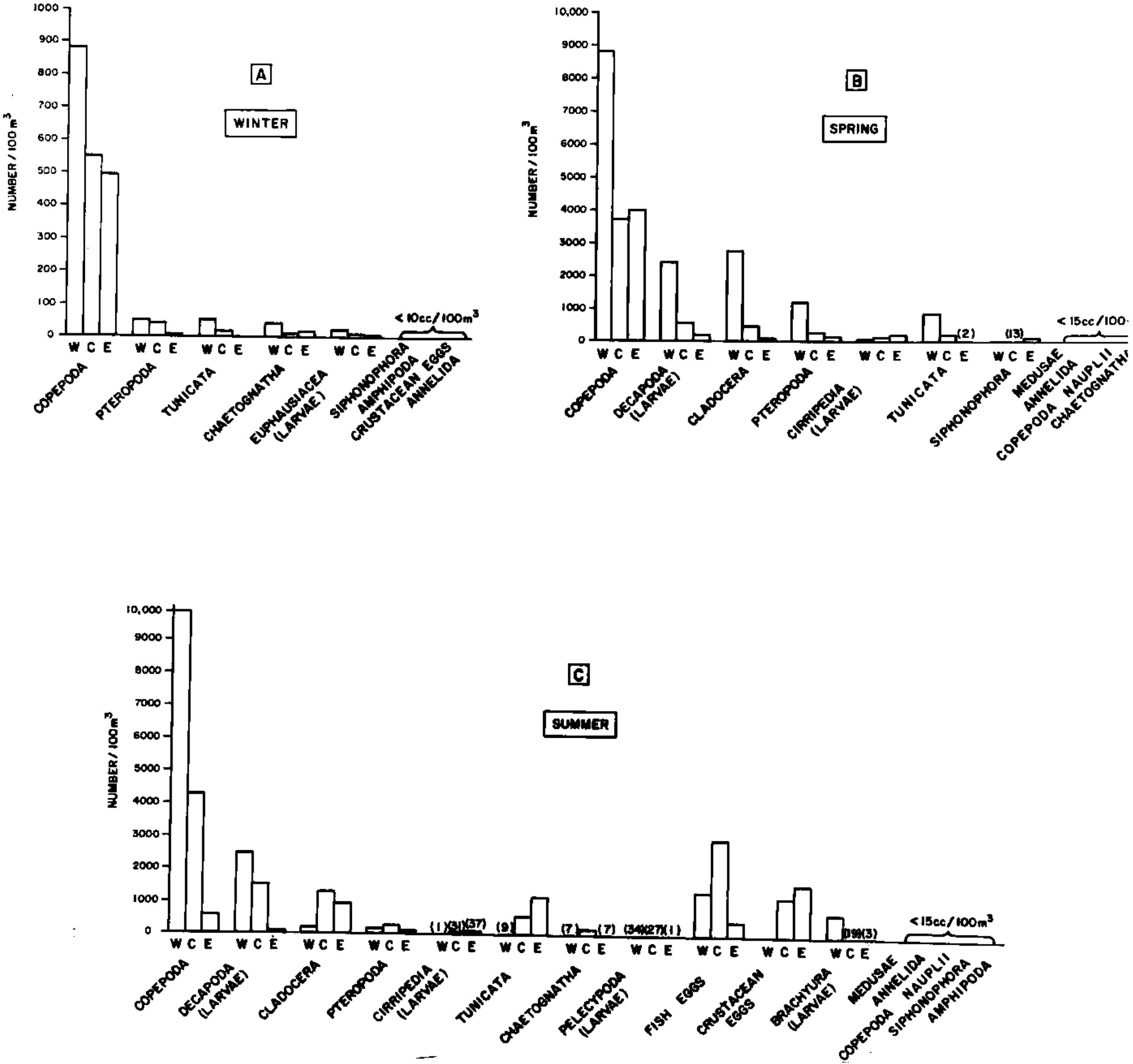

Fig. 4. Bar graph represents the mean number per 100 m^3 of water strained of the dominant zooplankton groups present in each of the three areas-west, central and east-during winter, spring, summer and fall.

(12,744/100 m^3) occurring in the western sector. Other groups more numerous in the western than in the eastern area were cladocera and pteropods. Of the four major groups, only one, brachyuran larvae, was more numerous in the central area. The low abundance of fish eggs, crustacean eggs, and larvae of other groups, indicated that the widespread breeding, characteristic of the summer period, was over and that the zooplankton population was approaching the winter minimum.

Copepod Species Occurrence

Copepods were the dominant zooplankters during all seasons. Species encountered are listed in Table 2. They have been arranged into two groupings; the common forms, those species exceeding

TABLE 2. COPEPOD SPECIES ENCOUNTERED DURING THE 1963 ZOOPLANKTON SAMPLING.

	Mean number/100 m^3	
	Common species >50/100 m^3	Less numerous species <50/100 m^3
Acartia longiremis (Lilljeborg)	204	
Calanus finmarchicus (Gunnerus)	1446	
Centropages typicus Kroyer	2308	
Metridia lucens Boeck	411	
Oithona similis Claus	141	
Pseudocalanus minutus (Kroyer)	398	
Temora longicornis (Muller)	160	
Tortanus discaudatus (Thomson and Scott)	76	
Acartia clausi Giesbrecht		3.17
Aetidius armatus Boeck		0.197
Calanus hyperboreas Kroyer		0.70
Candacia armata (Boeck)		3.21
Centropages hamatus (Lilljeborg)		0.704
Euchaeta norvegica Boeck		0.845
Eurytemora sp.		2.51
Oithona plumifera Baird		0.113
Oithona spinirostris Claus		23.00
Pleuromamma robusta (Dahl)		0.028
Pleuromamma xiphias Giesbrecht		0.028
Rhincalanus nasutus Giesbrecht		0.098
Scolecithricella minor Brady		0.042

a mean value of 50/100 m^3 for all cruises, and the less numerous species, with a mean value of <50/100 m^3 for all cruises. Of the eight common species, *Centropages typicus* was the dominant copopod, followed by *Calanus finmarchicus*, *Metridia lucens*, *Pseudocalanus minutus*, *Acartia longiremis*, *Temora longicornis*, *Oithona similis* and *Tortanus discaudatus* (Fig. 5).

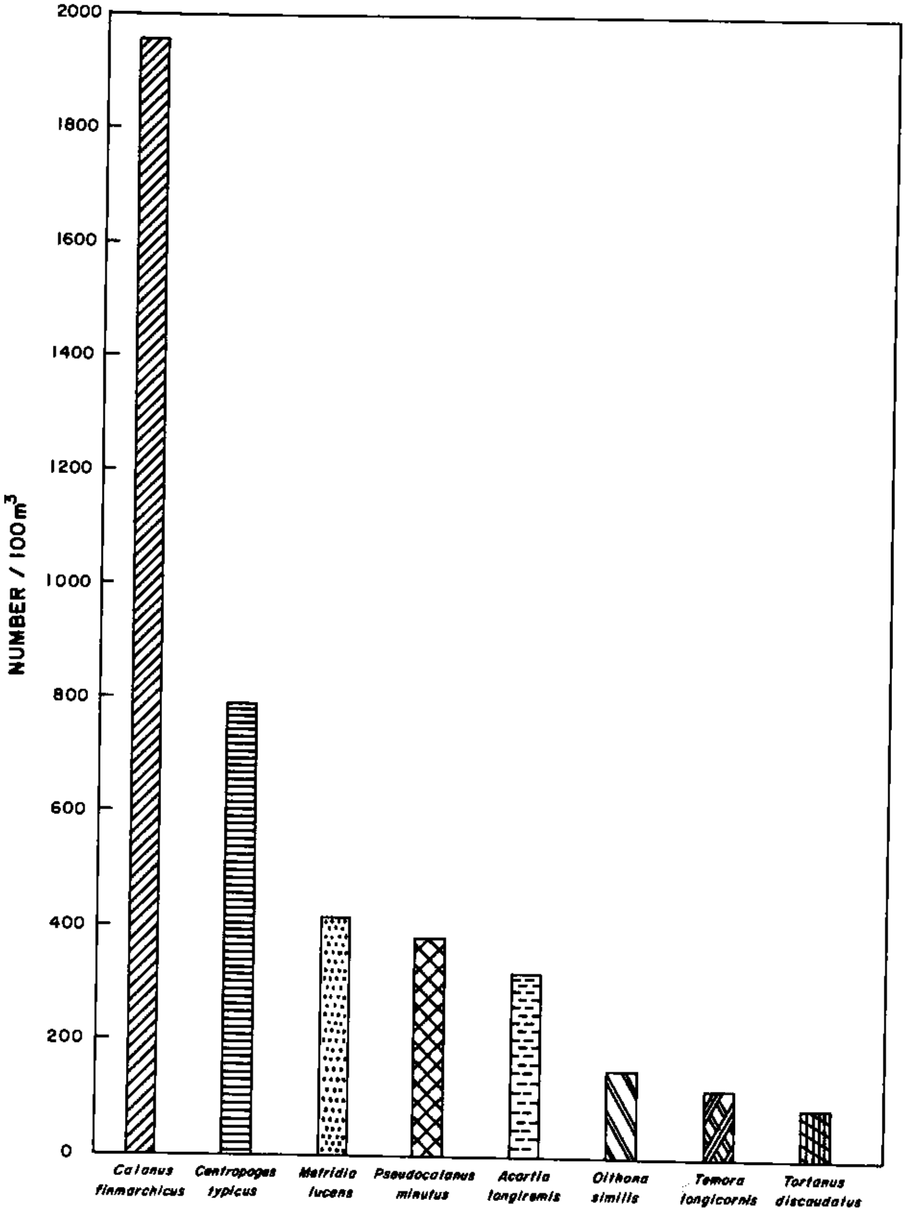

Fig. 5. Bar graph represents the mean number per 100 m^3 of water strained of eight commonly occurring copepod species during 1963.

Six of the eight commonly occurring species declined in abundance from west to east during all seasons (Fig. 6A to F). Differing patterns of occurrence were shown by two species, *C. finmarchicus*, and *P. minutus*, with the former species more abundant in the eastern area than in the western sector during spring and the latter reaching maximum numbers in the central area during summer (Fig. 6G and H).

Seasonal variability in species occurrence was observed among the eight common species. Five reached peak numbers in summer; *C. finmarchicus, M. lucens, O. similis, P. minutus* and *T. discaudatus*. Of the remaining three, *A. longiremis* was most numerous during spring, and *C. typicus* and *T. longicornis* reached peak numbers in the fall (Table 3).

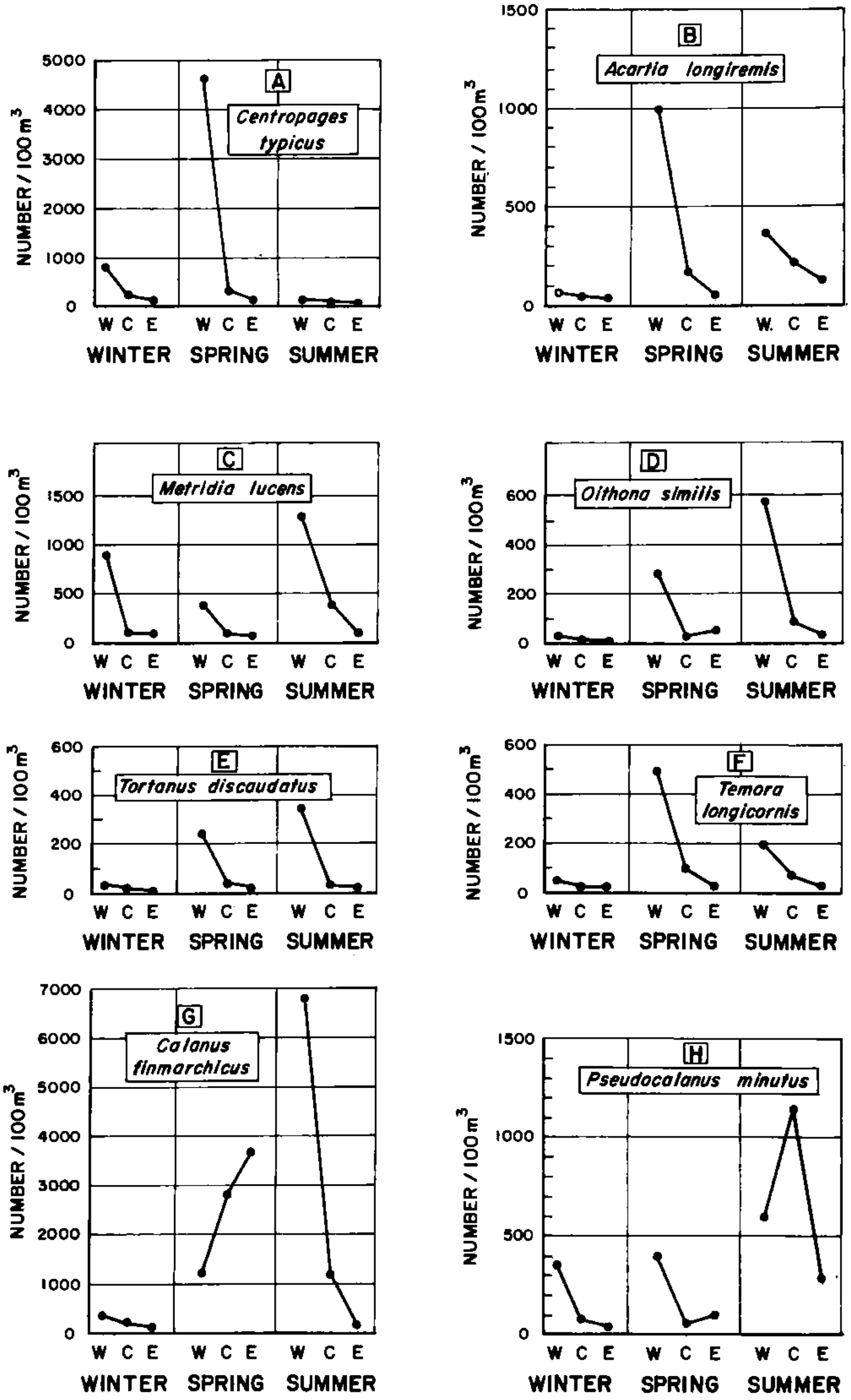

Fig. 6. The areal and seasonal variation in numbers per 100 m^3 of water strained of the eight commonly occurring copepod species.

TABLE 3. SEASONAL PERIODS OF MAXIMUM ABUNDANCE OF THE COMMONLY OCCURRING COPEPOD SPECIES.

Species	Winter 5-16 Jan.	Spring 25 May-2 June	Summer 10-22 July	Fall 11-20 Oct.
Acartia longiremis		0		
Calanus finmarchicus			0	
Centropages typicus				0
Metridia lucens			0	
Oithona similis			0	
Pseudocalanus minutus			0	
Temora longicornis				0
Tortanus discaudatus			0	

TABLE 4. SEASONAL AND AREAL OCCURRENCE OF THE LESS NUMEROUS COPEPOD SPECIES.

Species	Winter (+)			Spring (0)			Summer (X)			Fall (Ø)		
	west	central	east	west	central	east	west	central	east	west	central	east
Aetidius armatus	+											
Acartia clausi				0		0				Ø		
Calanus hyperboreas			+									
Candacia armata	+	+	+						X	Ø		
Centropages hamatus				0						Ø		
Euchaeta norvegica		+								Ø		
Eurytemora sp.				0			X	X	X	Ø		
Metridia longa											Ø	Ø
Oithona plumifera					0							
Oithona spinirostris	+	+			0	0			X	Ø		
Pleuromamma robusta						0						
Pleuromamma xiphias			+									
Rhincalanus nasutus			+									
Scolecithricella minor								X				

The less common species presented interesting patterns of occurrence (Table 4). Of the 14 species found, 8 occurred only during a single season. In winter 4 species, considered to be oceanic in origin, were found - *Aetidius armatus*, *Calanus hyperboreas*, *Pleuromamma xiphias*, and *Rhincalanus nasutus*. All but *A. armatus* occurred only in the eastern area. Other seasonally occurring species were: *Oithona plumifera*, and *Pleuromamma robusta*, present only during the spring, *Scolecithricella minor*, found in summer and *Metridia longa* present only in fall. Species occurring in more than a single season were: *Acartia clausi*, *Candacia armata*, *Centropages hamatus*, *Euchaeta norvegica*, *Eurytemora* sp. and *Oithona spinirostris*.

DISCUSSION

A comparison of mean displacement volumes for each of the areas and seasons revealed different patterns of abundance. The highest values for all seasons were found in the western area. The lowest values occurred in the eastern sector, and intermediate volumes in the central area. Based on data collected during the warmer months (April-October), Bigelow (1926), Fish and Johnson (1937) also found that the region west of Penobscot Bay was consistently higher in zooplankton volumes than the relatively "barren" area to the eastward, from Mt. Desert to the Bay of Fundy. The progression from a winter low to a summer high in the western area is also in agreement with Bigelow (1926); Fish and Johnson (1937) and Redfield (1941). In addition these authors have indicated a late summer reduction in volumes, followed by a short-lived fall increase. During 1963, this fall increase was not apparent in the western or central areas. However, a slight increase in zooplankton volumes occurred in the eastern area.

The seasonal variations of volumes in the central and eastern areas are not compatible with the findings of Bigelow (1926) or Fish and Johnson (1937). However, Redfield (1941) showed that the "Seguin" sector of the Gulf, an area comparable to the central area, had only moderate plankton volumes in summer which declined in fall, increased in winter, declined in spring and increased in summer. The present pattern of seasonal variability in volumes in the central area is in agreement with the description given by Redfield for 1933 data. The increase in volumes, however, from summer to fall of 1934, reported by Redfield (1941), indicated that annual variations can be expected in the central area. In the eastern area, the winter-spring increase in volumes although of a lesser magnitude than the western sector, is in agreement with previous reports. However, the summer decline observed in this region has not previously been reported. Future sampling is planned for this region to examine these results more closely.

Major zooplankton groups showed a seasonal variation both in numbers and areal distribution. Most of the groups were more numerous in the western sector than in the eastern. The most notable exceptions occurred during the summer period when six groups - cladocerans, pteropods, tunicates, chaetognaths, fish eggs and crustacean eggs - were more numerous in the central and eastern areas. The significance of this shift in areal distribution is not known. However, it was found that considerable breeding during the warmer months occurs in the northeastern sector of the Gulf of Maine eddy, as evidenced by the presence of large numbers of fish and crustacean eggs occurring in the central and eastern areas. The general southwesterly movement of surface waters in this eddy (Bigelow, 1926; Bumpus, 1960) may be one of the factors contributing to the concentration of zooplankton in the western area in the period succeeding the peak summer breeding.

Bigelow (1926): Fish and Johnson (1937) indicated that copepods were the most numerous and comprised the greatest volume of zooplankters occurring in Gulf of Maine waters. These investigators also found that volumes of zooplankton were consistently higher west of Penobscot Bay than east of this region. It would follow then, that most of the endemic copepod population would also decrease in abundance from west to east. Fish (1936 *a*, *c*) reported this decrease for the copepods *Calanus finmarchicus* and *Oithona similis* and noted two breeding stocks for each species - one located east of Penobscot Bay and the other, the principal breeding grounds, to the west.

The decrease in numbers from west to east of all but two species of the commonly occurring copepods found during the present study confirms the conclusions reached by earlier investigators. The apparent exceptions were the species, *Calanus finmarchicus* and *Pseudocalanus minutus*. In this regard, Fish (1936*a*) has shown that successive broods of *C. finmarchicus* produced in the western Gulf were transported initially to the outer Gulf and then to the inner reaches of the eastern and central areas by the upper waters of the Gulf of Maine eddy. These circulation features were thought to be the mechanism for transporting large numbers of *C. finmarchicus* to other areas of the Gulf from the principal western breeding area during spring and summer (Fish, 1936*a*). The large numbers of *C. finmarchicus* found in the eastern area during spring may have resulted from this type of current transport.

The large numbers of *Pseudocalanus minutus* found in the central area during summer is not entirely unexpected. Fish (1936*b*) reported the presence of three stocks of *P. minutus* for: 1) the outer Gulf, 2) the western coastal area, 3) the region east of Mt. Desert to the Bay of Fundy. He indicated that in early spring, the western brood hecame widely dispersed, and that in late summer, the larger part of the *P. minutus* population originated in waters of the outer Gulf. The presence of large numbers of *P. minutus* in the central area during late summer could have been related to the inshore movement of the Gulf of Maine eddy in this area during the late summer period. Copepod length frequency data could provide additional information regarding the origin of copepod populations and future effort will be directed toward providing this information.

Although occurring in relatively small numbers, immigrant zooplankton species have provided an insight into the origin and along-shore movements of the mixed waters of the Gulf of Maine eddy system (Bigelow, 1926; Fish and Johnson, 1937; Redfield, 1939, 1941; Colton, *et al.*, 1962). The presence of *Calanus hyperboreas*, *Pleuromamma xiphias*, and *Rhincalanus nasutus*, in the eastern area only during winter is in agreement with Redfield (1939, 1941), who reported the indraft of oceanic water from the Nova Scotian banks into the Gulf of Maine during winter.

In a discussion of the environmental characteristics of the Gulf of Maine, Bigelow (1927) concluded that the wide seasonal variations in temperatures of the Gulf are due to... "its geographic location to the leeward of the continent and to the vigorous land climate. Only in a much smaller degree is it influenced by warm or cold currents flowing into it". He further indicated that the wide seasonal variation in salinity characteristic of the Gulf is due to local conditions,..."the water freshening at the season of the spring freshet and then gradually salting again as this inrush of river water is incorporated by the mixings and churnings caused by the tides, winds, and waves". In this regard, it would appear that a great salinity influence on coastal waters would be exerted by the Penobscot Bay area.

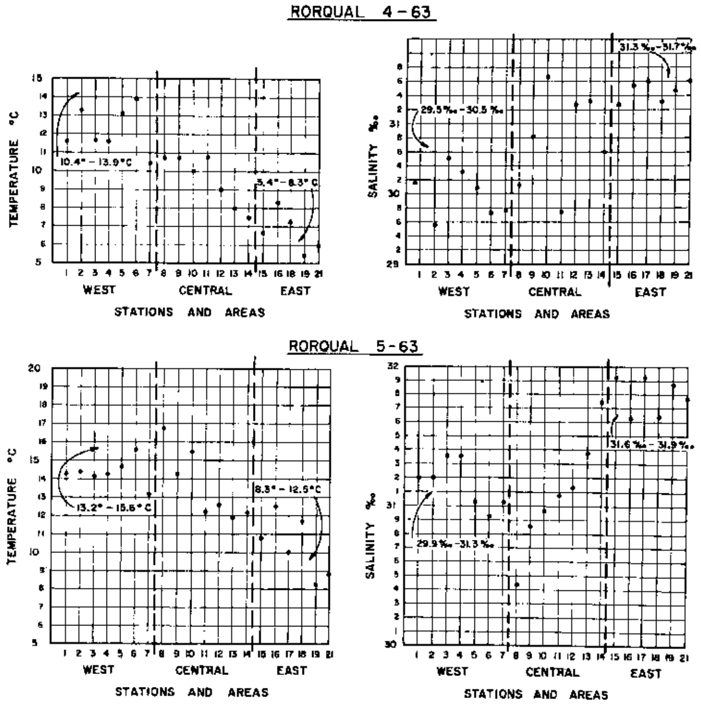

Fig. 7. Areal distribution of surface salinities and temperatures, *Rorqual* cruises 4, 5

Surface temperatures and salinities plotted for spring, summer, and fall by areas (Fig. 7) suggest that the Penobscot Bay region represents a transition zone between surface waters of lower salinity and higher temperature ranges located in the western sector and higher salinity, cooler waters of the eastern area. Whether these environmental differences are the result of local conditions or advection cannot presently be determined, but will be subject to future investigation. In addition to hydrographic differences, faunal changes east and west of Penobscot Bay occur for: 1) mean length at age of immature herring, 2) erythrocyte antigen frequencies of two-year-old herring, 3) myxosporidian parasite infestation of young herring, 4) differential herring spawning as evidenced by length frequencies of larvae. The high zooplankton volumes, greater numbers of groups, and copepod species found in the western Gulf, when considered with the surface temperature and salinity differences, suggest that the Penobscot Bay region represents a faunistic boundary between eastern and western coastal biota.

REFERENCES

BIGELOW, H.B. 1926. Plankton of the offshore waters of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, 40 (2): 1-509.

1927. Physical oceanography of the Gulf of Maine. *Bull. U.S. Bur. Fish.*, 40 (2): 511-1027.

BUMPUS, D.F. 1960. Sources of water contributed to the Bay of Fundy by surface circulation. *J. Fish. Res. Bd. Canada*, 17 (2): 181-197.

COLTON, J.B., R.F. TEMPLE and K.A. HONEY. 1962. The occurrence of oceanic copepods in the Gulf of Maine-Georges Bank area. *Ecology* 43 (1): 166-171.

FISH, C.J. 1936*a*. The biology of *Calanus finmarchicus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull., Woods Hole*, 70 (1): 118-141.

1936*b*. The biology of *Pseudocalanus minutus* in the Gulf of Maine and Bay of Fundy. *Biol. Bull., Woods Hole*, 70 (2): 193-216.

1936*c*. The biology of *Oithona similis* in the Gulf of Maine and Bay of Fundy. *Biol. Bull., Woods Hole*, 71 (1): 168-187.

1955. Observations on the biology of *Microstella norvegica*. *Deep-Sea Res. Suppl.* 3: 242-249.

FISH, C.J., and M.W. JOHNSON. 1937. The biology of the zooplankton population in the Bay of Fundy and Gulf of Maine with special reference to production and distribution. *J. Biol. Bd. Canada*, 3 (3): 189-322.

GEHRINGER, J.W. 1962. The Gulf III and other modern high-speed plankton samplers. *Contrib. Symposium on Zoopl. Prod., Rapp. Cons. Explor. Mer*, 153: 19-22.

REDFIELD, A.C. 1939. The history of a population of *Limacina retroversa* during its drift across the Gulf of Maine. *Biol. Bull., Woods Hole*, 86 (1): 26-47.

1941. The effect of the circulation of water on the distribution of the calanoid community in the Gulf of Maine. *Biol. Bull., Woods Hole*, 80 (1): 86-110.

REDFIELD, A.C., and A. BEALE. 1940. Factors determining the distribution of populations of chaetognaths in the Gulf of Maine. *Biol. Bull., Woods Hole*, 79 (3): 459-487.

SIEGEL, S. 1956. *Nonparametric Statistics*. New York. McGraw-Hill Co., 312 p.

SINDERMANN, C.J. 1961. Parasite tags for marine fish. *J. Wildlife Mgmt.*, 25 (1): 41-47.

1962. Serology of Atlantic clupeoid fishes. *Amer. Nat.* 96 (889): 225-231.

E-7

ECOLOGY OF HERRING LARVAE IN THE COASTAL WATERS OF MAINE

By

Joseph J. Graham and Harold C. Boyar[1]

ABSTRACT

The ecology of larval and juvenile herring, *Clupea harengus* (Linnaeus) in the coastal waters of the Gulf of Maine is being studied at the U.S. Bureau of Commercial Fisheries Biological Laboratory, Boothbay Harbor, Maine. This report is the first of a series and covers a period of a year beginning June, 1961. Hydrographic and biological observations were made in three embayments located along the central Maine coast; the Sheepscot, Boothbay and Damariscotta. Major seasonal environmental events were similar in the three areas. Average conditions for the year were somewhat different; eastward from the Sheepscot to the Boothbay and Damariscotta areas, average seasonal salinities, surface temperatures and surface standing crops of zooplankton increased. Meter-net catches showed marked differences in the seasonal and areal distribution of herring larvae. The seasonal distribution of herring larvae was inverse to other fish larvae. The source of the herring larvae, the influence of avoidance and migration by larval herring on meter net catches and the utilization of the estuarine environment during their larval stages are discussed.

INTRODUCTION

The U.S. Bureau of Commercial Fisheries Biological Laboratory, Boothbay Harbor, Maine, is studying the ecology of larval and juvenile herring, *Clupea harengus* (Linnaeus), in the coastal waters of the Gulf of Maine. The study is designed to determine trends in the distribution and abundance of the early life history stages of herring and their relation to variations in the environment. This is the first of a series of reports and covers the period from June 1961 to June 1962. The region investigated, an inshore habitat, is part of the rocky coast of Maine which is deeply embayed and dissected by drowned river valleys (Fig. 1). The sides of the lower estuaries and bays are usually steep and their basins relatively deep, the water is well mixed, and dilution evident only during periods of peak river discharge. Within the bays and lower estuaries, water exchange is influenced by the presence of islands and ledges in the areas of deep water, and by narrow guts (or passages).

The general ecology of the lower Sheepscot River estuary has been described by Stickney (1959) and a specific study of the bottom fauna has been made by Robert W. Hanks, whose paper, "A benthic community in a New England estuary", is in press in the Fishery Bulletin series of the U.S. Fish and Wildlife Service. The Sheepscot River has a drainage area of approximately 148 sq. mi. and an average daily discharge of 239 c.f.s. (U.S. Geological Survey, 1962, 1962*a*). During the study period, 83,840 c.f.s. was discharged by the river, with the highest monthly discharge (36% of the total) in April and the lowest(2%) in September. A secondary high (14%) and a low (3%) occurred during December and February, respectively. Similar data were not available for the Damariscotta River basin which is smaller than the Sheepscot. The Boothbay area does not receive discharge from any major stream.

METHODS AND MATERIALS

Each of the 18 stations shown in Fig. 1 was sampled biweekly, alternating hydrographic and fishing cruises. Weather conditions occasionally hampered sampling but of 26 cruises, only 5 were not completed and no more than 5 stations were abandoned on any one cruise. There were considerable variations in the sequence, stage of tide, and time of day that stations were sampled. These variations are not considered to detract from the average seasonal and areal data obtained. The sampling procedure is considered analagous to that of Hopkins (1963). He concluded that several tows spaced

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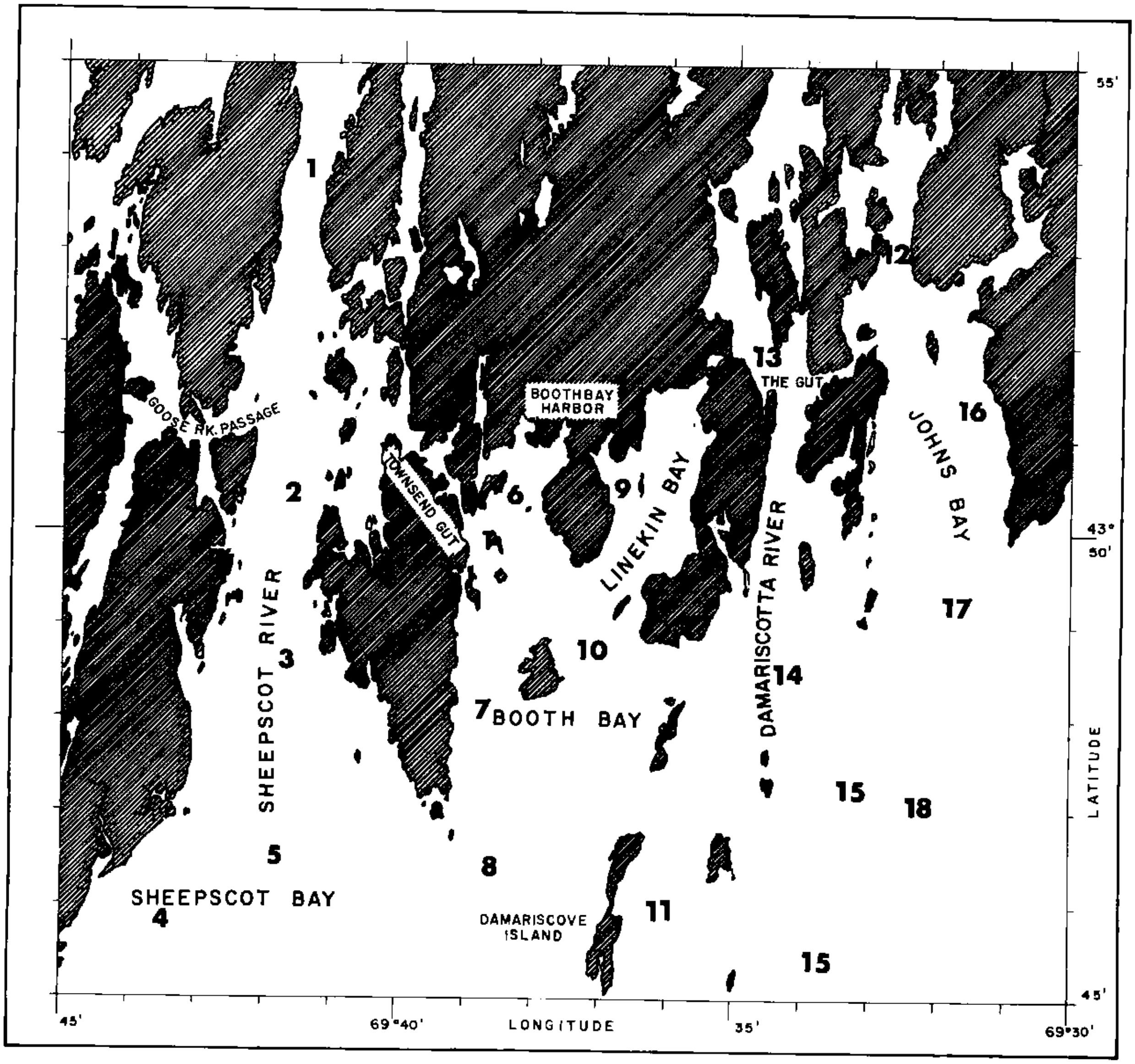

Fig. 1. Sampling stations in the Sheepscot-Boothbay-Damariscotta region of Maine. Two positions are shown for station 15. Because of obstructions in the water the original station position was shifted midway during the year of sampling.

over a single tidal cycle were more effective in estimating average biological characteristics at a station than one that filtered a large amount of water in a single tow.

Bathythermograph casts, surface temperatures and appropriate meterological observations were made during all cruises. On hydrographic cruises, Nansen bottle casts were made at 0, 10 and 20 m and just above the bottom. Plankton tows were made at the surface and vertically from the bottom. On fishing cruises an otter trawl with a 25-ft mouth opening and cod end liner (fine mesh) was towed along the bottom. The mesh at the mouth had a stretched measure of 4.4 cm; and the cod end, 3.2 cm. Sampling of salinity and plankton was confined to the surface. The 1-m plankton net used to capture

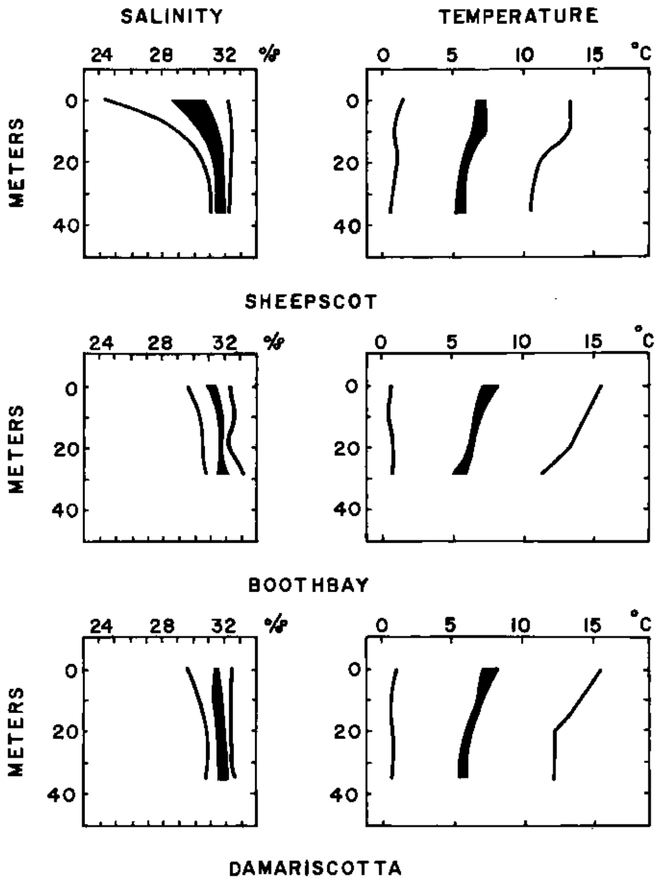

Fig. 2. Annual means and extremes of temperature and salinity. The mean range for each area at various depths is shaded.

larvae and plankton had a 0.51 mm mesh opening with 13 meshes per linear centimeter; no flowmeter was used during tows on station. The column of water strained on a vertical tow depended upon the depth of water. The amount strained during surface tows was determined by a calibrated Atlas flowmeter. The flowmeter was suspended in a meter net ring and towed over a known distance both with and without a net. This calibration, revolutions of the flowmeter per cubic meter of water strained, was applied with a net factor to metered tows. The average volume of water strained during the standard 10-min tow at 3 knots was 1,550 m^3.

In the laboratory, fish larvae were separated from plankton samples, identified and counted. Displacement volumes were calculated for the remaining plankton after removing foreign materials and organisms larger than 5 cm. Salinity samples were titrated by the Knudsen method.

RESULTS

Environmental conditions

Figure 2 summarizes, as profiles, the hydrographic data obtained during the year. The highest salinity values in each area were similar, reflecting a seasonal maximum in evaporation and a minimum of runoff common to the three areas. In the upper 20 m, Boothbay and Damariscotta were comparable, mean salinities were higher and their range less than in the Sheepscot, which receives a greater inflow of freshwater. Below 20 m mean salinities were similar in the three areas. The narrow range of mean salinities at the surface in the Damariscotta area was related to turbulence and mixing in the narrows above station 13. The Damariscotta estuary was not affected by the shallow gut leading to John's Bay, but water from the Sheepscot estuary flowed through the deeper Townsend Gut (6-15 m) reducing the mean salinity at station 7.

Average temperatures in the Sheepscot area indicated a relatively homogeneous distribution in the upper 10 m. A similar situation existed for highest temperatures. In the Boothbay area, mean and highest temperatures increased generally from the bottom upward because some of the shallow stations (6 and 9) were completely stratified throughout in the summer. The deeper stations of the Damariscotta area showed a relatively homogeneous layer from 20 m to the bottom. Lower temperatures reflected the lower winter air temperatures common to all of the areas.

At station 1 the seasonal progression of temperature and salinity was pronounced and was not obscured by advection of other water types or excessive turbulence, but represented seasonal events at other stations (Fig. 3). These were summer stratification, fall overturn, winter homogeneity and spring dilution. The estuary was coldest throughout its water column in late winter and coldest near the bottom during early spring. Salinity was highest in the winter, interrupted briefly by an increase in river discharge. With vernal warming and increased runoff salinity was lowered and the water column was stratified. By late spring to early summer this diluted water was mixed by the tides and removed from the estuary.

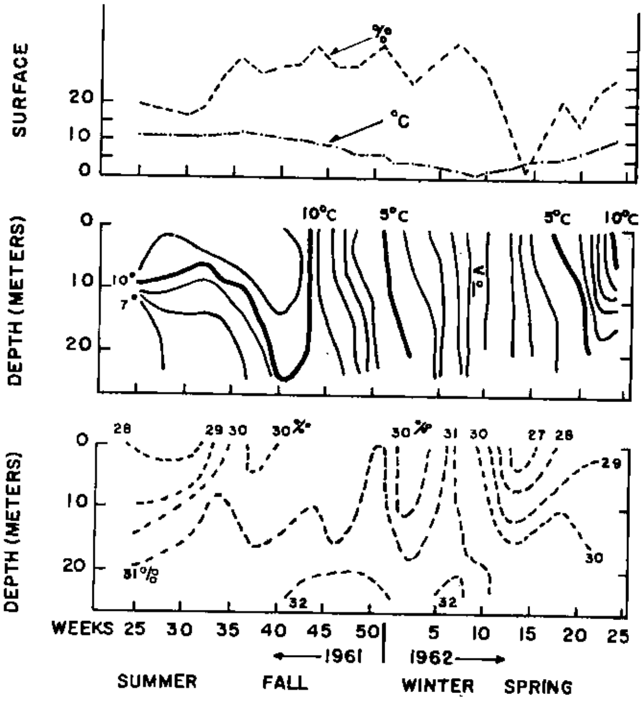

Fig. 3. Seasonal progressions of temperature and salinity at station 1 in the Sheepscot estuary. Original temperature measurements in degrees Fahrenheit and depths in feet.

During the year, either temperature or salinity controlled the density distribution. This is illustrated with selected shallow- and deep-water stations in Fig. 4. In April, the discharge of freshwater preceded thermal stratification and the steep density gradient at station 1 was more closely related to a change in salinity than temperature, although the gradient was accentuated by the colder bottom water. A steep gradient was not present during April at station 5 because the freshwater was well mixed through tidal action when it departed the estuary. Temperature was the dominant variable during the summer and fall, when the density of the entire water column was lowest. In the winter, the water column approached homogeneity except at stations in the Sheepscot area.

Displacement volumes of zooplankton obtained in meter net tows were not normally distributed and a median-quartile description (Snedecor, 1948) was used to summarize data from each of the 18 stations (Table 1).

TABLE 1. MEDIAN-QUARTILE DESCRIPTION OF PLANKTON VOLUMES

	Range in ml		
	Sheepscot	Boothbay	Damariscotta
Quartile 1	2.0 - 3.5	2.0 - 6.0	2.0 - 5.0
Median	4.0 - 6.5	4.0 - 8.0	4.0 - 9.5
Quartile 3	5.75 - 12.0	11.75 - 18.75	11.00 - 27.0
Extremes	< 1 - 70	< 1 - 197	< 1 - 341

The volumes in the first quartiles and medians overlap considerably between the three areas. This overlap is related, in part, to measuring small displacement volumes less than 5 ml. Very small volumes are present for all areas, but the third quartile, large volumes, showed a progressive increase from the Sheepscot to the Damariscotta. The three areas differed, as suggested above, in their average temperature and salinity distributions and in their resultant sigma-t values at the surface. In this regard, a positive correlation (r = 0.562, N-2 = 16, P < .05) was obtained between the third quartile of surface plankton volumes and sigma-t values at each station. Stations in the lower estuary of the Sheepscot River had the lower sigma-t values and lower plankton volumes while the Damariscotta area, particularly stations 17 and 18, more exposed to coastal waters, had the highest. The seasonal progression of zooplankton volumes from station 1 in the Sheepscot estuary was similar to those of the other stations and is shown in Fig. 5. The standing crop was high during late summer and early fall, low in the late fall and winter, high again in late winter and early spring, and low again during the late spring and early summer.

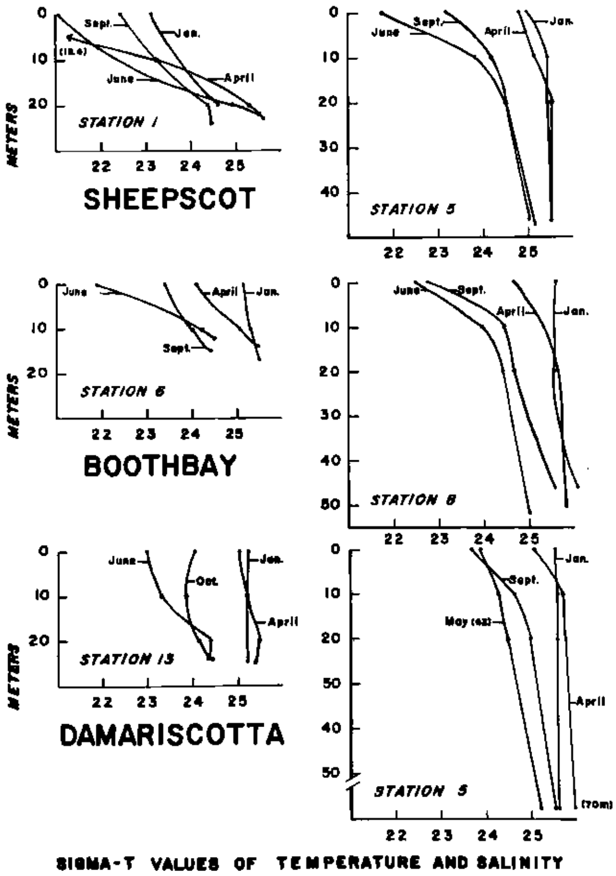

Fig. 4. Vertical distributions of density at selected shallow and deep water stations. See Fig. 1 for the location of numbered stations.

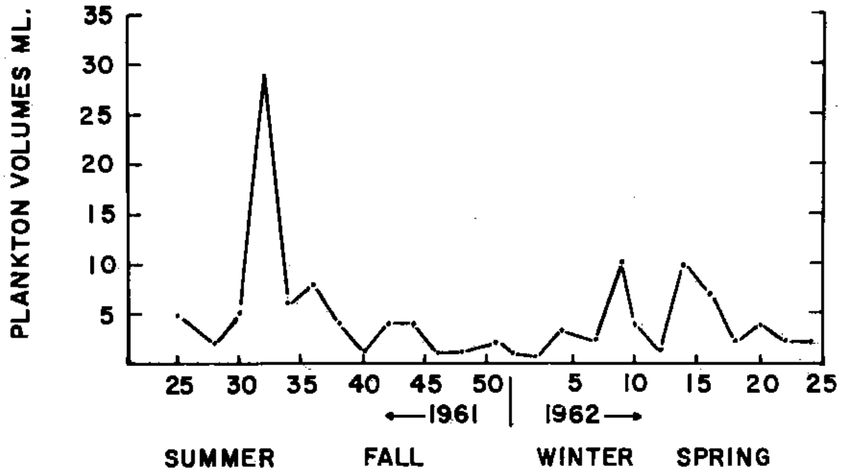

Fig. 5. Zooplankton volumes at station 1 in the lower Sheepscot estuary.

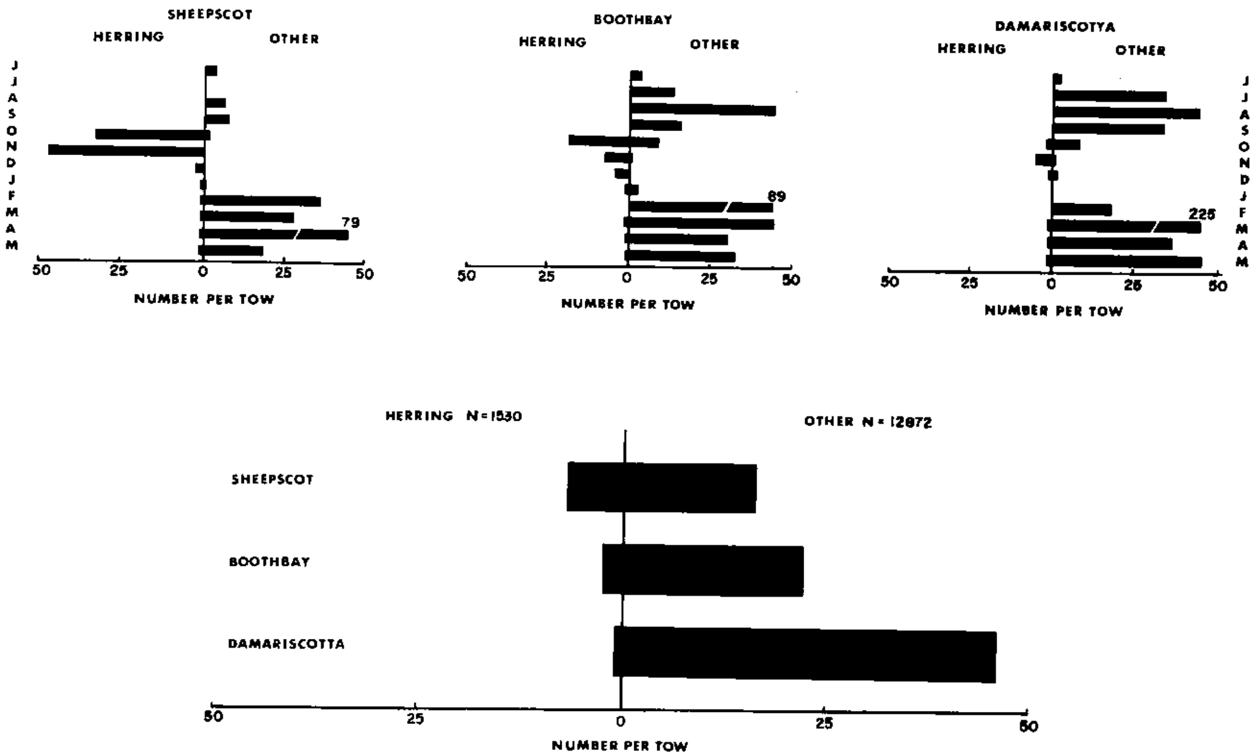

Fig. 6. Average number of herring and other fish larvae caught in surface tow

Larval distribution

Monthly meter-net catches of larval herring and other larval fishes had three notable features: 1) there were marked differences in the seasonal distributions of larvae, 2) the differences in areal distribution were equally marked, 3) the seasonal and areal distribution of herring larvae was inverse to that of other larvae (Fig. 6).

Herring larvae were first captured in October and were relatively abundant. Catches were largest in the Sheepscot and smallest in the Damariscotta area. Their numbers increased in the Sheepscot and Damariscotta areas during November but decreased in the Boothbay area. By December, there was a sharp drop in all areas and catches remained at a low level. During February, herring larvae were not captured in the Boothbay area, nor in January and February in the Damariscotta area. The average number per tow decreased from the Sheepscot to the Damariscotta area.

The number of larvae captured in vertical meter-net tows was small, 50 during October and November, a period of relative abundance at the surface. No particular pattern of areal distribution or relation to surface catches was discernible. Possibly the distances towed, 14-67 m, were too short and the amounts of water strained, 12-52 m^3, too little to register any distinct pattern of distribution. Surface samples strained 1,550 m^3 and were towed for 830 m. Otter trawling was largely unsuccessful in capturing the larger larval herring in the spring and summer. When larvae were captured, they were entangled in the leading meshes of the trawl with only a few reaching the cod end liner.

Very small herring larvae (< 9 mm standard length) were present in October and November. (Fig. 7). Recruitment of these small larvae ended in December when both the range and mean length increased considerably. From October through May there was a consistent increase in length. In the fall to early winter months, smaller larvae were captured in the Sheepscot than in the other areas. Most of the larvae (1,530) were captured in the fall with a surface meter-net tow; the remainder (188) were captured during the spring when otter trawling.

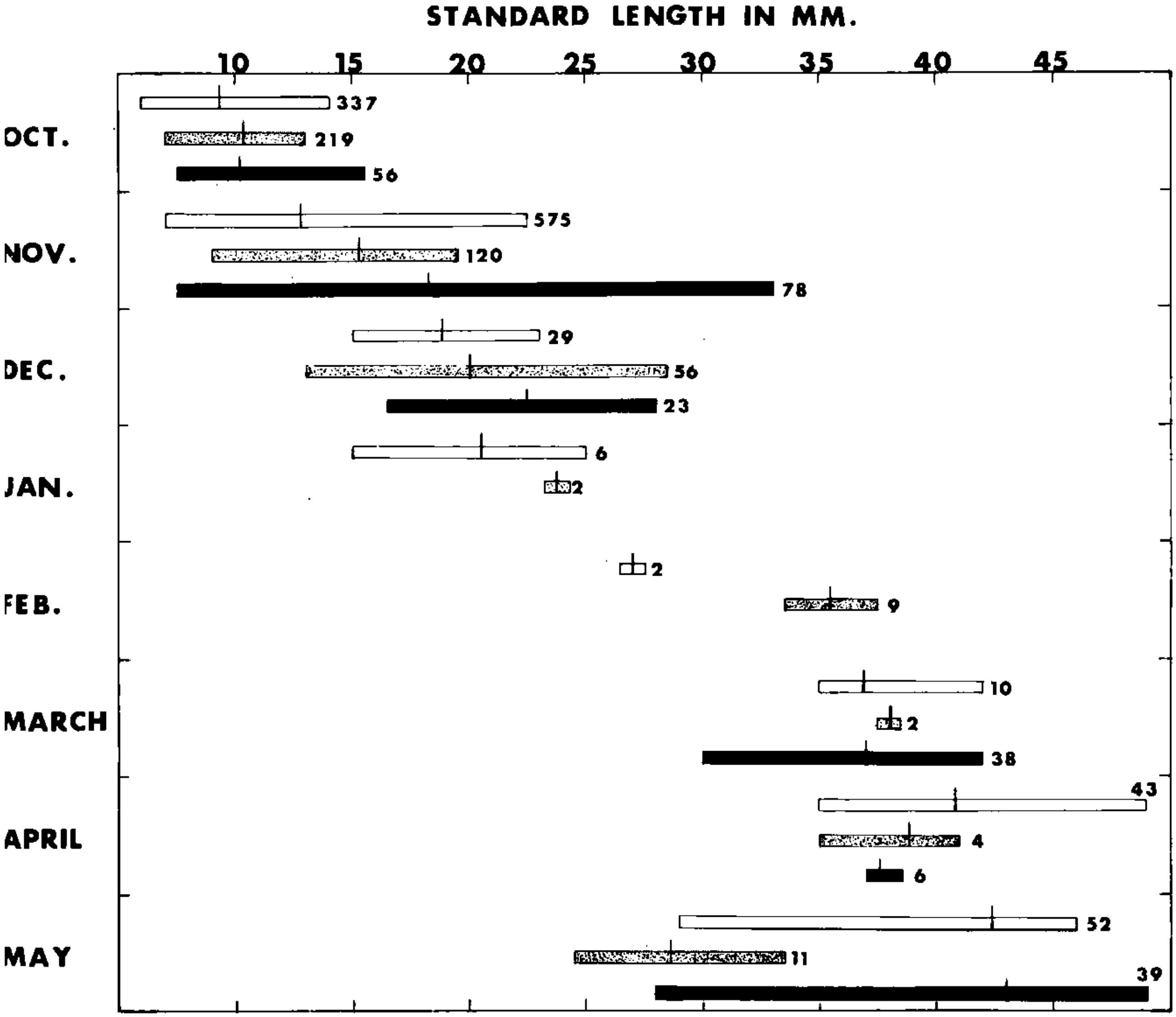

Fig. 7. Monthly average length (vertical line) and range (bars) of larval herring captured in meter net and otter trawl tows. The light, stipled, and dark bars represent the Sheepscot, Boothbay, and Damariscotta areas, respectively. The number of fish measured is given to the reader's right for each bar.

In contrast to the fall distribution of herring, larvae of other fishes were caught in largest numbers during the spring and summer. Monthly catches of other larvae were generally highest in the Damariscotta area and lowest in the Sheepscot; an extensive period of low catches occurred between October and February. The more abundant species during the spring months were: *Ammodytes americanus, Myxocephalus scorpius,* and *Pholis gunnellus;* and during the summer months: *Ulvaria subbifurcata, Enchelyopus cimbrius*, and *Cyclopterus lumpus*. The numbers, and mean standard lengths of larvae other than herring are given in Table 2. Unlike herring larvae, some species showed no consistent increase in mean length.

The seasonal occurrence of other juvenile and adult fishes in the otter trawl catches is shown in Fig. 8. Although there is some variation from month to month, peaks in relative abundance appeared in the fall and spring, with lows in the summer and winter.

TABLE 2. NUMBER AND MEAN LENGTH OF FISH LARVAE, OTHER THAN HERRING, CAPTURED IN THE SHEEPSCOT-BOOTHBAY-DAMARISCOTTA REGION OF MAINE, 1961-62. (EELS, *ANGUILLA ROSTRATA*, WERE IN THE ELVER DEVELOPMENTAL STAGE.)

	JUNE	JULY	AUG.	SEPT.	OCT.	NOV.	DEC.	JAN.	FEB.	MAR.	APR.	MAY
Cyclopterus lumpus	16/6.7	24/4.7	47/5.3	48/6.3	12/10.2	3/9.0		1/5.9	62/6.3	179/7.2	151/11.6	75/7.5
Ulvaria subbifurcata	18/7.9	826/7.3	861/8.7	378/8.8	36/7.9	4/11.8					6/7.0	1183/7.1
Gadus morhua	4/28.3											
Urophycis chuss	1/5.0	1/68.5	8/3.2	16/6.2	19/3.5	2/9.4						
Gasterosteus aculeatus	2/19.5	1/18.5	1/34.0			1/27.0						1/32.0
Enchelyopus cimbrius		1/42.5	53/4.4	143/4.2	208/3.5	1/23.5						
Syngnathus fuscus			9/16.7	1/18.5								
Scophthalmus aquosus			9/3.1	5/3.9	2/3.5							
Merluccius bilinearis			29/3.2	3/3.2								
Glyptocephalus cynoglossus			4/3.2	1/3.5	5/6.7							
Sebastes marinus				5/38.0								
Tautogolabrus adspersus			52/4.4	38/4.6	9/3.3							
Scomber species			5/3.3									
Pollachius virens							1/143.5					
Pholis gunnellus								19/11.9	426/10.2	4150/13.4	775/12.6	62/13.1
Gadus or Pollachius species									9/24.9	17/22.8	39/25.7	95/25.1
Lumpenus lumpretaeformis								6/17.8	16/18.2	16/18.6	6/18.8	15/18.4
Myoxocephalus scorpius								30/7.5	299/7.6	942/9.9	334/12.2	92/15.1
Cryptacanthodes maculatus									23/18.9	151/18.7	99/20.1	6/30.0
Anarhichas lupus									1/5.0	1/8.5		
Ammodytes americanus								1/6.5	2/5.4	115/5.4	200/18.3	196/21.2
Anguilla rostrata									1/55.0	3/56.8	9/57.6	3/59.3
Aspidophoroides monopterygius											5/9.6	30/12.2
Myoxocephalus octodecemspinosus											51/6.4	32/6.8
Melanogrammus aeglefinus											6/5.9	
Limanda ferruginea												7/5.2

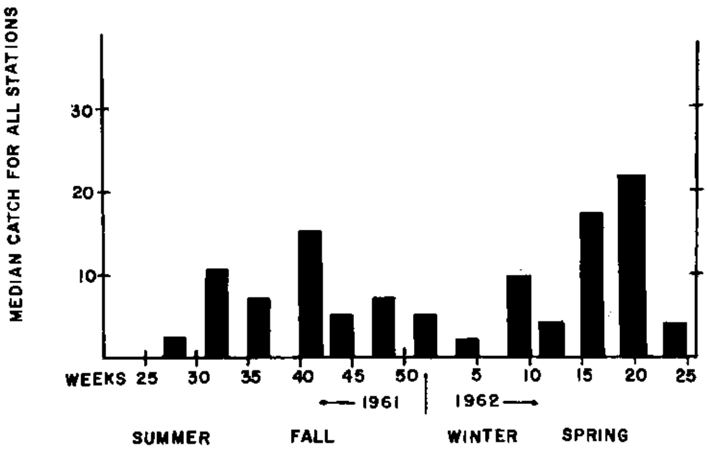

Fig. 8. Seasonal variation in the number (median) of fishes other than herring captured by 20-min otter trawl tows.

DISCUSSION

Distribution of larval herring

In the Gulf of Maine, the largest spawning grounds are found on the northern edge of Georges Bank and off the Nova Scotia coast (Tibbo *et al.*, 1958). Non-tidal drift suggested that some newly hatched larvae, determined by size (< 9 mm), were carried northward from Georges Bank to the Nova Scotia coast, but the majority were carried southward. Few inshore spawnings have been reported and confirmed and there is no evidence of large spawning grounds along the Maine coast.

The presence of very small herring larvae in the Sheepscot-Boothbay-Damariscotta region suggested that their source was local. Recent catches of herring with gonads in a running state and catches of yolk-sac larvae were recorded from the vicinity of station 11 during the fall of 1963. Regardless of their source, larvae in their early planktonic stage would have obtained some assistance from currents to introduce or maintain themselves in the bays and estuaries. This assistance could be in the form of both non-tidal and tidal currents. The presence of the greatest numbers of larvae in the Sheepscot area suggested that transport by non-tidal currents was important. The Sheepscot estuary is influenced by freshwater discharge while the Boothbay area has no major streams entering it. The Damariscotta area has a smaller stream entering it and its effects are masked by considerable turbulence. In the Sheepscot estuary the discharge of river water was lowest in the fall and vertical sigma-t gradients were largely a function of thermal stratification rather than changes in salinity. Vertical density gradients in the Sheepscot were not steep and a two layered estuary would be poorly developed for conveying larvae inward along the bottom. In contrast, a lateral flow would be accentuated by water of lower salinity entering from the Kennebec River. This water enters the Sheepscot from Goose Rock Passage and flows southward along the western side of the estuary. Tidal currents could transport larvae in water eddying behind promontories (Stommel, 1953) and other rugged features common to the region. Stranding of larvae in an eddy would make it possible for advancement upstream on the next flood tide.

The distribution of other larvae complements that of herring. Many of these larvae were obtained in a planktonic stage and presumably were susceptible to transport by currents, particularly in the spring when river discharge was at its height. Their distribution could be associated with their behavioral attributes or to the location of spawning grounds; little is known locally of either aspect of their biology.

Avoidance of net and migration

Catches of herring larvae decreased with an increase in larval size. Bridger (1956) found that more clupeid larvae were taken with a 1-m silk tow net and other nets at night. He suggested that the lower catches of larvae by daylight were related to avoidance of the net by larger larvae and discounted the possible effects of shoaling, dispersal, and congregation near the bottom by day. Colton (1961) found that escapement and diurnal migrations influenced the catches of larval herring in the Gulf of Maine. His tows were limited to 10 m and were made with a 1-m plankton net. The seasonal abundance of herring larvae in this study was similar to that obtained in the Gulf of Maine and the Bay of Fundy (Tibbo *et al.*, 1958; Colton *et al.*, 1961). That is, 1) larvae were captured in greatest numbers in the fall, 2) catches were subsequently small during the winter months, 3) recruitment of newly hatched larvae was completed by the winter months. While the sharp drop in larval catches was probably related to escapement as indicated by Colton *et al.* (1961) the movement of fish from the vicinity of the sampling stations was also suspect. Recently, explorations were made upstream of station 1 in the Sheepscot, during the winter and early spring, and a concentration of larvae was found. Their size (30 - 35 mm) agreed with the growth expected since the fall. Apparently, herring larvae overwinter in the Sheepscot. To test this hypothesis this upstream area is being sampled routinely with high speed sampling gear and samples are taken from the surface to the bottom.

CONCLUSIONS

This study provided the first evidence that herring larvae utilize the estuarine environment along the Maine coast. The distribution of herring larvae differed in the three adjacent embayments studied. More herring were captured in the Sheepscot area than the Boothbay and Damariscotta areas. Differences in the seasonal distribution of herring larvae were marked, with the greatest abundance occurring in the fall. The seasonal and areal distribution of other fish larvae was inverse to that of herring larvae. Eastward from the Sheepscot to the Boothbay and Damariscotta areas average salinities, surface temperatures, and surface standing crops of zooplankton increased.

REFERENCES

BHATTACHARYYA, R.N. 1957. The food and feeding habits of larval and post larval herring in the Northern Sea. *Mar. Res.*, no. 3, 16 p.

BRIDGER, J.P. 1956. On day and night variation in catches of fish larvae. *J. Cons.*, 22 (1): 42-51.

COLTON, J.B., Jr., K.A. HONEY and R.F. TEMPLE. 1961. The effectiveness of sampling methods to study the distribution of larval herring in the Gulf of Maine. *J. Cons.*, 26 (2): 180-190.

HOPKINS, THOMAS L. 1963. The variation in the catch of plankton nets in a system of estuaries. *J. Mar. Res.*, 21 (1): 39-47.

SMAYDA, THEODORE J. 1957. Phytoplankton studies in lower Narragansett Bay. *J. Limnol., Oceanogr.*, 11 (4): 342-359.

SNEDECOR, GEORGE W. 1948. *Statistical Methods*. Fourth Edition, Ames, Iowa, Iowa State College Press, 485 p.

STICKNEY, ALDEN P. 1959. Ecology of the Sheepscot River estuary. *Spec. sci. Rep. U.S. Fish Wildl. Serv. - Fish.*, No. 309, p. 1-21.

STOMMEL, HENRY. 1953. The role of density currents in estuaries. *Proceedings Minnesota International Hydraulics Convention*, 1-5 September, 1953. (Contribution no. 655, Woods Hole Oceanographic Institution, p. 305-312).

TIBBO, S.N., J.E. HENRI LEGARE, LESLIE W. SCATTERGOOD and R.F. TEMPLE. 1958. On the occurrence and distribution of larval herring (*Clupea harengus* L.) in the Bay of Fundy and the Gulf of Maine. *J. Fish. Res. Bd. Canada*, 15 (6): 1451-1469.

U.S. GEOLOGICAL SURVEY. 1962. Surface water records of Maine 1961. District Engineer, Surface Water Branch, *U.S. Geological Survey*, Augusta, Maine, 70 p.

1962*a*. Sheepscot River discharge, October 1961 to September 1962 (Provisional). District Engineer, Surface Water Branch, *U.S. Geological Survey*, Augusta, Maine, Mimeographed, 1 p.

E-8

DISTRIBUTION OF WINTERING HERRING IN THE SOUTHERN PART OF THE NORWEGIAN SEA ACCORDING TO TEMPERATURE CONDITIONS

By

L.R. Shmarina[1]

ABSTRACT

This contribution deals with the influence of the temperature conditions of the southern part of the Norwegian Sea on the distribution of herring concentrations in the wintering and spawning periods.

The main features of mature herring distribution in the Norwegian Sea while wintering are of a regular character. Due to the hydrological conditions, however, both the distribution of herring and the time and migration routes display certain divergences. In the present paper an attempt is made to demonstrate the influence of winter temperature conditions according to the data obtained in 1958-63.

In November - January great concentrations of pre-spawning herring form in the southern part of the Norwegian Sea, north of the Faroes. From January, herring move then to the spawning grounds located along the western coast of Norway.

The changes in the hydrological conditions in this above-mentioned region are defined by interaction of the cold East-Icelandic and the warm Atlantic waters and have a great influence on the movements of herring.

To show the temperature conditions of the wintering area, charts of surface temperature are compiled for the second half of November and December for the years 1958-62. Also schemes of vertical temperature distribution in the western part of the section along 65°46'N are drawn, with the locations of herring concentrations indicated. For estimation of temperature conditions in the areas of pre-spawning migrations and on spawning grounds, charts of surface temperatures for January, February and March, 1959-63, are constructed where the boundaries of herring distribution are traced (Fig. 1-6). Mean temperatures on standard sections in the southern part of Norwegian Sea are also calculated for these same years.

The month of November is the beginning of the wintering period for herring. In December commercial concentrations of herring are distributed over the small area along the western edge of the East-Icelandic Current. In January pre-spawning herring concentrations start moving eastward to the west coast of Norway. February is characterized by the ending of the wintering period for the pre-spawning herring concentrations and they leave the cold waters for the upper layers of the warm Norwegian Current and move to the spawning grounds.

WINTER SEASON OF 1958-59

In November-December 1958 at the section along 65°45'N "the dome" of the cold East-Icelandic Current with temperature 2° to 3°C was well developed and reached to the 50 m layer (Fig. 1a,b). Warm waters of the Norwegian Current, however, penetrated on the surface far out to the north-west. Herring concentrations kept at the western edge of the East-Icelandic Current in the 0-50 m layer at the temperature of 3° to 5°C. In the period from November to January considerable displacement of the wedge of the East-Icelandic Current to the south-east took place. In January at the section along 63°00'N, mean temperature in the 0-50 and 0-200 m layers of this Current was about 6.1° to

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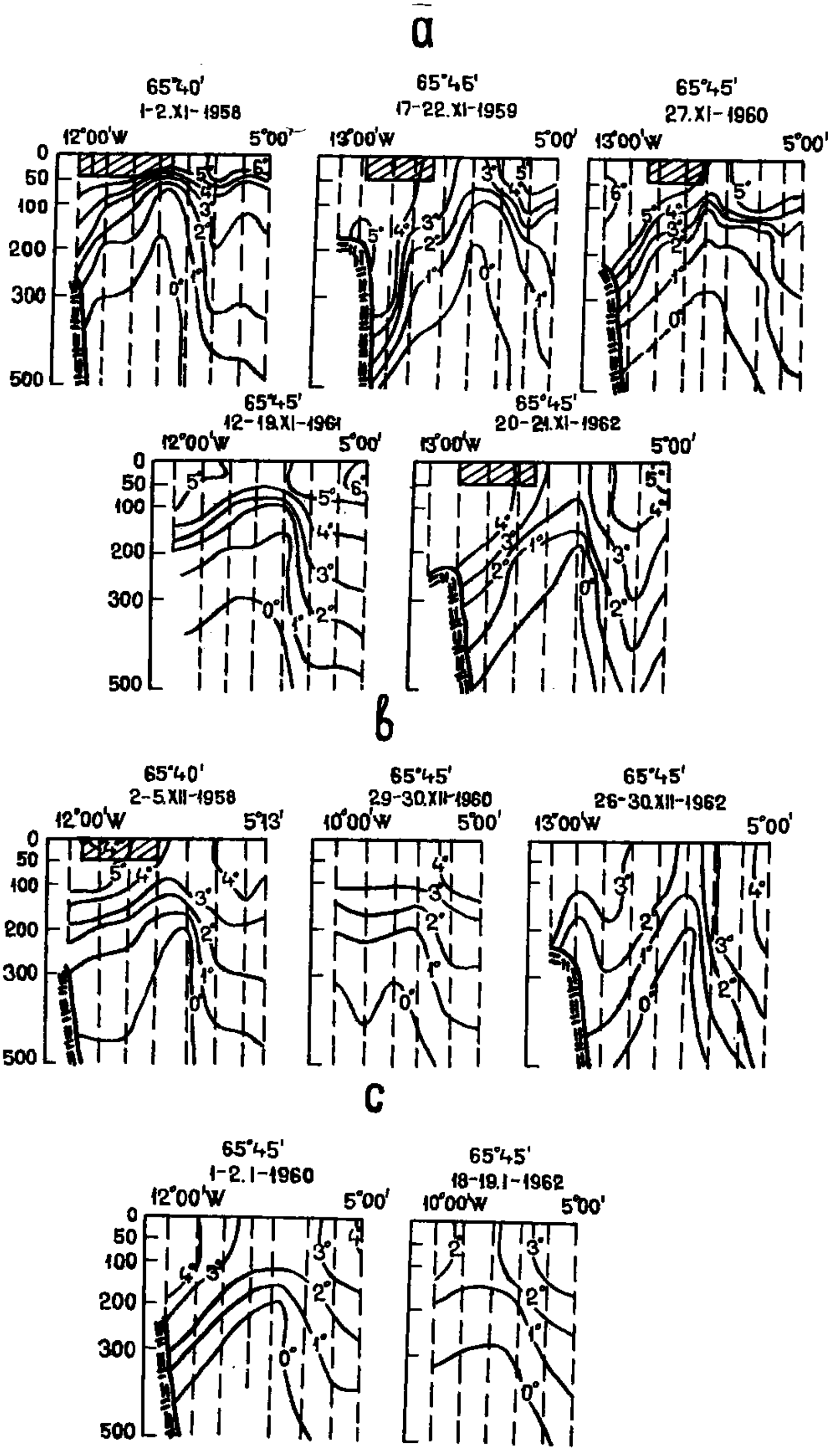

Fig. 1. Schemes of vertical temperature distribution and the limits of herring concentrations (shaded area) in the western part of the section along 65°45'N in winter.

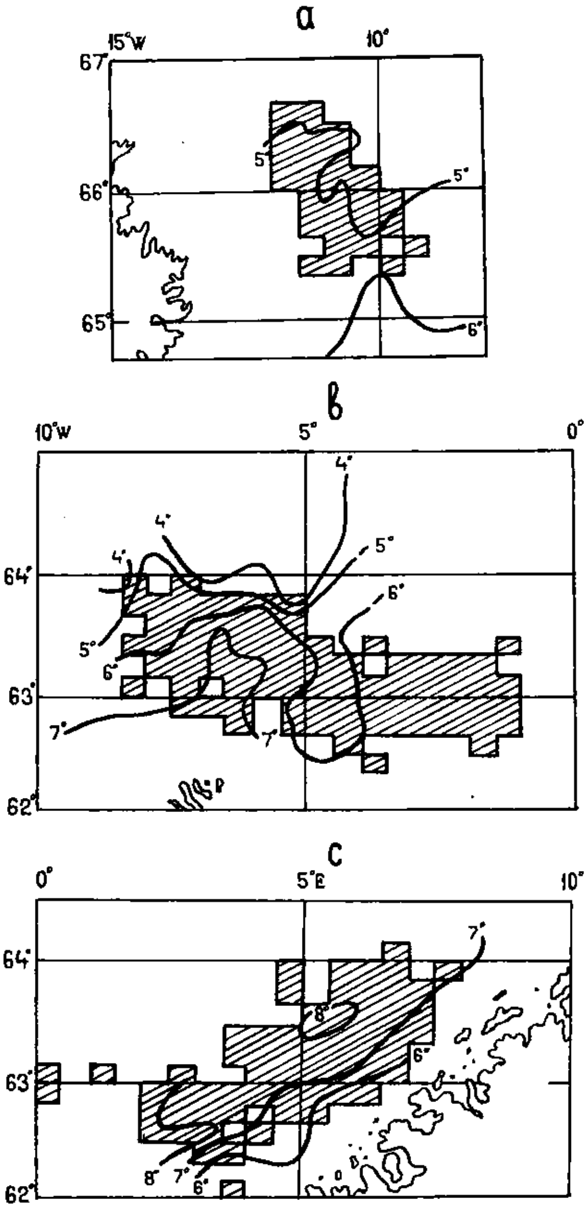

Fig. 2. Distribution of temperatures of the sea surface and the area of herring concentrations (shaded) in winter: 1958-1959.

6.4°C. Commercial herring concentrations were distributed northeast of the Faroes (Fig. 2b).

In January and at the beginning of February pre-spawning herring concentrations moved in the direction of the Norwegian Shallow. In early February, the water temperatures at the sections along 63°00'N in the Norwegian Current were homogeneous at 7.4°C.

In the waters of the continental shelf the highest mean temperature (7.73°C) for the period in question was observed. Herring came to spawn at the beginning of February and their concentrations were located near the coast (Fig. 2c).

WINTER SEASON OF 1959-60

Since the end of 1959 increased influx of the Atlantic waters into the Norwegian Sea was observed. In November 1959, however, "the dome" of the cold waters of the East-Icelandic Current at the section along 65°45'N was still well developed and its waters (2° to 3°C) reached the surface (Fig. 1a).

Herring concentrations were distributed along the western edge of the East-Icelandic Current about 20-30 miles farther to the south than in 1958 (Fig. 3a).

From November 1959 to January 1960, due to the increased inflow of the Atlantic waters, the wedge of the East-Icelandic Current displaced to the west, mean temperature at the section along 65°45'N in the 0-50 m layer having decreased by 0.9°C. Commercial herring concentrations were located over a small area north-west of the Faroes (Fig. 3b). Spawning migrations of the winter concentrations of herring to the Norwegian Coast took place in February and was a little bit prolonged (Fig. 3c). In February 1960 mean temperature in the 0-50 and 0-200 m layers at the section along 63°N in the Norwegian Current was 0.4° to 0.5°C higher than in the same period of 1959. The bulk of herring came to spawn in the beginning of February, but part of the concentrations kept north-east of the Faroes (Fig. 3c).

WINTER SEASON OF 1960-61

In November of 1960 in the waters of the East-Icelandic Current at the section along 65°45'N the highest mean water temperatures were registered, which in the 0-50 and 0-200 m layers were 5.37°C and 3.83°C respectively.

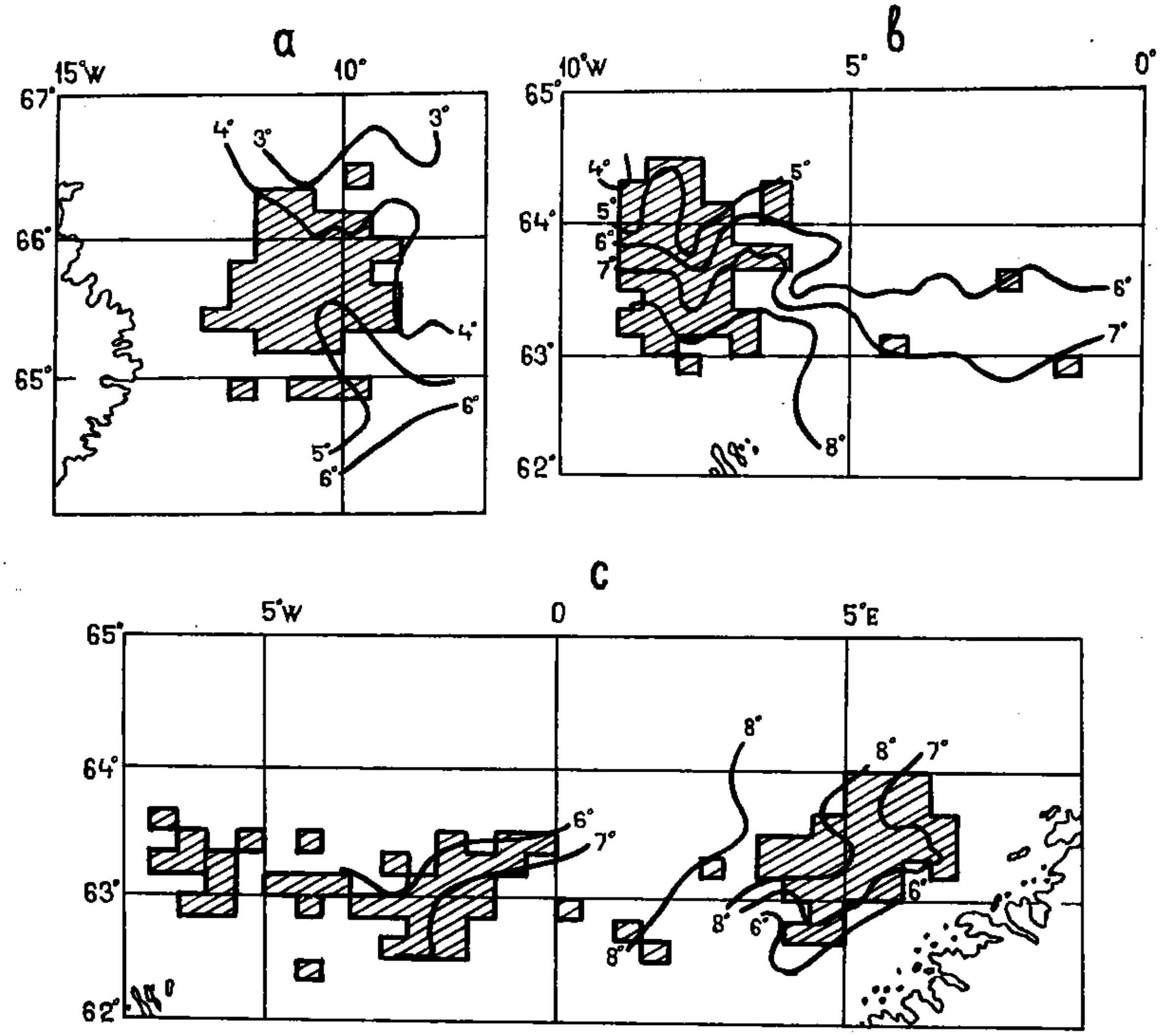

Fig. 3. Distribution of temperatures of the sea surface and the area of herring concentrations (shaded) in winter: 1959-1960.

"The dome" of cold waters was developed poorly (Fig. 1a). Warm waters of the Norwegian Current spread far out to the north-west. During December no appreciable changes in temperature distribution in the area of the wedge of the East-Icelandic Current took place.

In the beginning of January 1961, in the southern part of the Norwegian Sea (section along 63°00'N) the highest water temperature for the whole period examined was observed in the East-Icelandic and Norwegian Currents. In the East-Icelandic Current mean temperatures at the abovementioned section were 7.1° to 7.3°C in the 0-50 and 0-200 m layers, whereas in the same layers of the Norwegian Current 8.2° to 8.3°C. Commercial herring concentrations were distributed farther to the north-west than in 1959-60 (Fig. 4b).

At the beginning of February 1961, the mean temperature in the 0-50 and 0-200 m layers of the Norwegian Current at the section along 63°00'N decreased by 0.5° to 0.6°C in comparison with November 1960, but was somewhat higher than in February 1959, while temperature on the continental shallow was 0.9°C lower. Part of the herring concentrations approached the Norwegian coast for spawning in the early February and was distributed farther to the south-west in comparison with the same periods of 1959 and 1960. Main concentrations of herring delayed in the area north of the Faroes and came to spawn later (Fig. 4c).

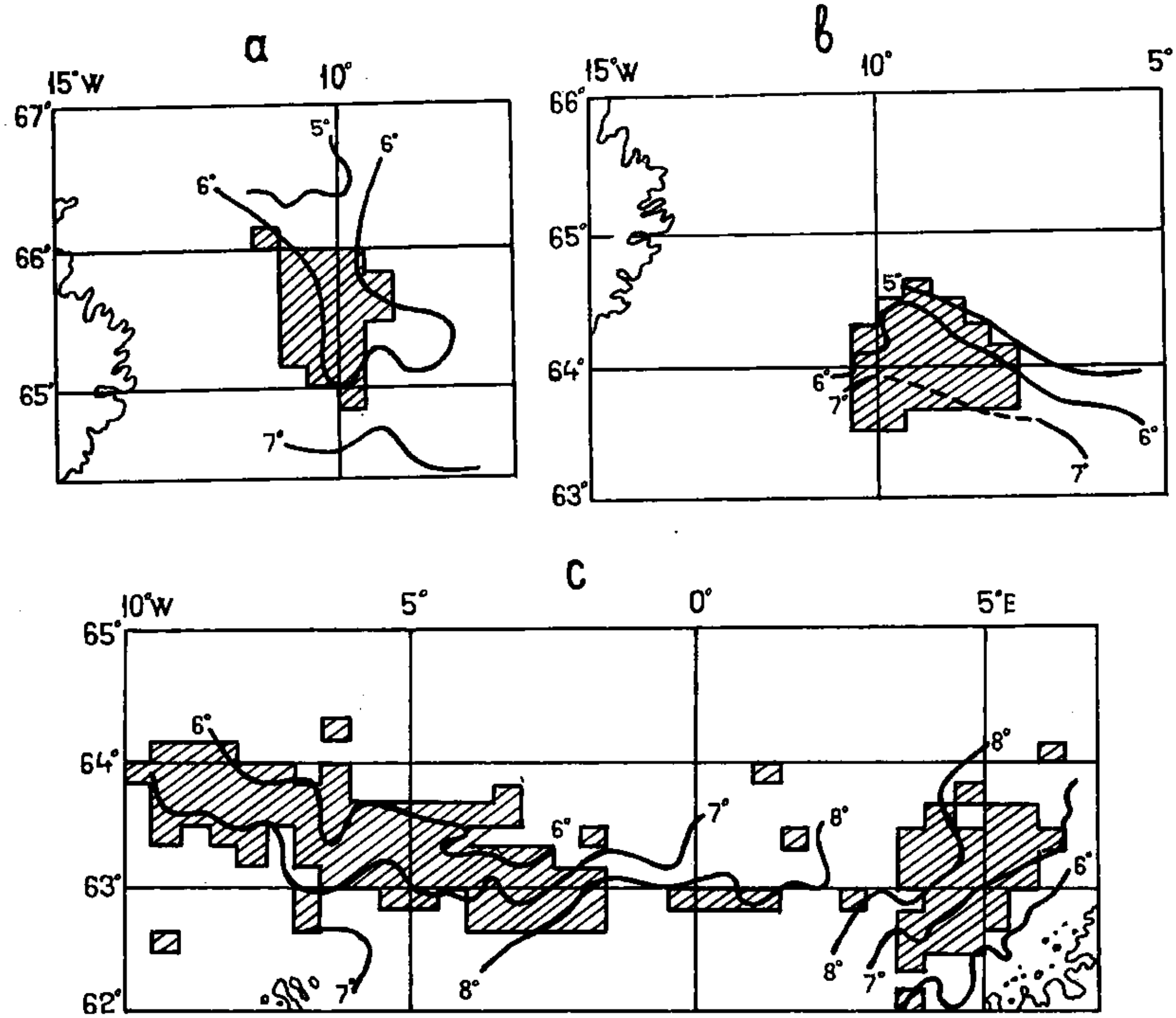

Fig. 4. Distribution of temperatures of the sea surface and the area of herring concentrations (shaded) in winter: 1960-1961.

WINTER SEASON OF 1961-62

In November 1961, in the southern part of the Sea, relatively great warming of the Norwegian Current was observed. At the section along 65°45'N "the dome" of the cold East-Icelandic Current was poorly developed (Fig. 1a). Mean temperature in this Current in the 0-200 m layer was at the level of the warm year of 1960. Herring concentrations were located in the north-western part of the area (Fig. 5a).

In November-January in the area of the wedge of the East-Icelandic Current considerable decrease in temperature took place. In January 1962 at the section along 65°45'N the waters of the East-Icelandic Current, the area of mixed waters, the western branch and the waters of the continental shallow were much colder than in 1959 and 1960. In the East-Icelandic Current mean water temperature in the 0-200 m layer decreased by 1.5°C in comparison with that in November 1961. In the period from November to January the southern boundary of herring concentrations displaced 60 miles to the south. In February, herring concentrations spread along the western edge of the cold current (Fig. 5d) and moved very slowly eastwards.

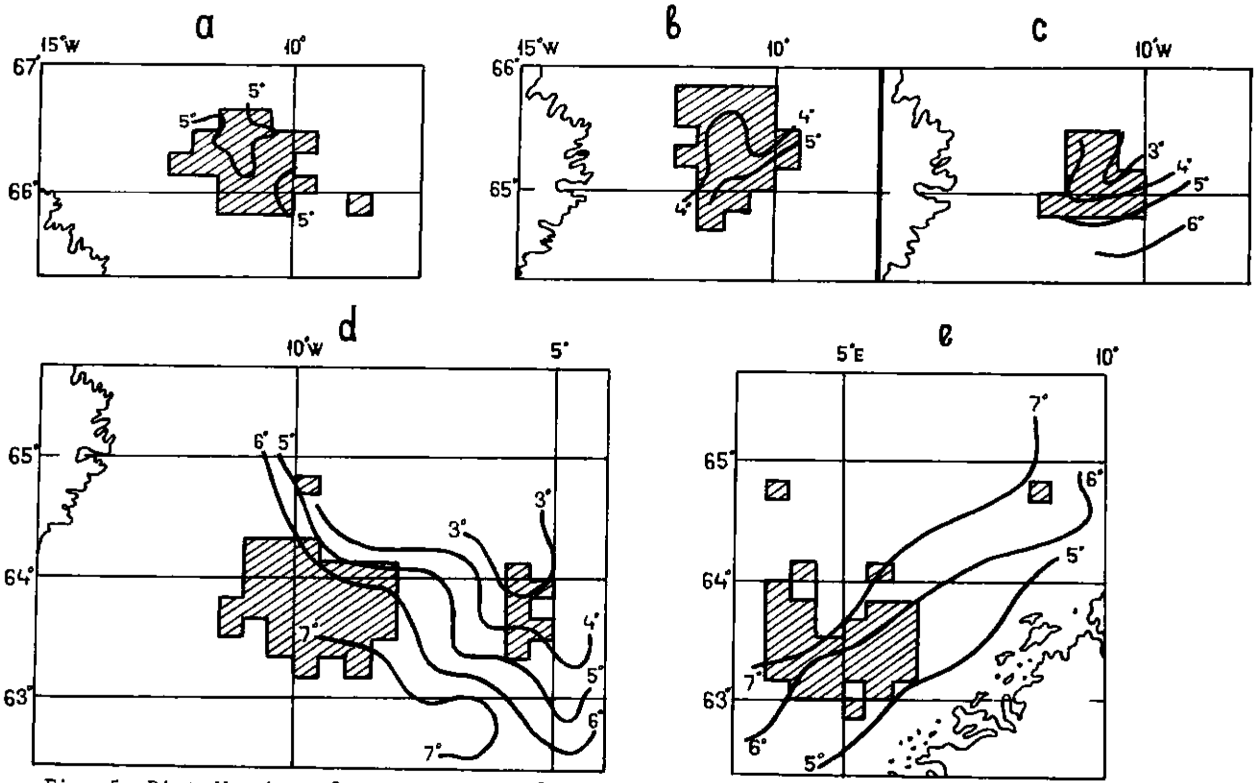

Fig. 5. Distribution of temperatures of the sea surface and the area of herring concentrations (shaded) in winter: 1961-1962.

In March of 1962 in the southern part of the Norwegian Sea (section along 63°00'N) mean temperature of the waters of the Norwegian Current in the 0-50 and 0-200 m layers was 0.9° to 0.6°C lower than that in 1959. Herring came to spawn to the western coast of Norway at the beginning of March, *i.e.* a month later than in 1959 (Fig. 5e).

WINTER SEASON OF 1962-63

In November - December of 1962, the cold waters of the East-Icelandic Current at the section along 65°45'N extended to the surface (Fig. 1 a,b); mean temperature in the 0-50 m layer was the lowest (3.77°C). Commercial concentrations of herring were displaced to a considerable extent to the south-east.

In December - January further cooling of the East-Icelandic and the Norwegian Current took place. In the middle of January 1963, mean temperature of the East-Icelandic Current (section along 63° 00'N) in the 0-50 and 0-200 m layers was at the level of the same period of 1962. In the 0-50 m layer the waters of the Norwegian Current were 0.3°C colder and those of the continental shallow more than 1°C colder. Herring concentrations were observed north-west of the Faroes (Fig. 6c).

In February 1963, in the waters of the Norwegian Current and those of the continental shallow minimum temperature was observed for the whole period considered. Herring concentrations were distributed in a large area from the Faroes along the edges of the East-Icelandic Current and in the warm waters of the Norwegian Current (Fig. 6d).

In March, in the waters of the Norwegian Current and the continental shallow temperature conditions analogous to those in March of 1962 were registered. As in the previous year, herring came to the Norwegian coastal shallows in the beginning of March (Fig. 6e).

For the characteristics of year-to-year displacement in the position of the wedge of the East-Icelandic Current in winter, a chart of the position of 5°C isotherm on the sea surface for the second part of November 1959-62 was drawn, where the boundaries of herring distribution were marked (Fig. 7).

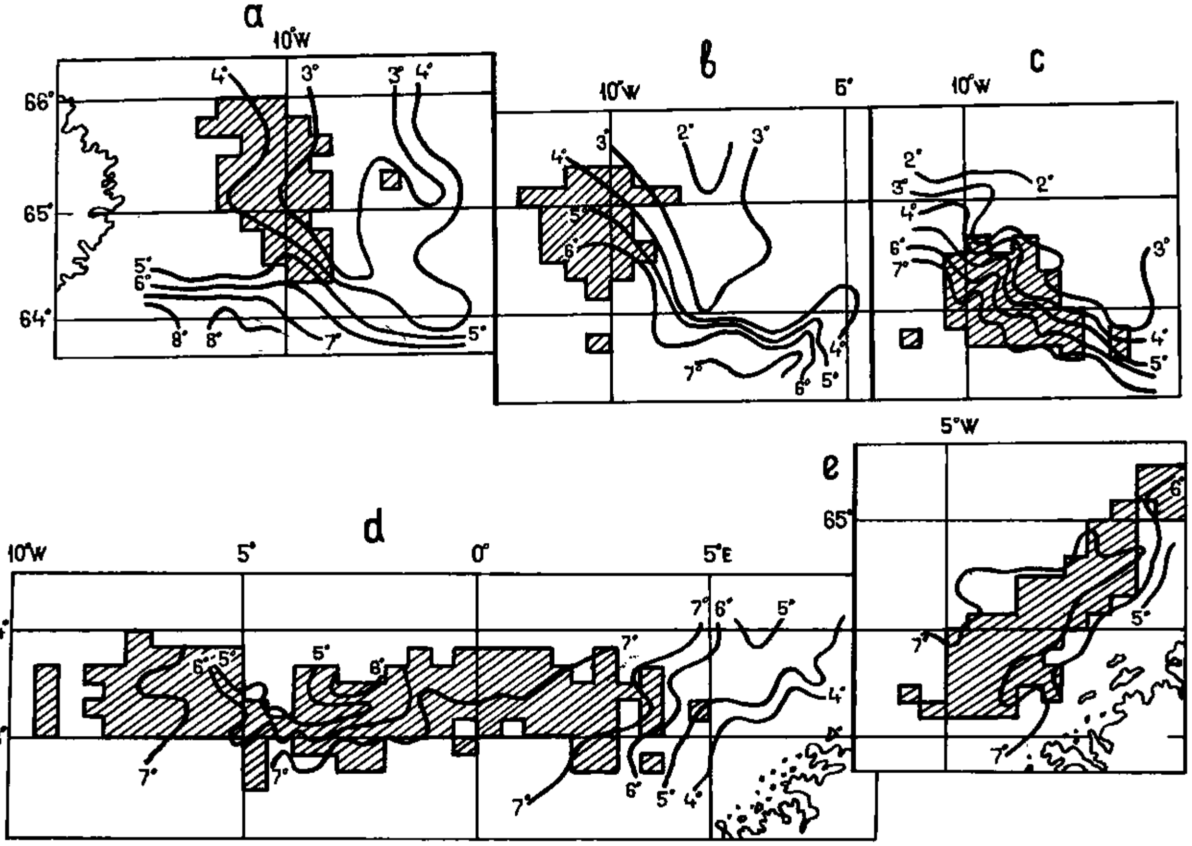

Fig. 6. Distribution of temperatures of the sea surface and the area of herring concentrations (shaded) in winter: 1962-1963.

As is evident from the chart, in November 1961, when in the waters of the East-Icelandic Current high temperatures were observed, the 5°C isotherm was in the most north-western position. In November 1962, considerable decrease in temperature in the surface layers of the Current was registered; the waters of the Current being wide spread on the sea surface. The 5°C isotherm was 120-130 miles farther south-east than in the previous years. In 1959 and 1960 the isotherm took the central position.

Thus, the distribution of herring concentrations in the southern part of the Norwegian Sea in winter (November-December) depends to a considerable degree on the temperature conditions in the wedge of the East-Icelandic Current. For example, in November - December 1961 when in the waters of the East-Icelandic Current high temperatures were observed, commercial concentrations of herring were displaced far to the north-west. In 1962, low heat content of the waters of this current was registered and herring concentrations were located at the most south-eastern position. In November-December 1959, 1960 (the years with moderate thermal conditions) the position of herring concentrations was intermediate (Fig. 7).

The water temperatures in the southern part of the Norwegian Sea in January - February 1959, 1960 being higher, herring came to spawn to the western coast of Norway earlier, whereas in the same period of 1961, 1962 and 1963 when the heat content of the waters of the Norwegian Current and those of the continental shallow was low, the arrivals of pre-spawning herring were late and their concentrations spread more to the west and south-west in comparison with the position they had in 1959 and 1960 (Fig. 8).

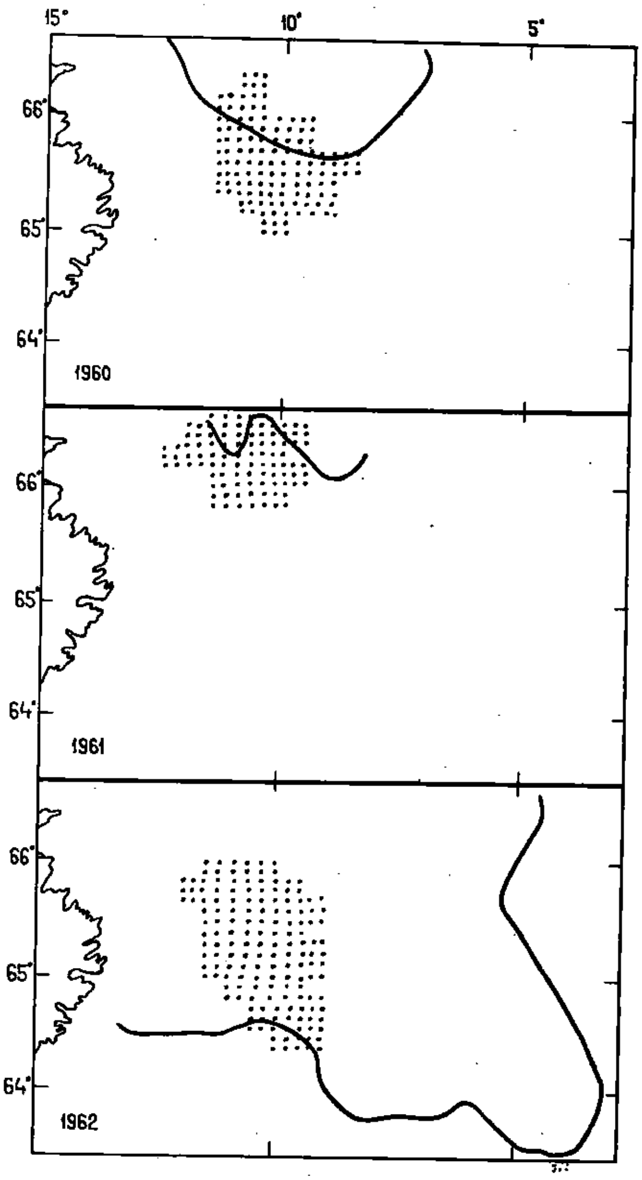

Fig. 7. Position of 5°C isotherm on the sea surface and boundaries of herring distribution in the wintering period, 1960–1962.

More north-western and south-eastern positions of herring concentrations in November - December in the wintering area are in good consent with the analogous displacement in the spawning area in February, which is due, apparently, to the temperature regime of the waters of the Norwegian and the East-Icelandic Currents in the southern part of the Sea in this period of time.

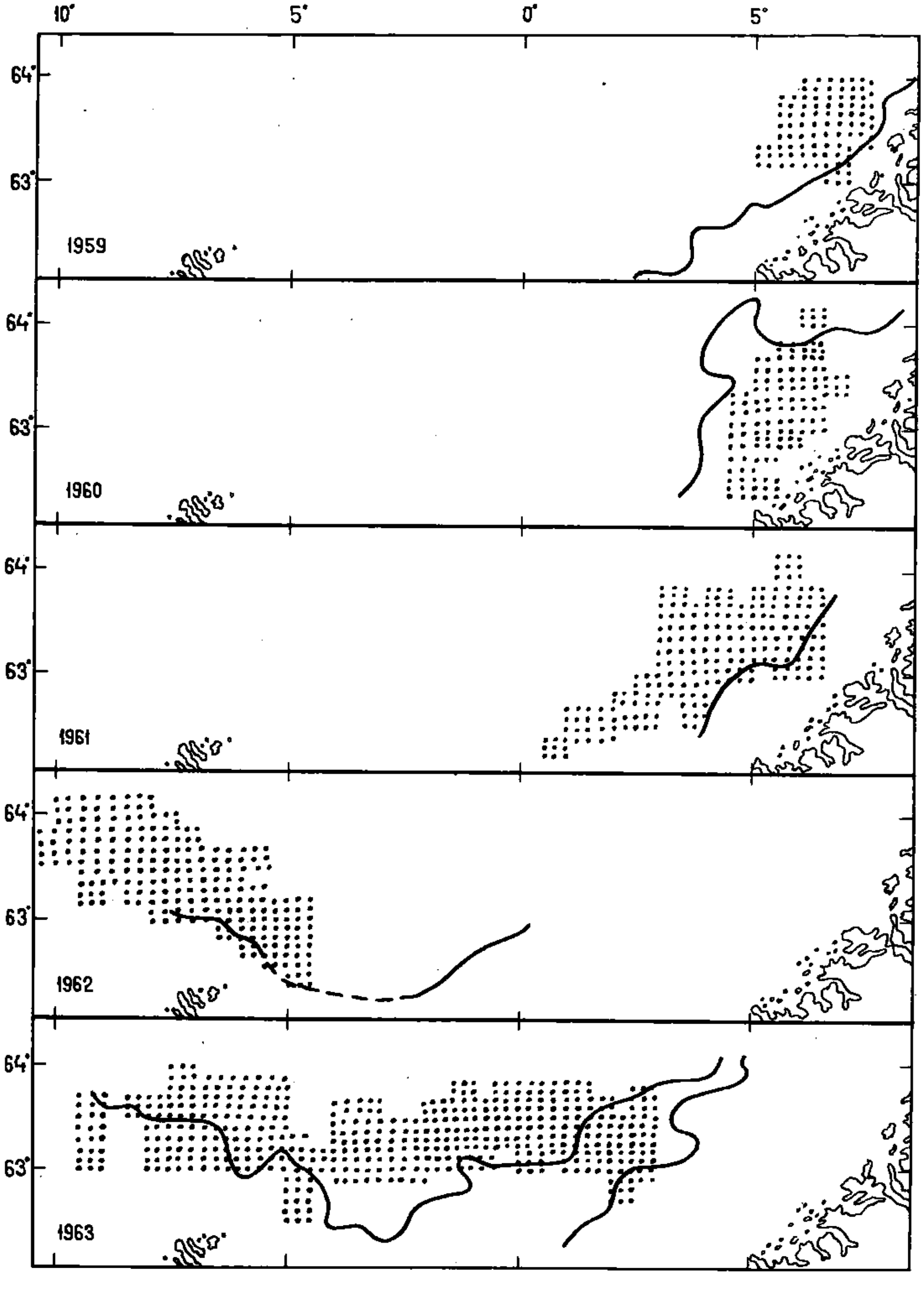

Fig. 8. Position of 7°C isotherm on the sea surface and the boundaries of herring distributions during the spawning period, 1959-1963.

SECTION

F

F-1

POSSIBLE EFFECTS OF OXYGEN LACK ON SHOALING FISH

By

K. Kalle[1]

ABSTRACT

This paper suggests that a critical shortage of oxygen may be the cause of the so-called vertical "swim" of dense herring shoals.

It is a well known fact in the herring fishery that herring shoals sometimes rise suddenly from the bottom layers to the surface. The vertical "swim", mainly observed in dense spawning shoals, is assumed to be due to a panic caused by predators chasing the herring. Other causes might be tidal effects, the narrowing of the shoal while approaching shallow water, or sudden internal stimuli. Besides these factors, decrease of oxygen below a critical level may be considered. In contrast to conditions for freshwater fish the oxygen supply for marine fish is normally sufficient. In very dense aggregations of fish with a high metabolic rate, however, a shortage of O_2 may occur. A hypothesis may be produced to explain the swim as a result of decreasing O_2 supply in a densely-packed shoal of herring. As long as the shoal is moving through the water and as long as the tidal currents cause some turbulence the O_2 content of the water occupied by the shoal will always remain high by continuous renewal.

Critical reduction of O_2 within the shoal may occur under the following conditions:
(a) during the slack period when turbulence is at a minimum
(b) in calm weather
(c) while the shoal is not moving, *e.g.* while it is concentrated on the spawning ground.

In addition to this reduction in exchange of water, an increase of shoal density or of the metabolic rate, or both, of the single fish due to external and internal stimuli will accelerate the reduction in O_2 inside the shoal.

The reduction of O_2 by the respiratory activity of the shoal may be estimated as follows:
(1) Weight of herring 150 g
(2) (a) O_2 consumption 90 mg O_2/kg/hr
    therefore
  (b) O_2 consumption per herring 13.5 mg O_2/hr
(3) (a) space occupied by a single herring assumed as about ten times its volume of 1500 ml,
    therefore
  (b) volume of water available 1350 ml per fish
(4) (a) O_2 saturation in seawater 9.6 mg O_2/l. (Salinity 35 /oo, temperature, 8°C)
    therefore
  (b) O_2 available to herring in 1350 ml is 12.96 mg.
(5) (a) minimum level of O_2 content for unrestricted respiration 3.5 mg O_2/liter, *i.e.*
    4.73 mg O_2 in 1350 ml.
(6) No replacement of O_2 within the shoal.

Each of the statements in this balance sheet may now be discussed.

(1) The average weight of herring in a shoal varies considerably within and between the different races but an individual weight of 150 g is reasonable for adult North Sea herring.

However,

(2) data on the metabolic rate of herring are not available. The value given was derived from measurements by Sundnes (1959) on gadoid fish. A cod of 1,750 g total weight had an O_2 consumption

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[1] Hamburg 13, Rothenbaumchaussee, 22, Germany.

of 50 mg O_2/kg/hr, and a coalfish of 1,020 g had an average consumption of 67 mg O_2/kg/hr. For herring, with its much smaller body size and rather high activity, the value of 90 mg/kg/hr should be regarded as an underestimate. Several measurements by Fry (1957) and other workers suggest that for salmonids of comparable size and under similar temperature conditions, values of 150-200 mg O_2/kg/hr are reasonable.

(3) Not much is known so far about the water volume per herring within the shoal because measurements of the volume of a herring shoal and the number of fish in this shoal are very difficult. The individual swimming space, *i.e.*, volume of the shoal divided by the number of fish in the shoal, is not constant. Observations in tanks show that fish close up if they are irritated and scatter while feeding. In the open sea an increase in shoal density may occur due to stimulation by gear or predators or during spawning.

(4) A temperature of 8°C will apply for the northern spawning grounds of the North Sea herring. It is an overestimate for Atlanto-Scandian spring spawners but an underestimate for the herring spawning in the central and southern North Sea and the English Channel and for some groups of Baltic herring. At higher temperature the O_2 saturation is reduced while the metabolic rate is increased. In addition the O_2 content of the bottom water is slightly lower than that of the upper layers.

(5) The critical level of the respiratory demand of herring is not known. But compared with other fish *e.g.* gadoids and salmonids (Sundnes, 1957 and Job 1955) 3.5 mg O_2/liter seems reasonable.

(6) The prerequisites for this assumption were listed earlier.

Using the above figures the O_2 supply available per herring for unrestricted respiration will be 8.23 mg O_2, *i.e.* the difference between the values for O_2 in (4b) and in (5a) above. The duration of unrestricted respiration is given by this amount of O_2 available and the respiratory rate of herring (2b).

$$8.23/13.5 \text{ hr} = 36.5 \text{ min}.$$

Thus, under the circumstances assumed in these calculations,critical shortage of O_2 in the shoal will occur after about half an hour. This figure should be taken as an upper estimate. If O_2 consumption of the stimulated herring is higher than assumed, or if the water temperature is above 8°C, the time will be much shorter. When herring approach the critical level they possibly show a panic-like behaviour and move up to the surface to search for aerated water.

Tank experiments with shoals of juvenile herring are planned to study the influence of reduced O_2 on shoaling behaviour. Measurements on the reduction of O_2 by herring shoals are also needed and should be conducted in the sea and in aquaria. New instruments for continuous recording of oxygen under sea conditions may facilitate those measurements.

REFERENCES

FRY, F.E.J. 1957. The aquatic respiration of fish. *In:* M.E. Brown, The physiology of fishes. Vol. I, New York, Academic Press, p. 1-63.

JOB, S.V. 1955. The oxygen consumption of *Salvelinus fantinalis*. Univ. Toronto Studies Biol. Ser. No. 61. *Publ. Ontario Fisheries Research Lab.* 73: 39 p.

KALLE, K. 1945. *Der Stoffhaushalt des Meeres,* Leipzig.

1963. Zur Frage des Schwarmverhaltens von Heringen, *Arch. FischWiss.*, 13: 89-92.

SUNDNES, G. 1957. On the transport of live cod and coalfish. *J. Cons.*, 22: 191-196.

F-2

EFFECT OF CHANGE OF LIGHT INTENSITY ON FISH

By

J. H. S. Blaxter[1]

CONTENTS

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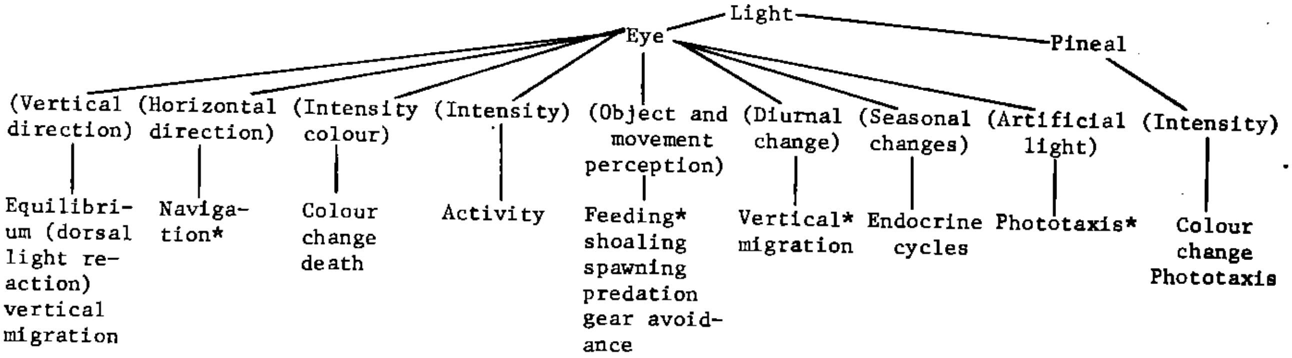
[1] Marine Laboratory, Aberdeen.

INTRODUCTION

Light may be considered as providing the most useful sensory information for fish. Due to its speed it gives the earliest possible warning of the environment at a distance, and its directional properties are also of great value in the perception of form and movement and in orientation. Diurnal and seasonal changes in light coordinate patterns of behaviour and physiology within a fish species. It is possible that the total integrated effect of light over an extended period may also be of importance.

The effects of light on fish may be shown by the following diagram:



This paper reviews some of the work done on the importance of light for different behaviour patterns (*) and especially refers to work done in recent years at the Marine Laboratory, Aberdeen.

CHARACTERISTICS OF LIGHT IN THE SEA

A brief outline of this subject will be given based on papers by Jerlov (1951, 1963).

1. Changes in Intensity

The intensity of light depends on time of day, cloud cover and the altitude of the sun, especially on a clear day. Surface reflection varies, in some cases only amounting to 1-3%, where the surface is calm. Reflection may be increased by wave action and absorption at the surface, by a turbid layer may be considerable. Below the surface light is attenuated due to absorption and scattering. Scattering will be low in clear oceanic water and high salinity is often associated with low particle content. High particle content will greatly affect attenuation; for instance, the blue component of daylight was reduced to 1% of the surface value in 8 m in Woods Hole Harbor, in 32 m in the deep basin of the Gulf of Maine, in 100 m in average oceanic conditions and only in 149 m in the Sargasso Sea (Clarke, 1936). The general extinction of light in various types of water is shown in Fig. 1. At night or in very deep water the light intensity may be more affected by bioluminescence than by light from the surface.

2. Changes in Colour

The colour of light changes with depth due mainly to absorption, scattering being less selective. The maximum penetration is by light of 460-490 mμ (blue) in oceanic water, but is at somewhat longer wavelengths in coastal water, see Fig. 2, (Jerlov, 1951; Atkins and Poole, 1958; Kampa, 1961). This is partly due to the presence of yellow substance (Kalle, 1961) which absorbs light of shorter wavelength. Red light is absorbed very rapidly; for example light of 600 mμ may be reduced to 2% of the surface value within 20 m. Ultra-violet light down to a wavelength of 230-240 mμ may be transmitted fairly well in clear water (Armstrong and Boalch, 1961; Jerlov, 1950). Light of 310 mμ for instance, was found to be absorbed only at the rate of 14%/m and of 375 mμ at 5%/m, compared with 3%/m for blue light. Absorption of ultra-violet light may be much greater in coastal water (for example 90%/m for light of about 310 mμ (?) in the Skagerrak) and may be substantial at 350 mμ when phytoplankton blooms are present.

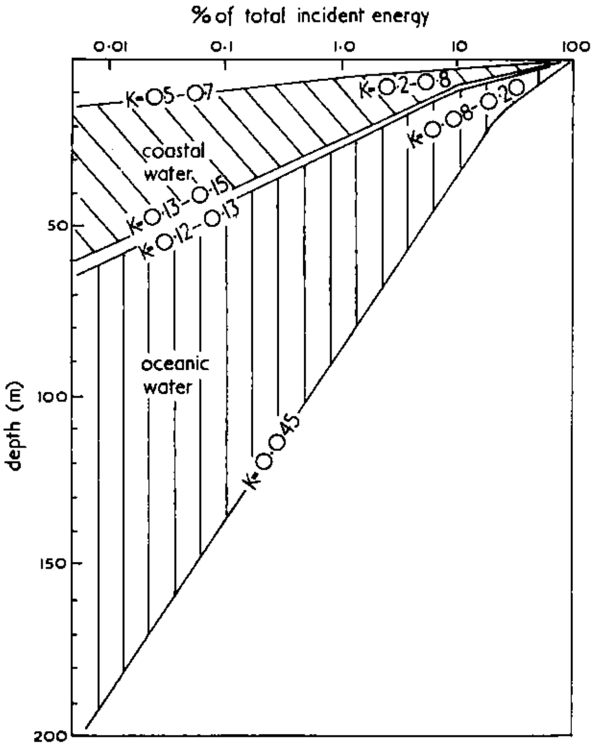
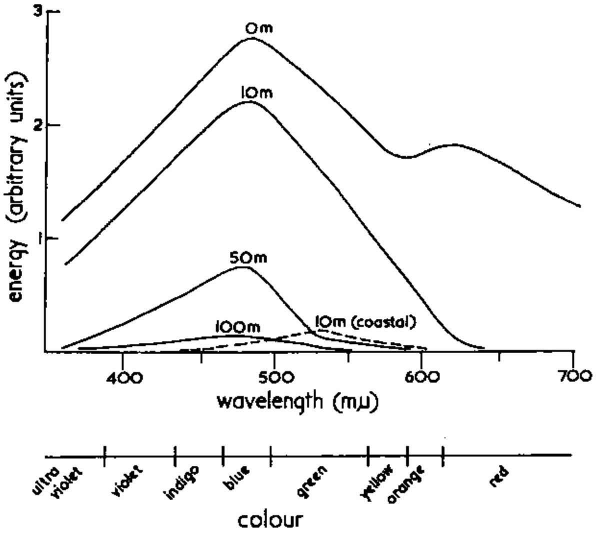


Fig. 1. Extinction of light at different depths in different types of water. (K is extinction coefficient in the relationship $K = 2.3 (\log I_z - \log I_z + 1)$, I being the intensity of a given wavelength at depth z and z + 1) (adapted from Jerlov, 1951).



Spectral absorption of sea water at 0, 10, 50 and 100 m off Bermuda (from Jerlov, 1951) with comparable curve for typical coastal water at 10 m (from Sverdrup *et al*, 1946).

It is of interest that luminescent organisms appear to produce light with a spectral peak at about 470 mμ (Clarke and Denton, 1962).

3. Angular Distribution

The angular distribution of light could be important for orientation of animals. The direction of highest light intensity is partly controlled by the altitude and azimuth of the sun, refraction tending to offset extreme obliquity. Theoretically the maximum obliquity would be about 48° to the vertical, this being the angle of refraction at the critical angle of incidence, but surface effects and scattering reduce obliquity, which becomes less extreme with depth. However, Atkins and Poole (1958) found an average obliquity of 30-40° from the vertical in the English Channel which was not very much affected by depth and altitude of the sun. The average ratio of light intensity measured vertically to the maximum value was 1:1.25. Jerlov (1951) and Sasaki, Okami, Watanabe and Oshiba (1958) found a dependence between the angle of maximum light intensity and the direction of the sun. This obliquity was lost gradually with depth, Jerlov estimating an equilibrium of distribution with vertical light predominant at 300 m in clearest ocean water. The upwelling light amounted to 1-4% of the downward light and had a peak of spectral composition at about 450 mμ. Sasaki *et al.* (1958) measured the extent of the horizontal light component and found that even at 80 m some directionality remained, related to the azimuth and altitude of the sun.

Clarke and Denton (1962) mentioned work on polarisation of light in the sea which showed that it diminished rapidly in the first 10-40 m. It seems possible it would be sufficient to permit azimuthal orientation of animals which can perceive polarised light.

4. Relationship to Fish Behaviour

In relation to fish vision, only few data of light intensity at different depths are available for the ICNAF area though more work has been done in the NE Atlantic. Estimates of light intensity at different depths using known average surface values and measurements of turbidity from Secchi disc readings (as taken in ICNAF NORWESTLANT Surveys) are not really satisfactory, because higher turbidity readings at the surface are likely to cause calculations of bottom light intensities which are much too low. Joseph (1961) estimated the turbidity at different depths in the North Atlantic using a transparency meter with a red light source. His extinction coefficients are related to water of very high clarity and do not permit calculations of light intensity at different depths very easily.

Information on fish vision is usually based on light intensity measurements in lux. The following values of lux are given for various light conditions at the surface:

10^{-7}	10^{-6}	10^{-5}	10^{-4}	10^{-3}	10^{-2}	10^{-1}	10^{0}	10^{1}	10^{2}	10^{3}	10^{4}	10^{5}	lux
				overcast night	clear new moon summer	full moon		dusk dawn		dull day		zenith sun	

In the wide variety of latitudes found in the North Atlantic there may be great variations in "night" and "day" values of light intensity. For instance during the summer Arctic "nights" the light may not fall below 10^3-10^4 lux (Digby, 1960).

Because the absorption of red light by water gives a spectral composition of light below 5 m not dissimilar from the spectral sensitivity of the human eye, especially when dark-adapted, lux values may be approximately equated with total energy values (Ångstrom, 1936).

LIGHT PERCEPTION

1. Vision

Vision in fish and its numerous adaptations to different environments has been reviewed recently by Sverdrup *et al.* (1946), Brett (1957), Polyak (1957) and Nicol (1963). The brief account in this paper is based on these four publications. The work on marine commercial species is inadequate and is mainly anatomical.

Generally speaking, the fish eye is not dissimilar in structure from the human eye. The retina contains both rods and cones, but accommodation is brought about by movement of the whole lens towards or away from the retina. The arrangement of the cones in many marine species has recently been reviewed comprehensively by Engstrom (1963). The adaptations of the lens to the marine environment and the optical system in fish are discussed by Clarke and Denton (1962). Teleosts are generally considered to be myopic (Brett, 1957). There is little pupillary movement and adaptation to light or dark results from migration of retinal pigment or of the visual cells. In elasmobranchs a reflecting layer, the tapetum, is found at the back of the retina.

Vision in high light intensities is due to the cones and in low light intensities to the rods. The rods summate giving added sensitivity but poor acuity. A fovea seems to be uncommon in fish, though there are often areas of the retina in which the density of cones is greatly increased, giving a higher acuity (Tamura, 1957*a*). The optic nerve decussates completely. The structure of the brain reflects the main sensory basis of the life of the fish. Thus, Evans (1935) correlated the brain structure of gadoids with their mode of life. The "visual" feeders such as cod, haddock, whiting, saithe, pollock and ling, had enlarged optic and small olfactory, lobes, while the three-bearded rockling had rather small optic, but large olfactory, lobes related to its mode of feeding. In the same way Blaxter and Holliday (1958) noted that the herring, which is also a visual feeder, had large optic lobes. Polyak (1957) and Tamura (1957*a*) discussed the anatomical basis and role of binocular vision in fish and its importance for the localisation of prey and predators. Some fish have a projecting cornea and siting grooves in the dermal bones in front of the orbit to improve the overlap of the visual field of the two eyes.

2. Colour Perception

This is generally accepted as being a function of the cones. So far no teleosts have been shown *not* to have colour vision. Walls (1942) considered that a duplex retina, containing rods and cones, was a reasonable indication of the presence of colour perception. The absence of cones in elasmobranchs suggests that they cannot perceive colour.

The lenses of diurnal and surface oceanic fish appear to absorb ultraviolet light, but in nocturnal and deep sea fish the lens may transmit light down to 310 mμ. As mentioned in the section on light in the sea, ultraviolet light may be transmitted quite well by oceanic water, but not inshore. This light may, therefore, be of use to some species. Craig and Baxter (1952) reported what might have been a reaction of fish to artificial ultraviolet light and Breder (1959) stated that *Jenkinsia* was photopositive to ultraviolet light. Care must be taken in this type of experiment to exclude the possible effects of longer wavelength fluorescence, which may also occur.

3. Optimum Light

The optimum light for the performance of behaviour patterns has not been studied much. Tamura, Mitarai and Sugita (1957) measured the minimum light intensity for the maximum cone response, using a micro-electrode on the retina, and found values of 64-175 lux for *Sparus*, 175 lux for *Cyprinus*, 800+ lux for *Lateolabrax*.

4. Intensity Perception

4.1 As the light decreases dark adaptation takes place and photopic (cone) vision changes to scotopic (rod) vision. There is usually a "Purkinje shift" in the spectral sensitivity of the eye, the maximum sensitivity shifting to shorter wavelengths.

Thus Borisov and Protasov (1960)[2] gave the following values:

	Maximum sensitivity in mμ	
	Light adapted	Dark adapted
Cod	550	504
Haddock	565	520
Saury	580	510
Catfish	545	470
Plaice	580	525
Star-like skate	500	500
Anchovy	560	500
Horse mackerel	555	505
Red mullet	590	505
Grey mullet	557	500

This shift has been shown by electrophysiological means, the response by the retina to lights of different colours being recorded on an electro-retinogram. (It should be stressed that this is not necessarily concerned with colour vision. The visual cells are more, or less, sensitive to different wavelengths; this may not result in subjective colour discrimination, but only that the colour to which the cells are most sensitive will appear brightest.) It should be noted that no shift was found in skate, which has no cones. There is very little other evidence for a "Purkinje shift" due to a lack of data on spectral sensitivity of fish when light-adapted. There are more data on scotopic spectral sensitivity, however, in freshwater fish, but few on marine fish. Blaxter (1964), using various behaviour techniques, found a maximum at 510-520 mμ in dark-adapted *Clupea harengus* and Blaxter and Little (unpublished results) maxima around 500 mμ for *Gadus merlangus* and *Limanda limanda*, though the spectral sensitivity curves were very plateau-like at the blue-green end of the spectrum. It should be stressed that the spectral sensitivity determined by behaviour techniques (such as feeding in different coloured lights) may, in a sense, be subjective. In other words fish may cease to feed in red light of low intensity, for instance, although they can still see the food. A more objective measure of spectral sensitivity might be found by an electro-physiological technique, for instance by electrodes placed on the retina or optic nerve, but even this is not evidence of a "central" perception of light.

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[2] "Some aspects of light perception in fish and selective light sources"
I.C.E.S. Comp. Fish Committee. Paper 139, 1960.

4.2 More data are to be found on the absorption spectra of the retinal pigments, which are often in close agreement with the spectral sensitivity obtained by other means. In general, dark-adapted fish have a peak absorption at about 500 mμ (due to the pigment rhodopsin), dark-adapted freshwater fish at about 530 mμ (due to porphyropsin) and dark-adapted deep water fish at 485 mμ (due to chrysopsin). It should be noted that these correspond well with the spectral make-up of light in the water at the depths these fish are found. Thus the fish are most sensitive to the colour of light which is predominating in their environment. Those species which change their environment may or may not change their visual pigment. Thus Atlantic salmon retain porphyropsin throughout their life; whereas the eel acquires a pigment similar to deep sea fish before migrating into deep water.

The importance of vitamin A, which is concerned in the photochemical cycle of rhodopsin, in the visual sensitivity of fish, was shown by Kampa (1953) who found in *Gillichthys* that a diet free of vitamin A resulted in a loss of sensitivity.

4.3 The change from light to dark adaptation may be judged from a study of behaviour patterns and especially from the "photo-mechanical" movements in the retina. In the light-adapted state the sensitive rods are invested by pigment and the cones contracted away from the pigment. In the dark the pigment contracts, leaving the rods free, and the cones lengthen. The light intensities at which this change occurs in various species are shown in Table 1.

TABLE 1. LIGHT INTENSITIES AT WHICH EYES CHANGE FROM THE LIGHT-ADAPTED TO DARK-ADAPTED STATE, BASED ON PHOTO-MECHANICAL CHANGES IN THE RETINA.

Species	Light intensity for light to dark adaptation (lux)	Author
Atherina mochon pontica	$10^1 - 10^0$	Protasov *et al.*, 1960.
Sargus annularis	$10^{-1} - 10^{-2}$	
Engraulis encrasicholus	$10^0 - 10^{-1}$	
Clupea harengus	$10^1 - 10^0$	Jones and Blaxter, unpubl.
Lateolabrax japonicus	$4 \times 10^{-2} - 10^{-2}$	Tamura, 1957*b*.
Cyprinus sp.	$5 \times 10^{-4} - 6 \times 10^{-5}$	
Oncorhynchus spp	$10^1 - 10^{-1}$	Ali, 1959.
Salmo salar	$10^0 - 10^{-2}$	Ali, 1961.
Leuciscus rutilus	$10^{-3} - 10^{-4}$	Engström and Rosstorp, 1963.

Except for *Cyprinus* and *Leuciscus* sp. the values in Table 1 are similar to the light intensity at dusk and dawn.

The "photo-mechanical" changes are fairly slow, varying from 20 to 70 min in different species (Nicol, 1963). Usually light adaptation is faster than dark adaptation. When fish are placed in darkness after being at a high light intensity there may be a latent period (Ali, 1962). Ali (1959) has suggested that the light intensity at dusk may decrease at a greater speed than the process of dark adaptation in the retina, thus giving an especially vulnerable period of night-blindness just after dusk. If this were so in other species, it might mean that fish capture would be most advantageous at this time. It is possible, also, that fish descending fast in turbid water might also undergo such a "blind" period.

The control of the "photo-mechanical" changes seems to be unknown. Only rarely have any signs of a diurnal rhythm (in constant experimental conditions) been found and it seems that the changes in light themselves mediate the adaptation by nervous or hormonal stimuli.

4.4 The structure of the retina may sometimes hint at the habitat and light conditions occupied by a species. This is especially true for species living in low light intensities. For instance, Ali and Hanyu (1963) studied the retinae of fish off the Labrador coast. The cod, *Gadus callarias*, had many cones and a well-developed pigment epithelium, suggesting eyes that could function at high light intensities and yet be efficient under diurnally changing illumination.

Sebastes species, however, often found at 300 m or more, had many rods and a degenerating pigment epithelium, suggesting life at greater depths. Interesting differences in the size and density of the cones were apparent in two specimens of *Sebastes marinus mentella*, one found at 270 m and the other at 540 m. The cones were larger and denser in the fish nearer the surface. Differences in the retinal of *Sebastes* spp. found at varying depths was also reported by Wunder (1958).

4.5 Vision in dark-adapted fish will cease at the absolute rod threshold. This is not easy to measure except by electro-physiological methods, because behaviour techniques may only give the subjective level. In other words a fish may still be able to perceive light even though its behaviour patterns in low light intensities have ceased. Presumably conditioned response techniques could be used to determine the absolute threshold though this has not been done. Clarke (1936) quoted a threshold value based on a behaviour technique of 1.5×10^{-6} μW/cm^2 (about 3×10^{-6} lux) for *Lepomis*, a pond fish, which suggests fish can detect light at least 10^{-10} or less that of full sunlight. Thus fish like *Lepomis* might be able to detect light (but not necessarily see an object) ranging from 430 m in the Sargasso Sea (depth 4500 m) to only 75 m in water of a similar turbidity to that found in Woods Hole Harbour. According to Clarke and Denton (1962) some fish may well have a threshold as good as, or better than, the human eye (3×10^{-8} μW/cm^2 at the pupil, or equivalent to about 6×10^{-8} lux). It is possible that deep sea fish which possess better light collecting properties in the eye (a large lens in relation to the whole eye), a very transparent lens and very dense retinal pigment, and because of certain other neurophysiological considerations, may have a sensitivity of 10-100 times that of the human eye. This might mean that deep sea fish could detect light for a while each day down to nearly 900 m, or perhaps to 1,000 m, in exceptionally clear water with an extinction coefficient between 0.03 and 0.04. In coastal water with an extinction coefficient of 0.13, the threshold would be reached at 250 m. However, the light intensities at great depths are sometimes enhanced by luminescent organisms. It has been found that flashes may give off more light than that penetrating from the sky, even as high as 10^{-2} μW/cm^2, enabling fish to locate each other and their prey at sub-threshold overall intensities.

BEHAVIOUR PATTERNS

1. General

Many behaviour patterns will depend on form perception which will not be possible at light values near the rod threshold. The sharpness and contrast of objects underwater is frequently much impaired even at high light intensities. However, such patterns as phototaxis may depend only on the perception of light down to the threshold. In some behaviour there may be a gradual changeover of the dominant stimuli from visual ones at high light intensities to olfactory or other stimuli in darkness. There are some reports of a decrease in activity at low light intensities. This could be mediated by the pseudobranch (Holliday and Parry, 1962) which may be an endocrine organ controlled by the choroid gland at the back of the eye.

2. Feeding

The importance of light for a high rate of feeding in some species has been observed by a number of workers. Some other species may feed equally well by day and night (Girsa, 1961) if food is readily available, while others still may reduce feeding by day, because their food becomes more difficult to catch (*Corvina*, *Silurus*, ling).

The range of light intensity at which various daylight feeders cease to feed is given in Table 2.

These values may be compared with those for the change from light to dark adaptation. From this it appears that feeding becomes much reduced in dark-adapted fish, presumably due to the loss of acuity. However, some feeding may still be possible when the food is silhouetted against the light. That is why in experiments with light from the side (Table 2) rather lower values were found.

Feeding in deep sea fish, where it is visually controlled, must almost certainly be by the detection of phosphorescence which produces flashes of 10^{-7} to 10^{-2} μW/cm^2 (about 2×10^{-7} to 2×10^{-2} lux), (Clarke and Denton, 1962). The large mouths of deep sea fish may not only allow large food organisms to be taken on rare occasions, but may also assist the taking of food where location of the prey and the efficiency of snapping are poor.

An optimum light intensity for feeding was found in herring ranging from 100 to 1,000 lux (Blaxter and Holliday, 1958).

TABLE 2. RANGE OF LIGHT INTENSITY OVER WHICH "VISUAL" FEEDERS CEASE TO FEED.

Species	Range of light intensity (lux)	Remarks	Author
Cod	10^0 - 10^{-2}	some residual feeding in dark	Girsa, 1961
Boreogadus saida) *Alburnus alburnus*) *Trachurus trachurus*)	10^0 - 10^{-2}		ditto
Trachurus) *Leucaspius*)	10^1 - 10^{-1}		Protasov *et al.*, 1960
Clupea harengus	10^1 - 10^{-1}	light from above, juvenile fish	reviewed in Blaxter and Holliday, 1963
" "	c.10^{-2}	light from the side, juvenile fish	Blaxter, 1964*a*[3]
" "	10^0 - 10^{-1}	light from above, larvae	Blaxter, 1964*b*[4]
Gadus virens	- 10^{-3}	blue light from the side	Blaxter unpbl.
Gadus merlangus	- 10^{-4} - 10^{-5}	ditto	Blaxter & Little unpubl.
Limanda limanda	- 10^{-3} - 10^{-4}	ditto	ditto
Phoxinus phoxinus	10^{-3} - 10^{-4}	some feeding in dark	Jones, 1956
Oncorhynchus kisutch	10^0 - 10^{-3}		Brett and Groot, 1963
Oncorhynchus spp.	10^1 - 10^{-4}	varied in different species	Ali, 1959

3. Schooling

Schooling is used here in the sense of a group of fish which are polarized or orientated to one another as a result of mutual interaction. Much of the work on schooling has been reviewed by Breder (1959). In the main schools appear to break up in the dark, though the fish may remain as a group, perhaps kept aggregated (but not necessarily polarized) by other stimuli, as well as by a decrease in activity.

The literature on the importance of light for shoaling has been reviewed by Loukashkin and Grant (1959) and Shaw (1961). The results of work where the light intensity was measured when shoaling ceased are given in Table 3.

There are some instances of fish schooling without visual cues. Blinded *Anchoviella* (Moulton, 1960) will school with intact fish as long as they are moving sufficiently rapidly. Shlaifer (1942) showed a dispersion of the mackerel *Pneumatophorus grex* in darkness, but nevertheless some polarization was still evident. Jones (1962), for instance, reported that groups of herring in the southern North Sea remained at least partially intact (as observed by echo-sounder) at night, but this and other reports of groups of various species remaining together by night as observed on echo-trace records cannot be considered as evidence for polarization, but only for aggregation. Nor can reported instances of "schooling" in the dark be used as evidence for polarization by non-visual means unless they are accompanied by a definition of schooling and measurements of light intensity.

Perhaps the best evidence for apparent schooling at night by clupeids are photographs of *Clupea harengus* polarized near the sea bed during darkness (Craig and Priestley, 1961). Whether the fish were reacting to each other or to some common external stimulus is uncertain. A mass rheotropism is considered to be impossible without visual or tactile cues. Clearly the analysing and defining of schooling behaviour becomes difficult if fish can polarize by a common reaction to external stimuli other than each other.

4. Spawning

This is not often directly observed in marine fish. Holliday (1958) reported that herring in

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[3] in Journal of Experimental Biology (in press)

[4] "The feeding of herring larvae and their ecology in relation to feeding" in CalCOFI Report of Symposium on "Larval Fish Biology" held in 1963 (in press)

TABLE 3. RANGE OF LIGHT INTENSITY OVER WHICH SCHOOLING CEASES.

Species	Range of light intensity (lux)	Remarks	Author
Clupea harengus	$10^{-2} - 10^{-3}$	8 m^3 aquarium	See Blaxter & Holliday (1963)
" "	$10^{\circ} - 10^{-1}$	225 m^3 aquarium	ditto
Sardinops caerulea	$< 10^{-1}$	aquarium	Loukashkin & Grant (1959)
Alburnus alburnus) *Atherina*) *"Anchovy"*)	$< 10^{-1}$		Girsa (1961)
Engraulis encrasicholus) *Atherina mochon pontica*)	$10^{1} - 10^{-1}$		Protasov *et al* (1960)
Hepsitia stipes) *Bathystoma rimator*)	5×10^{-1}		Steven (1959)
Oncorhynchus spp.	10^{-3}		Ali (1959)
Phoxinus phoxinus	$10^{-2} - 10^{-3}$		Jones (1956)
Menidia	$10^{\circ} - 10^{-1}$		Shaw (1961)

captivity ceased to spawn in darkness, the pattern of the bottom and the presence of the opposite sex being important stimuli. Brawn (1961) found that cod spawned in very dim light, but did not observe whether they continued to spawn in complete darkness. Doubtless the importance of light varies in different species, depending on the role of vision in courtship, display and pairing.

Spawning may so affect fish that their reactions to other stimuli become weaker. Thus, Mohr (1964) found that spawning *Clupea harengus* were much less reactive to a mid-water trawl than non-spawning fish.

5. Avoidance of predators

The study of predation in marine fish has received very little attention from research workers. The effectiveness of predation in light and dark will depend on the searching activity of the predator and its success in taking food, as well as on the perceptibility and availability of food organisms. Girsa (1961) found that some predators tended to be more active in low light intensities and caught their prey by means other than sight. Shoaling prey species may be less active by night, perhaps making them easier to catch, but they may also be more dispersed, making them more difficult to locate. Bioluminescence, while showing the presence of organisms, may also act as a warning to, or elicit fright reactions from, predators. At very low light intensities, where the detection of objects may only be by silhouette against light from above, the avoidance of predators is probably an easier process than the taking of prey.

6. Avoidance of Fishing Gear

6.1 The importance of sight in the avoidance of nets and the scaring effect of different colours has been reviewed by Mohr (1960) and Blaxter and Holliday (1963). Blaxter *et al.* (1964) reported that herring started to swim into stationary nets (which they avoided in daylight) at 10^{-3} - 10^{-4} lux in a small tank and 10^{-2} - 10^{-3} lux in a big tank. The use of drift nets made of polyamide fibres of low visibility has resulted in improvement of catches in a number of species. Blaxter *et al.* (1964) also studied the reaction of *Clupea harengus*, various gadoid fish and flatfish to moving nets in tanks, and found that the reaction distance and extent of herding depended on their conspicuousness. At light intensities below 0.5 - 0.05 lux herding dropped substantially and at lower intensities only a residual degree of herding was left, due mainly to tactile stimulation. In experiments at sea photographs were taken of fish in front of the ground rope of a trawl and confirmed, especially in herring, the reduction in orientation to the ground rope and herding by night.

It is of interest that in elasmobranchs, where sight seems to be of less importance than in many teleosts, the reaction to nets may be poor.

6.2 Artificial barriers have been used to control fish. For example, curtains of air bubbles may be used to guide schools of *Clupea harengus* (Smith, 1961) and a moving barrier composed of chains to deflect salmonids (Brett and Groot, 1963). Visual stimulation seems to be necessary in these reactions.

6.3 Recently diurnal differences in catch by bottom trawl have been reported as relevant to the estimation of population abundance (*e.g.* reviews by Woodhead, this symposium and Parrish *et al.*, 1963[5]). Woodhead found mainly higher catches by day in plaice, cod, haddock and coalfish, but not with soles. Parrish *et al.* reported higher catches by night in flatfish (including plaice), whiting and sometimes haddock and in general in species fished in Faroese waters. Woodhead gave the possible reasons for the differences in catch, which are certainly not consistent from area to area, or season to season, within a species. There may be differences in diurnal cycles of swimming activity and feeding or differences of physiological condition. Where night catches are lower there is good evidence that vertical migration away from the bottom is occurring. Where day catches are lower it seems possible that avoidance of the trawl is taking place (Blaxter *et al.*, 1964). It is possible though that the trawl tends to pass over flatfish by day, and that they leave the bottom by night and become more vulnerable.

7. Attraction to Light and Activity

7.1 Attraction (to artificial light). Phototaxis would appear to be mainly under nervous control. Phototaxis and preference for different lights has been reviewed by Breder (1959). The use of artificial lights to attract fish, reviewed in general by Schärfe (1953), and on clupeids by Blaxter and Holliday (1963), provides artificial stimuli for fish which may well cause abnormal behaviour patterns. Various explanations such as curiosity, feeding, positive phototaxis, hypnosis and following an optimum light intensity have been put forward to explain light attraction. Verheijen (1958) considered it was due to a mass disorientation, such as found in birds and insects attracted to lights at night. In this case the lamp would need to act as a point source and the explanation appears unlikely for attraction in turbid water, or where the fish remain at a distance from the light. Russian workers consider the attraction to be due to a conditioned response brought about by the association of light with feeding. This could be tested experimentally.

Blaxter and Parrish (1958) attracted fish to underwater lights and found that whiting collected at a distance from the lamp where the intensity was about 10^{-1} lux and herring and sprats aggregated near the lamp at 10^3-10^4 lux.

7.2 Activity. This subject has been considered by Woodhead in this symposium and will not be referred to further here.

LIGHT IN ORIENTATION

1. General

Light can control both vertical and horizontal orientation in fish as well as allowing for the more intimate orientation required for capturing food, shoaling and rheotropism.

2. Diurnal Vertical Migration

A rise towards the surface by night has been observed in a number of marine species, especially clupeids, by echo-sounder. It may also be shown from results of decreased catch of fish near the bottom during the night. The subject has been reviewed generally by Hela and Laevastu (1962) and is also discussed by Woodhead in this symposium. In particular Richardson (1952) related the downward movement of shoals in the North Sea to light intensity, but it was apparent that they were found in a light intensity at night which was much lower than the "preferred" day intensity. Postuma (1957)[6] showed that herring in the North Sea tended to remain in light intensities below 1 lux and Chestnoy (1961) that the depth of herring shoals could be correlated with isolux lines. However, Brawn (1960) could find no relationship between mean solar radiation and the depth of shoals of immature herring in Passamaquoddy Bay. What is probably the dominant influence of light in most cases may be modified by other factors such as temperature gradients.

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[5] "Diurnal variations in size and composition of trawl catches". ICES Abundance Symposium Paper 34.

[6] "The vertical migration of feeding herring in relation to light and vertical temperature gradient". ICES Herring Committee 1957.

Studies on vertical movements and distribution of gadoids such as cod, haddock, hake and coalfish (Woodhead, this symposium 1963) have not been related to light intensity to the same extent. However, Woodhead cited an interesting paper by Konstantinov showing that there was little or no sign of vertical migration in Arctic cod in the months of January and July when there was a minimal variation in light intensity, but there was vertical movement in spring and autumn when the greatest variation in light intensity occurred.

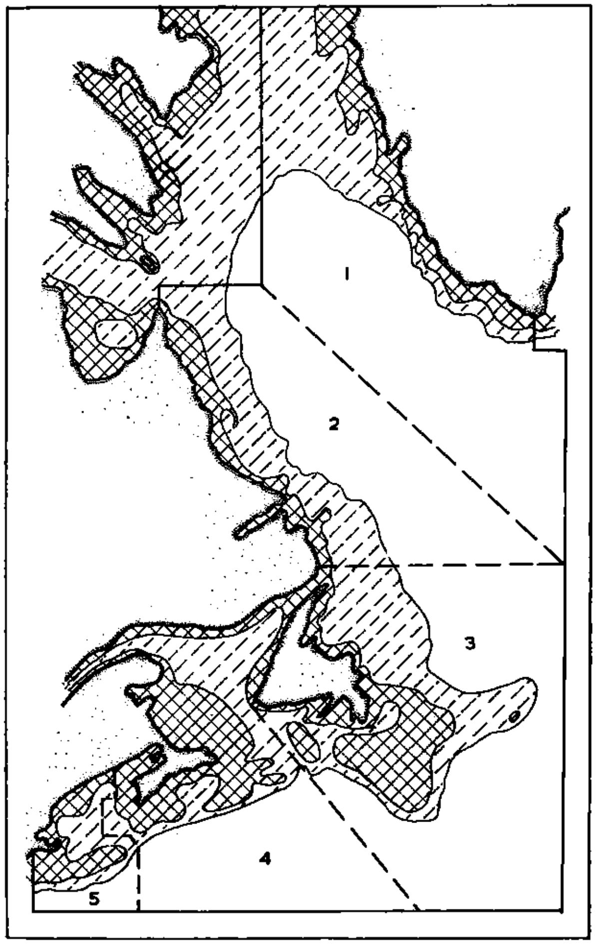

Fig. 3. The ICNAF area showing tentatively:

a. in cross hatching, the area within which diurnal changes in light intensity should occur on the bottom sufficient to bring about changes in light and dark adaptation of fish (on the assumption that the light will reach at least 10^{-1} lux on the bottom at some time during the day, the extinction coefficient being 0.13).

b. in broken hatching, the additional area within which the light will at least reach the absolute threshold on the bottom at some time during the day (based on an absolute threshold of 10^{-10} lux and an extinction coefficient of 0.045).

Diurnal vertical movements have often been correlated with the need to follow food organisms towards the surface at night. There is some evidence that feeding activity may be most intensive at dusk and dawn. It is interesting to speculate whether these periods are more favourable (in terms of light intensity) for predation or for escape from predators, or whether movements to the surface prevent the "night blindness" which fish might undergo if the light intensity falls too rapidly in the evening.

3. Sun Orientation

In an earlier section the directional nature of light in the sea was considered, a horizontal component being found to depths of 80 m or more. Light may be oblique to much greater depths with the greatest intensity in the direction of the sun's azimuth. Experimental work on freshwater fish (*Lepomis*, salmonids) has shown that they have the *ability* to navigate by the sun and that they possess a clock system which allows them to compensate for changes in azimuth bearing, depending on the time of day, longitude, and season (Hasler 1960; Hasler and Schwassmann, 1960; Brett and Groot, 1963). Saila and Shappy (1963) analysed the migration of Pacific salmon to the American coast and concluded that only a very rough ability to orientate by the sun is necessary, plus a great deal of searching; too good an orientation would result in displacement by currents. Some other species undertake considerable migrations (eel, tunny) but it is not certain to what extent homing is involved. It seems doubtful whether the type of overall movement North and East described by Wise (1959) in the cod off the East American coast would require sun navigation. In fact while sun navigation has been shown *experimentally* to exist in some species it is not known to what extent the faculty is utilised by these fish.

The existence of polarized light in the sea and its directional properties have also been considered earlier. Although the effect of polarized light on fish is not known, it is interesting that Stewart (1962) reported an adipose eyelid in a large number of families of fish. He found that it was birefringent in *Clupea pallasii* with different degrees of transmission depending on the plane of polarization of the incident light. The possible role of this in orientation is intriguing.

LIGHT AS A RHYTHMICAL STIMULUS

Both diurnal, lunar and seasonal periodicity play a part in the life of fish. Wynne-Edwards (1962) has developed the idea that the numerical density of animals may be regulated at certain times, for instance during a nightly vertical migration. This could be considered in relation to fish. There is sometimes considerable lunar periodicity in catches of clupeids. Seasonal changes of light may affect the reproductive cycle (Holliday, this symposium). They may even control the temperature tolerance of some species (Hoar, 1956) making them more resistant to high temperature in summer and low temperature in winter.

CONCLUSIONS

Despite the abundant evidence of the importance of light in the biology of fish, it is often one of the more neglected of the physical conditions which are recorded. It is intended to produce before long charts showing diurnal changes of light conditions in different areas of the sea bed in Scottish waters throughout the year. If possible only the light which is "useful" to the fish should be measured. Thus, the light meter should have the same spectral response as that of the fish eye. As a first attempt to show the possible value of further light intensity measurements, for instance in the ICNAF area, Fig. 3 has been drawn. It shows the areas where the diurnal variation in light intensity is probably sufficient for light and dark adaptation to take place during each period of 24 hr and the somewhat more extensive area, within which the light, at least during part of the day, reaches the absolute threshold for dark-adapted fish when surface illumination is at a maximum.

REFERENCES

ALI, M.A. 1959. The ocular structure, retinomotor and photobehavioural responses of juvenile Pacific salmon. *Canad. J. Zool.,* 37: 965-96.

1961. Histophysiological studies on the juvenile Atlantic salmon (*Salmo salar*) retina. II. Responses to light intensities, wavelengths, temperature and continuous light and dark. *Canad. J. Zool.,* 39: 511-26.

1962. Influence of light intensity on retinal adaptation in Atlantic salmon (*Salmo salar*) yearlings. *Canad. J. Zool.,* 40: 561-70.

ALI, M.A., and I. HANYU. 1963. A comparative study of retinal structure in some fishes from moderately deep waters of the western North Atlantic. *Canad. J. Zool.,* 41: 225-41.

ÅNGSTROM, A. 1936. On the unit for radiation in oceanic research. *Rapp. Cons. Explor. Mer, Cons. Explor. Mer,* 101(2)(5): 6 p.

ARMSTRONG, F.A.J. and G.T. BOALCH. 1961. Ultra-violet absorption of sea water and its volatile constituents. *In* Jerlov, N.G. *Symposium on radiant energy in the sea.* International Union of Geodesy and Geophysics Monograph. 63-66.

ATKINS, W.R.G. and H.H. POOLE. 1958. Cube photometer measurements of the angular distribution of submarine daylight and the total submarine illumination. *J. Cons.,* 23: 327-36.

BLAXTER, J.H.S. 1964.*a*. Spectral Sensitivity of the Herring, *Clupea harengus* L. *J. exp. Biol.*

1964.*b*. The feeding of herring larvae and their ecology in relation to feeding. *Calif. Coop. Oceanic Fish Investig. Rep.* (In press).

BLAXTER, J.H.S. and F.G.T. HOLLIDAY. 1958. Herring (*Clupea harengus* L.) in aquaria. II. Feeding. *Mar. Res.* No. 6: 22 p.

1963. The behaviour and physiology of herring and other clupeids. *In* Russell F.S. *Advances in Marine Biology Vol. 1.* London and New York, Academic Press. 261-393.

BLAXTER, J.H.S. and B.B. PARRISH. 1958. The effect of artificial light on fish and other marine organisms at sea. *Mar. Res.* No. 2: 24 p.

BLAXTER, J.H.S., B.B. PARRISH and W. DICKSON. 1964. The importance of vision in the reaction of fish to driftnets and trawls, modern fishing gear of the world, Vol.2, London: Fishing News Books.

BRAWN, V.M. 1960. Seasonal and diurnal vertical distribution of herring (*Clupea harengus* L.) in Passamaquoddy Bay. *J. Fish. Res. Bd, Canada,* 17: 699-711.

1961. Reproductive behaviour of the cod. (*Gadus callarias* L.) *Behaviour,* 18:177-198.

BREDER, C.M. Jr. 1959. Studies on social groupings in fishes. *Bull. Amer. Mus. Nat. Hist.,* 117: 397-481.

BRETT, J.R. 1957. The eye. *In* Brown, M.E. *The Physiology of Fishes Vol. 2.* New York Academic Press. 121-154.

BRETT, J.R. and C. GROOT. 1963. Some aspects of olfactory and visual responses in Pacific salmon. *J. Fish. Res. Bd, Canada,* 20: 287-303.

CHESTNOY, V.N. 1961. Vertical migrations of herring and the methods of their utilization in the fishing practice. *Ryb. Khoz.* 37(6): 53-57. In Russian.

CLARKE, G.C. 1936. Light penetration in the western North Atlantic and its application to biological problems. *Rapp. Cons. Explor. Mer,* 101(2)(3): 14 p.

CLARKE, G.L. and E.J. DENTON. 1962. Light and animal life. *In* Hill, M. N. *The Sea, vol.1 Physical Oceanography.* New York, London. Interscience Publishers. 456-68.

CRAIG, R.E. and I.G. BAXTER. 1952. Observations in the sea on the reaction to ultra-violet light of certain sound scatterers. *J. Mar. biol. Ass. U.K.* 31: 223-227.

CRAIG, R.E. and R. PRIESTLEY. 1961. Photographic studies of fish populations. *Nature, Lond.,* 188: 333-334.

DIGBY, P. 1960. Midnight sun illumination above and below the sea surface in Sörgat, N.W. Spitzbergen and its significance to the plankton. *J. Anim. Ecol.,* 29: 273-297.

ENGSTROM, K. 1963. Cone types and cone arrangements teleust retinae. *Acta, Zoologica,* 44: 179-243.

ENGSTROM, K. and E. ROSSTORP. 1963. Photomechanical responses in different cone types of Lencisus rutilus. *Acta Zoologica,* 44: 145-160.

EVANS, H.M. 1935. The brain of *Gadus* with special reference to the medulla oblongata and its variations according to feeding habits of different Gadidae. *Proc. roy. Soc.* (B) 117: 367-399.

GIRSA, I.I. 1961. Availability of food animals to some fishes at different conditions of illumination. *Trud. Soveshch. ikhtiol. Kom.,* No.13: 355-359.

HASLER, A.D. 1960. Guideposts of migrating fishes. *Science,* 132: 785-792.

HASLER, A.D. and H.O. SCHWASSMANN. 1960. Sun orientation of fish at different latitudes. *Cold Spring Harbour Symposium on Quantitative Biology,* 25: 429-441.

HELA, I. and T. LAEVASTU. 1962. *Fisheries Hydrography.* London, Fishing News Books Ltd. 137 p.

HOAR, W.S. 1956. Photoperiodism - thermal resistance in goldfish. *Nature, Lond.,* 178: 364-365.

HOLLIDAY, F.G.T. 1958. The spawning of the herring. *Scot. Fish. Bull.,* No. 10: 11-13.

HOLLIDAY, F.G.T. and G. PARRY. 1962. Electron-microscopic studies of the acidophil cells in the gills and pseudobranchs of fish. *Nature, Lond.* 193: 192.

JERLOV, N.G. 1950. Ultra-violet radiation in the sea. *Nature, Lond.,* 166: 111-112.

1951. Optical studies of ocean waters. *Report of the Swedish Deep Sea Expedition 1947-1948.*

1963. Optical oceanography. *In* Barnes, H. *Oceanography and Marine Biology* London. George Allen and Unwin, p. 89-114.

JONES, F.R.H. 1956. The behaviour of minnows in relation to light intensity. *J. of exp. Biol.,* 33: 271-281.

1962. Further observations on the movements of herring (*Clupea harengus* L.) shoals in relation to tidal current. *J. Cons.,* 27: 52-76.

JOSEPH, J. 1961. Trübungs- und Temperatur-Verteilung auf den Stationen und Schnitten von V.F.S. "Gauss" sowie Bathythermogramme von F.F.S. "Anton Dohrn" und V.F.S. "Gauss" im Internationalen Geophysikalischen Jahr 1957-1958. *Deutschen Hydrographischen Zeitschrift Ergänzungsheft Reihe B(4°) No. 5.*

KALLE, K. 1961. What do we know about "Gelbstoff"? *In* Jerlov, N. G. *Symposium on radiant energy in the sea.* International Union of Geodesy and Geophysics. 59-62.

KAMPA, E.M. 1953. Effects of Vitamin A supplementation and deprivation on visual sensitivity, rhodopsin concentration and retinal histology of a marine teleost, *Gillichthys mirabilis. Bulletin of the Scripps Institution of Oceanography,* 6: 199-221.

1961. Daylight penetration measurements in three oceans. *In* Jerlov, N. G. *Symposium on radiant energy in the sea.* International Union of Geodesy and Geophysics. 91-95.

LOUKASHKIN, A.S. and N. GRANT. 1959. Behaviour and reactions of the Pacific sardine *Sardinops caerulea* (Girard) under the influence of coloured lights and darkness. *Proc. Calif. Acad. Sci.,* 29: 509-548.

MOHR, H. 1960. Zum Verhalten der Fische gegenüber Fanggeräten. *Prot. Fisch. Tech.,* 6: 296-326.

1964. Reaction of herring to fishing gear studied by means of echo-sounding. Modern fishing gear of the world, Vol. 2, London: Fishing News Books.

MOULTON, J.M. 1960. Swimming sounds and the schooling of fishes. *Biol. Bull., Woods Hole,* 119: 210-223.

* PARRISH, B.B., J.H.S. BLAXTER and HALL. 1964. Diurnal variations in size and composition of trawl catches. *Rapp. Cons. Explor. Mer,* (in press).

POLYAK, S. 1957. *The Vertebrate Visual System.* Chicago. University of Chicago Press. 1390 p.

PROTASOV, V.P., Y.P. ALTUKHOV and N.D. KOVALEVA. 1960. Morphological and functional features of the transition from day vision to twilight vision in some Black Sea fish. *Dokl. Akad. Nauk SSSR,* 134: 195.

RICHARDSON, I.D. 1952. Some reactions of pelagic fish to light as recorded by echo-sounding. *Fish. Invest.,Lond.,* (2) 18(1): 19 p.

SAILA, S.B. and R.A. SHAPPY. 1963. Random movement and orientation in salmon migration. *J. Cons.,* 28: 153-166.

SASAKI, T., S. WATANABE, G. OSHIBA and N. OKAMI. 1958. Measurements of angular distribution of submarine daylight by means of a new instrument. *J. oceanogr. Soc., Japan*, 14(2): 1-6.

SCHÄRFE, J. 1953. Über die Verwendung Rünstlichen lichtes in der Fischerei. *Protokolle zur Fischereitechnik* 8: 1-29.

SHAW, E. 1961. Minimal light intensity and the dispersal of schooling fish. *Bull. Inst. océanogr., Monaco, No. 1213:* 8 p.

SHLAIFER, A. 1942. The schooling behaviour of mackerel: A preliminary analysis. *Zoologica*, 27: 75-80.

SMITH, K.A. 1961. Air curtain fishing for Maine sardines. *Comm. Fish. Rev.*, 23(3): 14 p.

STEVEN, D.M. 1959. Studies on the shoaling behaviour of fish. 1. Responses of two species to changes of illumination and to olfactory stimuli. *J. exp. Biol.*, 36: 261-280.

STEWART, K. 1962. Observations on the morphology and optical properties of the adipose eyelid of fishes. *J. Fish. Res. Bd., Canada*, 19: 1161-1162.

SVERDRUP, H.U., M.W. JOHNSON and R.H. FLEMING. 1946. *The Oceans. Their Physics, Chemistry and General Biology.* New York. Prentice-Hall. 1087 p.

TAMURA, T. 1957*a*. A study of visual perception in fish - especially in resolving power and accommodation. *Bull. Jap. Soc. sci. Fish.*, 22: 536-57.

1957*b*. On the relation between the intensity of illumination and the shifting of cones in the fish retina. *Bull. Jap. Soc. sci. Fish.*, 22: 742-46.

TAMURA, T., G. MITARAI and Y. SUGITA. 1957. The lowest intensity of illumination to produce the maximum cone potential in the fish retina and its ecological meaning. *Bull. Jap. Soc. sci. Fish.*, 23: 86-91.

VERHEIJEN, F.J. 1958. The mechanisms of the trapping effect of artificial light sources upon animals. *Arch. néer. Zool.* 13: 1-107.

WALLS, G. 1942. *The Vertebrate Eye and its Adaptive Radiation.* Bloomfield Hills, Michigan. The Cranbrook Press. 785 p.

WISE, J.P. 1959. Emigration of cod, *Gadus morrhua* L. *International Oceanographic Congress 1959.* p. 358.

WUNDER, W. 1958. Biologie und Bau der Netzhaut beim Rotbarsch (*Sebastes marinus* L.) *Zoologischer Anzeiger*, 160: 94-105.

WYNNE-EDWARDS, V.C. 1962. *Animal dispersion in relation to social behaviour.* Edinburgh and London: Oliver and Boyd, 653 p.

* NICOL, J.A.C. 1963. Some aspects of photoreception and vision in fishes. *In* Russell F.S. *Advances in Marine Biology Vol. 1.* London and New York. Academic Press. 171-208.

F-3

THE SIGNIFICANCE OF ENVIRONMENT/ENDOCRINE STUDIES TO THE INVESTIGATION AND EXPLOITATION OF FISH STOCKS

By

F.G.T. Holliday[1]

ABSTRACT

In any investigation of an exploited fish stock prominent among the factors considered are those concerned with a) location and b) the maintenance of the stock. Relevant data come from studies of migratory behaviour, activity levels, growth rates, maturation and spawning cycles, and estimates of natural mortality at various stages in the life history of the fish.

Almost all of these aspects of fish biology are associated with variations in the levels of circulating hormones. The fish react to a series of internal stimuli which in turn are geared to changes in single, or combinations of variables in the external environment such as day length, temperature and salinity.

Measurements of seasonal changes in the levels of endocrine activity are an important step towards the accurate prediction of the availability and accessibility of stocks.

INTRODUCTION

There have been many reviews of the relationships existing between specific factors, or combinations of factors, in the environment and the activity of endocrine glands in fish. Although experimental studies of the activity of endocrine glands have been made on only a few species, and these mostly estuarine or freshwater fish, the consistency of the results obtained is an indication of the existence of a fairly uniform pattern of endocrine activity and reactivity to the environment. The close link between day length, pituitary activity and gonad maturation is now so well established that Pickford & Atz (1957) were able to state that "with one possible exception...it has never been demonstrated that light fails to effect the reproductive system of fishes". It would now be surprising if an endocrine control system were discovered that did not conform in a general way to the pattern that has so far been found.

It is not the primary intention of this contribution to repeat information which can be found in many well known and comprehensive reviews such as Dodd (1960), Fontaine (1954), Hoar (1953, 1957), Pickford and Atz (1957). In particular Pickford and Atz devote a section of their book specifically to review 'The effects of the external environment on the gonadotrophic activities of the pituitary of fishes.' The main emphasis here will be on the relevance of environment/endocrine studies to fisheries problems, and to consider the position such investigations might take in a fisheries research programme.

As was pointed out by Kesteven (1958) fishery science ultimately deals in problems of fish behaviour, which in turn is the external expression of a particular physiological state. The secretions of the endocrine glands result in profound variations in this state; a change in the level of a circulating hormone is effectively a change in the internal environment of the fish.

Figure 1 shows, in schematic form, the principle endocrine organs in fish, their secretions and target organs. The scheme is much simplified and does not indicate several important factors, one being the inherent rhythm of certain endocrine activities which although normally reinforced by the environment have been shown to be independent of it. Bullough (1941) demonstrated the presence of a reproductive rhythm in *Phoxinus* which persisted under constant environmental

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conditions. An organism may be responsive to specific factors in its environment or blood only if these impinge on target organs in a state capable of response. The gonads of an immature or spent fish may be refractory to environmental and pituitary influences that at a different time would result in the onset of maturation (*e.g.* Harrington, 1957).

ENDOCRINES AND THE COMPONENTS OF A FISHERY

At the joint scientific meeting of ICNAF, ICES and FAO on 'Fishing effort, the effect of fishing on resources and the selectivity of fishing gear' (Lisbon, 1957), certain of the concepts, elements and properties relating to fishing effort and mortality were defined. As was pointed out in this report, each characteristic represents the end result of a long chain of cause and effect, with the organism and the environment interacting together. The properties of a fish stock which make it potentially useful to a fishery are

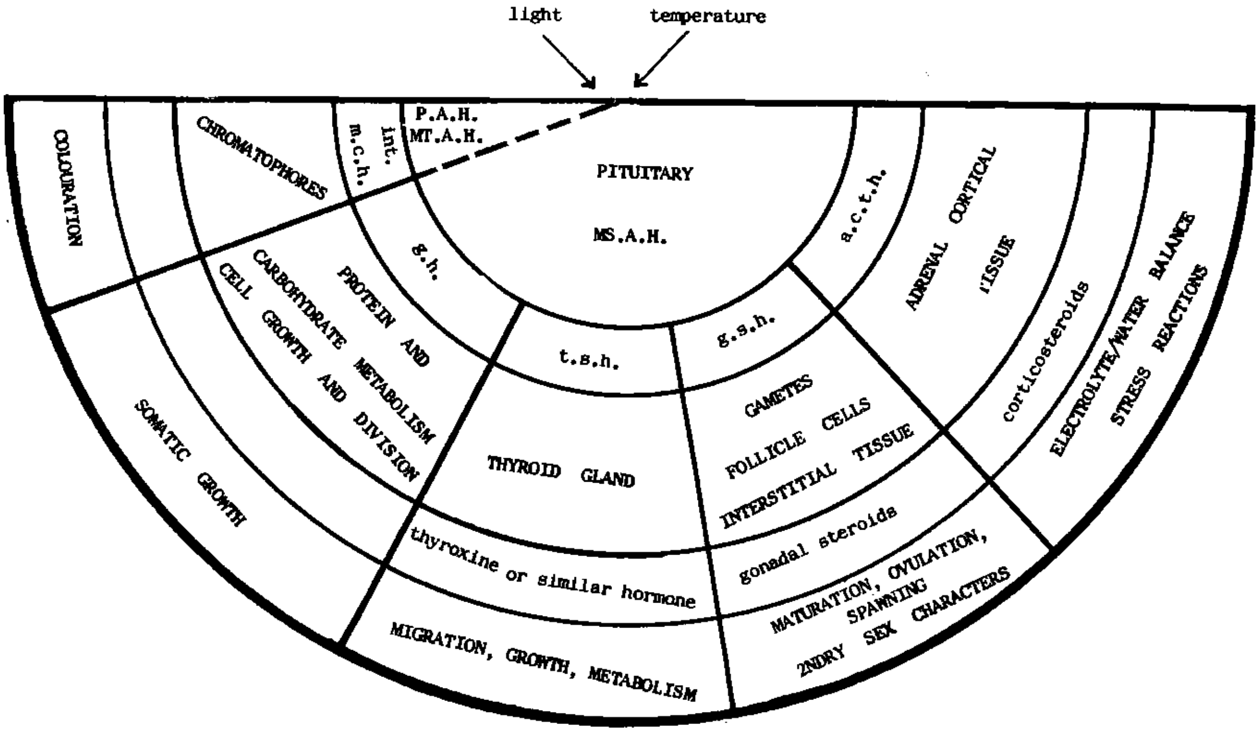

Fig. 1. The principal endocrine glands, hormones and target organs or processes in teleosts. Each radial segment represents a functionally linked sequence of events.

Key: Stimulating factors in lower case. Target organs or processes in capitals. P.A.H. Proadenohypophysis; M.S.A.H.-Mesoadenohypophysis; M.T.A.H.-Metaadenohypophysis (Regions of pituitary gland). int.-Intermedin. m.c.h.-melanophore contracting hormone. g.h.-growth hormone. t.s.h.-thyroid stimulating hormone. g.s.h.-gonad stimulating hormone. a.c.t.h.-adrenocorticotropic hormone.

1. Location and Availability
2. Magnitude and Structure
3. Distribution and Accessibility
4. Vulnerability to the fishing force exerted on it.

It is interesting to consider the relevance of endocrine studies to these characteristics.

Location and Availability.

A species is available to a fishery by reason of its presence in a known area at a specific time. Any force, internal or external, which makes fish migrate into or holds them on such an area is a factor to be considered in relation to location and availability.

The influence of the thyroid gland on migratory activity was discussed by Hoar (1953) and by Woodhead (1959*a*). The latter obtained good circumstantial evidence for this influence in *Gadus morhua* of the Barents Sea. Thyroid gland activity, as estimated from the height of the follicular cells, was greatest during the spawning migration. Buchmann (1940) found increased thyroid activity in the herring, associated with spawning. Woodhead (1959*b*) demonstrated that the changes in the cod thyroid were not due to gonad activity alone. She found increased thyroid activity in immature cod during an overwintering migration in the Barents Sea. Migration of these fish continued for as long as the thyroid gland remained active.

Hoar and his co-workers (Hoar, 1955; Hoar *et al.*, 1952; Hoar *et al.*, 1955) in investigations on young salmon obtained experimental evidence for the association between high levels of locomotor activity and the presence in the water of thyroxine. Conversely, decreased activity levels were found if the thyroid was inhibited by immersing the fish in thiourea. Baggerman (1959, 1960) found that treatment with thyroxine induced a change in the salinity preference of *Gasterosteus* and young *Oncorhynchus;* this change was associated with the onset of the breeding migration. There are many other instances of increased thyroid activity associated with migrations (Fontaine and Callamand, 1943 on the eel; Fontaine *et al.*, 1948 on the salmon). What is still not clear is the link between the environment and the initiation of thyroid activity. Baggerman (1957), in the light of her own and other work, suggested that in cases where external conditions were able to induce a change in salinity preference (associated with migration) then this was the result of increased production of thyrotropic hormone from the pituitary. This production was closely associated in *Gasterosteus* with increasing day length and rising temperature in the spring.

Reproductory drives would appear to motivate migratory behaviour in many marine teleosts. It is on the predictable regulatory of the reproductive cycle that many fisheries are based.

There have been a relatively large number of experiments to demonstrate the effects of light, temperature, water conditions etc. on the reproduction of fishes easily kept in the aquarium (Pickford and Atz, 1957). For many of these species the critical levels and sequences of illumination and temperature necessary to control reproduction have been established. Most experiments support the view that these external factors influence reproduction by way of the production of pituitary gonadotropin. One fact of particular significance emphasised by Pickford and Atz is that light can affect the pituitary - gonad system by means other than the eye, perhaps via the pineal organ or other area of the fish brain responding to light transmitted through the thin bones of the skull. Hoar's (1961) analysis of the andocrine control of the complex behaviour patterns involved in reproduction in *Gasterosteus* illustrates the potential value that lies in such investigations.

The factors that influence and control the timing of maturation and spawning in commercially important fishes are virtually unknown. The maturation of the gonads is made up of a number of phases; Holliday (1960*a*) and Iles (1964) suggest that in the herring these stages differ in duration and control. The early stages (to about stage III-IV) appear to be influenced primarily by the availability of suitable food, whereas the later stages are under pituitary control and may, by analogy with other fish, be responsive to daylength and temperature. Naumov (1956) correlated the maturity stage of herring with water temperature, solar radiation etc., but while it was clear that different stages were associated with different environmental conditions, it was not possible to identify a particular initiating or controlling factor. The picture is complicated by the fact that the gonads of male and female herring mature at different rates when under the same environmental conditions (Holliday, 1963; Iles 1964). There is a seasonal variation in gonadotropic activity of the pituitary in herring, a peak of maximum potency being found at spawning. It is not known what factors initiate spawning. The process is two-part; first ovulation occurs, *i.e.* the release of the egg from the follicle, then after a variable time interval that might be as long as seven days, the gametes are shed. Control of the two phases is almost certainly by different mechanisms, and although these mechamisms are presumably the same within a species the environmental releasing agents are not so specific. Different groups of *Clupea harengus* may mature and spawn under very different conditions at different places and times of the year. These groups are apparently showing different responses to the same stimuli, as they often share a common environment (Blaxter, 1958). Dragesund (1960) suggested that a sharp rise in temperature induced spawning in *Clupea harengus;* Outram (1951) suggested that a sudden decrease in salinity stimulated *Clupea pallasii* to spawn. Holliday (1960*b*) could find no direct effect on the spawning of *Clupea harengus* of either temperature or salinity changes. Ovulation in the herring is under pituitary control, but it is not known what stimulus is required for the release of the appropriate hormone from this gland. Direct visual factors (the amount of light, the nature of the substrate) appear to release egg deposition. Barr (1963 *a, b, c*) demonstrated that maturation of the gonads in plaice (*Pleuronectes platessa*) was controlled by the pituitary. He also obtained evidence that egg deposition in this fish was dependent on pituitary activity.

The spawning of the herring is a mass process (see review by Blaxter and Holliday 1963). On the other hand Brawn (1961 *a, b*) has shown that aggregation and spawning in cod is preceded by complex aggressive and nuptial behaviour. Aggressive behaviour between individuals leads to dispersal, and Brawn correlated a high incidence of aggression with a decrease in catch. It is possible that these behaviour patterns in cod are under the hormonal control of the steroids formed in the gonads of this fish (Gottfried *et al.*, 1962).

Magnitude and Structure.

The recruitment of fish as a result of growth and migration, and the loss of fish by death or emigration are major factors in determining the magnitude and structure of the available stock. The part played by endocrine secretions in migration has been considered, and applies to movements into and from a given area. Growth rate and recruitment are closely linked. The control of growth in fish by a pituitary hormone is well established (Pickford and Atz, 1957 review the literature) and clearly the measurement of the production and release of growth hormone is relevant to the study of growth patterns in the sea, especially as the annual rings on scales and otoliths are influenced by this hormone. Unfortunately the relationships, if any, between the environment and the production of growth hormone are not known. Swift and Pickford (1962) showed that the onset of rapid growth in May of *Perco fluviatilis* was accompanied by a sharp rise in pituitary growth hormone at this time, demonstrating that there is a seasonal variation in the production of this hormone.

Losses by way of natural mortality are difficult to measure, and little is known of the factors contributing to this process. Mass mortality as a result of spawning is known in the Pacific salmon (*Oncorhynchus*), and on a smaller scale similar deaths may take place in the sea. Barr (1963*a*) and Holliday (1958) found that after spawning, plaice and herring are exhausted, in poor condition and probably at this time incapable of withstanding stress.

A good deal of work has been done on the changes in the level of blood corticosteroids and tissue structure of *Oncorhynchus* during its spawning migration (Idler *et al.*, 1958; Robertson and Wexler, 1960). A large increase in the levels of adrenal steroid hormones was found in the blood, and histological studies showed that prior to death the salmon showed symptoms comparable with Cushing's syndrome in man *i.e.* hyperplasia of adrenal cortical tissue, degenerative changes in the pituitary and pathological changes in other organs. The influence of the environment on the production of these hormones is not clear. The pituitary gland (usually the mediator of environmental factors) certainly influences corticosteroid production, (Pickford and Atz, 1957). Rasquin and Rosenbloom (1954) demonstrated the effects of keeping fish in total darkness, when hypertrophy of adrenal tissue was followed by its atrophy. Return to the light could reverse the early stages of these stress responses. Cold shock was also found to induce adrenal cortical changes (Rasquin, 1951). Fontaine and Hatey (1953) found that response to pituitary corticotropin could be varied by a change in temperature.

Distribution and Accessibility.

The same endocrine factors which influence the availability of a species to a fishery will also operate in a general way with regard to distribution and accessibility to the fishing gear. Whether or not a fish lies within the range of operation of a particular gear depends on its position within the fishing area. A drive which results in the localisation of the fish in relation to substrate or a point in depth will to some extent determine its accessibility.

Some components of the complex pattern of diurnal vertical migrations found in pelagic fish such as clupeids may well be due to diurnal differences in the metabolism. There are indications (Holliday and Parry, 1962; Blaxter and Holliday 1963) that the pseudobranch gland, by regulating the availability of oxygen to the tissues, may control the general level of activity of the fish.

It is interesting that Copeland (1952) found that the pseudobranch also controlled gas secretion into the swim-bladder - a factor which is of importance in vertical migration. The pseudobranch is linked with the eye by a common blood supply, and light may in this way control diurnal differences in pseudobranch activity and hence metabolism and vertical migration.

In describing the reproductive behaviour of cod, Brawn (1961*a*) suggested that succeeding phases in the pattern of reproductive behaviour would tend to stratify the fish. There was a downward movement of non-aggressive males, immature fish of both sexes and spent females. There was an upward movement of spawning males and females with spawning in the surface waters.

Vulnerability to fishing force.

Vulnerability is defined as the degree to which an organism is open to attack by a specific force or process. Clearly an animal is most vulnerable to a force designed to exploit its innate or acquired behaviour patterns; for example a particular bait might appeal to a specific appetite or a series of nets might be interposed in a known migration route. Of special relevance to these problems are studies of sensory physiology and behavioural motivation. The effects of endocrines on sensory physiology is not well understood. Apart from inducing patterns of innate behaviour at the time of reproduction, sex hormones may alter acquired behaviour patterns. Vanderplank (1938) found that treatment of rudd (*Leuciscus leuciscus*) with oestrone inhibited conditioned responses to light.

As far as motivation is concerned, cyclical changes in metabolism resulting from hormone action may underlie changes in feeding drives and reactivity to lures and nets. A change in the threshold for the release of escape reactions, or a change in sensory thresholds may alter the vulnerability of fish. Mohr (1963) found that following ovulation herring were less responsive to the approach of a trawl and more easily captured. Skadovskii (1939 *a* and *b*) showed an increase in phototactic responses of *Gambusia* and *Rhodeus* immersed in dilute solutions of chorionic gonadotropin.

THE POSITION OF ENVIRONMENT/ENDOCRINE STUDIES IN A RESEARCH PROGRAMME.

Environmental surveys.

The fundamental study of endocrine control of physiological systems and the initiating and regulating effects of the environment is one that must be based primarily on laboratory experiments. Environmental surveys can provide valuable background data for these experiments. Any attempt to induce or interpret changes in fish kept in aquaria must have relevance to the range of conditions in which the fish normally live. The demonstration of sensitivity to unphysiological doses of hormones or unnatural levels of external stimuli is of value only in so far as it demonstrates the presence of systems which have a <u>potential</u> to respond. On the other hand, environmental surveys alone generally do not demonstrate true cause and effect relationships between the organism and any specific environmental factor. Useful pointers may be obtained if a year or season presents an abnormal factor; Sahrhage (1954) found that in 1952, when sea temperatures in December were 2°C below normal the herring of the southern North Sea were not ripe, whereas in December 1953 when sea temperatures were 2°-3°C above normal the majority of the herring sampled were ripe. The usefulness of such data is limited by the fact that other unmeasured factors in the environment may have interposed between the fish and the temperature stimulus.

Laboratory experiments.

To determine the primary relationships existing between the environment and target organs in fish it is necessary to study the effects of varying a single factor or specific combination of factors while all others are held constant. Not only should the environment be strictly controlled, but the experimental fish should be of uniform physiological background. Only in long term aquarium experiments can these conditions be met. However, as already pointed out, these experiments should be designed and interpreted in the light of measurements of the environment and endocrine activity in the sea.

Endocrine activity measurements in fish caught at sea.

Useful indices of activity can be obtained from the histological appearance of the cells of the gland *e.g.* cell height in the thyroid or ratios of different types of cells in the pituitary. Assay of the glands either chemically or, more often, by a bio-assay technique have been used to determine seasonal variations of potency *e.g.* Gerbil'skii (1940). The most reliable, but also the most difficult technically, of measurements would be the level of circulating hormones in the blood. Changes in target organs *e.g.* the gonads may be indirect indicators of endocrine activity. The sensitivity of the fish to injected hormones may be used to indicate its physiological condition. Gerbil'skii (1951, 1953) used sensitivity to pituitary injections as a criterion for differentiating the spawning races of *Aciperser*.

CONCLUSIONS

In discussing a programme of organized research Parrish (1956) drew attention to some of the physiological problems associated with fisheries biology, but suggested that at the time many could be regarded as largely academic and not essential to the accomplishment of a rational fishery. However as environmental investigations in relation to fisheries problems are almost invariably interpreted in the light of the actual or expected responses of the fish, direct measurements of the fishes' capacity to respond should be available to complement these studies.

REFERENCES

BAGGERMAN, B. 1957. An experimental study on the timing of breeding and migration in the three-spined stickleback. (*Gasterosteus aculeatus* L.) *Archives néerl. Zool.*, 12: 105-318.

1959. The role of external factors and hormones in migration of sticklebacks and juvenile salmon. *In* Gorbman, A. *Symposium on Comparative Endocrinology.* New York. John Wiley and Sons. 24-37, illus., bibl.

1960. Salinity preference, throid activity and the seaward migration of four species of Pacific salmon (*Oncorhyncus*). *J. Fish. Res. Bd. Canada,* 17 (3): 295-322.

BARR, W.A. 1963*a*. The endocrine control of the sexual cycle in the plaice, *Pleuronectes platessa* L. 1. Cyclical changes in the normal ovary. *Gen. comp. Endocr.*, 3 (3): 197-204.

1963*b*. The endocrine control of the sexual cycle in the plaice, *Pleuronectes platessa* L. II. The endocrine control of oogenesis. *Gen. comp. Endocr.*, 3(3): 205-215.

1963*c*. The endocrine control of the sexual cycle in the plaice, *Pleuronectes platessa* L. III. The endocrine control of spermatogenesis. *Gen. comp. Endocr.*, 3 (3): 216-225.

BLAXTER, J.H.S. 1958. The racial problem in herring from the viewpoint of recent physiological, evolutionary and genetical theory. *Rapp. Cons. Explor. Mer.*, 143: 10-19.

BLAXTER, J.H.S., and F.G.T. HOLLIDAY. 1963. The behaviour and physiology of herring and other clupeids. *In* Russell, F.S. *Advances in Marine Biology*, 1. London and New York. Academic Press. 262-394. Illus., bibl.

BRAWN, V.M. 1961*a*. Aggressive behaviour in the cod (*Gadus callarias* L.). *Behaviour*, 18 (1-2): 107-146.

1961*b*. Reproductive behaviour in the cod. (*Gadus callarias* L.). *Behaviour*, 18 (3): 177-198.

BUCHMANN, H. 1940. Hypophyse und Thyreoidea im Individualzyklus des Herings (Hypophysis and Thyroid in the Individual cycle of the Herring). *Zoologischer Jahresbericht*, 66 (2): 191-262.

BULLOUGH, W.S. 1940. A study of the reproductive cycle of the minnow in relation to the environment. *Proc. zool. Soc. Lond.*, Series A, 109: 79-102.

COPELAND, D.E. 1952. The function of the pseudobranch gland. in teleosts.. *Amer. J. Physiol.*, 167: 775.

DODD, J.M. 1960. Gonadal and gonadotrophic hormones in lower vertebrates. *In* Parkes, A.S. *Physiology of Reproduction*, 1 (2), London, Longmans.

DRAGESUND, O. 1960. Observations on the spawning of herring in captivity. *Fauna*, 4: 137-144.

FONTAINE, M. 1954. Du determinisme physiologique des migrations. (Physiological determinants of migrations). *Biological Reviews*, 29: 390-418.

FONTAINE, M., and O. CALLAMAND. 1943. Les aspects physiologiques d'une "vie cyclique de l'Anguille d'Europe", *Anguilla anguilla*, (Physiological aspects of a cyclic life of the European eel, *Anguilla anguilla*). *Bull. Mus. Hist. nat., Paris.*, 15: 373-378.

FONTAINE, M., F. LACHIVIER, J. LELOUP, and M. OLIVEREAU. 1948. La fonction thyroidienne du Saumon (*Salmo salor*) au cours de sa migration reproductrice. (The thyroid function of the salmon during its reproductive migration). *J. Physiol.*, 40: 182-184.

FONTAINE, M., and J. HATEY. Recherches sur le controle hypophysaire de l'interrenal anterieur d'un poisson teleosteen, l'anguille.(*Anguilla anguilla* L.). I. Variations ponderales de l'interrenal anterieur. *C.R. Soc. Biol., Paris.*, 147: 217-226.

GERBIL'SKII, N.L. 1940. Seasonal changes of the gonadotropic potency of the pituitary glands in fishes. *Dokl. Akad. Nauk, SSR*, 28: 571-573.

1951. Intraspecific biological groups of acipenserine fish and their reproduction in the mouths of rivers with regulated flow. (In Russian). *Ryb. Khoz.*, 27 (4): 24-27.

1953. Intraspecific biological groups of acipenserines and the importance of their understanding for the development of acipenserine culture in connection with hydroconstruction. *Trud. Soveshch. ikhtiol. Kom.*, 1: 291-300.

GOTTFRIED, H., S.V. HUNT, T.H. SIMPSON, and R.S. WRIGHT. Sex hormones of fish; the oestrogens of cod (*Gadus callarias*). *J. Endocrin.*, 24: 425-430.

HARRINGTON, R.W. 1957. Sexual photoperiodicity of the cyprinid fish, *Notropis bifrenatus* (Cope), in relation to the phases of its annual reproductive cycle. *J. exp. Zool.*, 135: 529-556.

HOAR, W.S. 1953. Control and timing of fish migration. *Biological Reviews*, 28: 437-452.

1955. Reproduction in teleost fish. *Mem. Soc. Endocrin.*, 4: 5-24.

1957. Endocrine Organs. *In* Brown, M.E. *The Physiology of Fishes* Vol. 1. New York. Academic Press. 245-285, illus., bibl.

1961. Hormones and reproductive behaviour of the Poikilothermic Vertebrates Physiology of reproduction. *Proceedings of the 22nd Biology Colloquium Oregon State University, 1961.*

HOAR, W.S., M.H.A. KEENLEYSIDE, and R.G. GOODALL. 1955. The effects of thyroxine and gonadal steroichs on the activity of salmon and goldfish. *Canad. J. Zool.*, 33: 428-439.

HOAR, W.S., D. MACKINNON and A. REDLICH. 1952. Effects of some hormones on the behaviour of salmon fry. *Canad. J. Zool.*, 30: 273-286.

HOLLIDAY, F.G.T. 1958. The spawning of the herring. *Scot. Fish. Bull.*, 10: 11-13.

1960*a*. The control of maturation in the herring. *I.C.E.S. Herring Committee*, Paper No. 38 (mimeo.).

1960*b*. The control of spawning in the herring. *I.C.E.S. Herring Committee*, Paper No. 39 (mimeo.).

1962. Hermaphroditism in the herring (*Clupea harengus* L.). *Proc. roy. Soc. Edinb.*, 68: 218-224.

HOLLIDAY, F.G.T., and G. PARRY. 1962. Electron microscope studies of the acidophil cells in the gills and pseudobranchs of fish. *Nature*, London. 193: 192.

IDLER, D.R., A.P. RONALD, and P.J. SCHMIDT. 1959. Biochemical studies on sockeye salmon during spawning migration. VII. Steroid hormones in the plasma. *Canad. J. Biochem. Physiol.*, 37: 1227-1238.

ILES, T.D. 1964. In press. *J. Cons.*

LISBON. 1957. Fishing effort, the effect of fishing on resources and the selectivity of fishing gear. *Proceedings of the joint scientific meeting of ICNAF, ICES and FAO.* 1 (reports): 45 p.

MOHR, H. 1963. Reaction of herring to fishing gear studied by means of echo-sounding. *Second World Fishing Gear Congress, London 1963.* Paper 21.

NAUMOV, V.M. 1956. The ovogenesis and ecology of the sexual cycle of the Murmansk herring (*Clupea harengus* L.). In Russian. *Trudy* PINRO. 9. (Translation in *Special Scientific Reports of the U.S. Fish and Wildlife Service*, 327: 203-262, 1959).

OUTRAM, D.N. 1951. Observations on the retention and spawning of the Pacific herring. *Progress Reports of the biological stations at Nanaimo and Prince Rupert*, 87: 32.

PARRISH, B.B. 1956. The cod, Haddock and Hake. *In* Graham, M. *Sea Fisheries, their investigation in the United Kingdom.* London. Edward Arnold. p. 252-331., illus. bibl.

PICKFORD, G.E. and J.W. ATZ. 1957. *The physiology of the pituitary gland of fishes.* New York. New York Zoological Society. 613 p., tabl., bibl.

RASQUIN, P. 1951. Effects of carp pituitary and mammalian A.C.T.H. on the endocrine and lymphoid systems of the teleost *Astyanax mexicanus*. *J. exp. Zool.*, 117: 317-357.

RASQUIN, P., and L. ROSENBLOOM. 1954. Endocrine imbalance and tissue hyperplasia in teleosts maintained in darkness. *Bull. Amer. Mus. nat. Hist.*, 104: 359-426.

ROBERTSON, O.H., and B.C. WEXLER, 1960. Histological changes in the organs and tissues of migrating and spawning Pacific salmon (Genus *Oncorhyncos*). *Endocrinology*, 66 (2): 222-239.

SAHRHAGE, D. 1954. Beobachtungen zur Frage der Heringslaichplätze. (Observations on the problems of herring spawning places). *Mitt. Inst. Seefisch.*, 6: 24-32.

SKADOVSKII, S.N. 1939*a*. Change of physiological processes in aquatic animals in dependence on conditions of the inorganic medium. *Uchen Zap. Moskow Univ.* (*Hydrobiol*), 33: 4-6.

1939*b*. The influence of prolan upon the phototaxis motions in *Daphnia pulex* and in *Rhodeussamarus*. *Uchen Zap. Moskow Univ.* (*Hydrobiol*), 33: 247-251.

SWIFT, D.R. and G.E. PICKFORD. 1962. Seasonal variations in the growth hormone content of pituitary glands of the perch, *Perca fluviatilis*. *General and Comparative Endocrinology*, 2 (6): 627.

VANDERPLANK, F.L. 1938. Sex hormones and their effect upon conditioned responses in the rudd (*Leuciscus leuciscus*). *J. exp. Biol.*, 15: 385-393.

WOODHEAD, A.D. 1959*a*. Variations in the activity of the thyroid gland of the cod, *Gadus callarias* L., in relation to its migrations in the Barents Sea. I. Seasonal changes. *J. Mar. biol. Ass., U.K.*, 38 (2): 407-416.

1959*b*. Variations in the activity of the thyroid gland of the cod, *Gadus callarias* L., in relation to its migrations in the Barents Sea. II. The "dummy run" of the immature fish. *J. Mar. biol. Ass., U.K.*, 38 (2): 417-422.

F-4

EFFECT OF ABIOTIC FACTORS IN YOUNG STAGES OF MARINE FISH *

By

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CONTENTS

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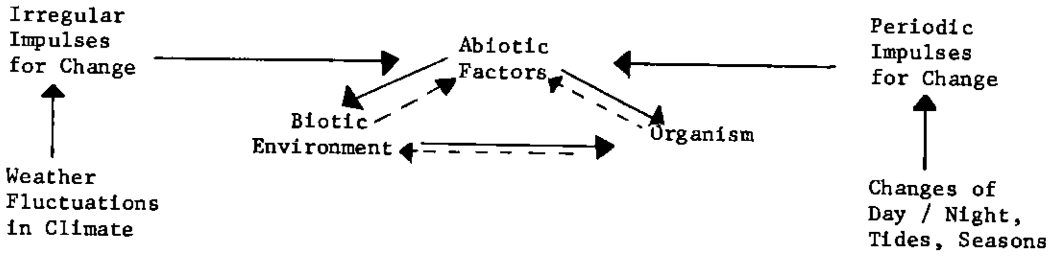
* This paper is dedicated to Prof. Dr R. Kändler on the occasion of his 65th birthday.

INTRODUCTION

The relationship between an organism and its biotic and abiotic environment and the causes which lead to a change in environmental conditions can be roughly schematized as follows:



As the above scheme shows, there should be distinguished between the *direct* effect of environmental factors on the specific organisms, and the *indirect* effect via the biotic environment. Moreover it seems to be useful to distinguish between two further possible effects,

(a) direct effect of a rather *constant* abiotic environmental factor
(b) direct effect through *changes* in the existing abiotic environmental conditions.
ad (a): In this connection the following facts are of special interest: the mode of action of the environmental factor on the organism; the ranges of tolerances and of optimum development of the species concerned.
ad (b): The effect of changing abiotic environmental conditions on fish eggs and larvae to a great extent depends on the speed and the range of change. It may be taken for sure that organisms have a resistance to periodic and unperiodic changes *normally* occurring in their biotop.

Among the abiotic environmental factors the following seem to be of special influence on fish eggs and larvae:

temperature
salt content
content of dissolved oxygen
light
currents
waves

In the following a review is given on investigations on the effect of abiotic factors in young stages of marine fish with special references to experimental results.

1. TEMPERATURE

1.1 General Remarks

The development of eggs and larvae is influenced to a high degree by water temperature. Many investigations have shown that the position of the spawning place, the beginning and duration of spawning depend on the water temperature. Furthermore, the intensity of spawning is closely related to the temperature, as indicated by Poulsen (1936) for the autumn-spawning herring of the Belt Sea and the Western Baltic. There is, however, less information on the effects these factors have on the success of fertilization and the survival rate of eggs and larvae.

Extremely low temperature in winter may lead to a late beginning of spawning for spring-spawners. In this way it becomes more probable that eggs and larvae develop during a period of rapidly increasing water temperatures. Qasim (1956) indicated that in such a case larvae of northern fish will be affected by too high water temperatures. On the other hand, the rich fauna caused by rapidly increasing water temperatures is favourable for the development of larvae.

1.2 Experiments on the Effect of Temperature on Egg Development

1.2.1 Time of Incubation

Recent investigations have shown that in many species there is no straight-line relation between temperature and time of incubation (Krüger, 1961; Barlow, 1961; Blaxter and Hempel, 1961; Lillelund, 1961; Hempel, 1962).

As the time to hatching is shorter at higher temperatures, the time during which hatching takes place in areas of rising water temperatures becomes shorter than the spawning period. For example, Lillelund (1961) computed for *Osmerus eperlanus* a mean spawning period of 29 days, whereas the difference between first and last hatching date of larvae was only 14 days.

1.2.2 Limits of Tolerance

Intensive investigations on the limits of tolerance during the time of incubation of eggs of *Salmo gairdneri* were made by Hamdorf (1960). These showed that the upper lethal temperature increased as the embryos develop. Immediately after fertilization, upper lethal temperatures were 14° to 15°C, and in later stages 20° to 24°C. This relation was confirmed by Lillelund (1961) for *Osmerus eperlanus*.

During breeding experiments, the rate of survival of cod eggs decreased at low water temperatures near the lower tolerance limit (Dannevig and Hansen, 1952). It is not known to what degree lethal temperatures during egg development are influenced by acclimatization of the eggs.

1.2.3 Size of Larvae at Hatching

The size at hatching to some extent depends on the temperature. In spite of a few contradictory results the size at hatching in general seems to decrease with increasing breeding temperatures. Thus, at low temperatures larvae hatch at a later stage, with smaller yolk supply, than at higher temperatures (Gray, 1928; Lindroth, 1946; Hamdorf, 1961; Blaxter and Hempel, 1961; Lillelund, 1961; Hempel, 1962).

1.2.4 Meristic Characteristics

There are several studies on the relation between temperature and the number of vertebrae (or myomeres) (among others, Tester, 1938; Tåning, 1952; Hempel, 1953; Blaxter, 1957; Lillelund, 1961). According to these studies there is a correlation between the number of vertebrae and the breeding temperature, differing from species to species.

1.2.5 Change of Temperature during Breeding

Such experiments have been carried through by Dannevig and Hansen (1952) with eggs of Norwegian cod, showing that the changes in temperature from 2° to 10°C. caused a high egg mortality. Temperature shocks at a sensitive period may influence the number of myomeres and vertebrae (Tåning, 1952; Hempel and Blaxter, 1961).

1.3 Experiments on the Relation between the Development of Larvae and Young Fish and Temperature

1.3.1 Absorption of Yolk Sac

According to the higher speed of metabolism at higher temperatures, the duration of the yolk sac stage (until absorption of yolk sac) decreases with increasing temperature. On this, thorough investigations have been made by Blaxter and Hempel (1963) on larvae of *Clupea harengus*.

1.3.2 Limits of Tolerance

The range of temperature tolerated by organisms depends to a high degree on the acclimation temperature, as some investigations have shown (Doudoroff, 1946; Fry *et al.*, 1942; Fry *et al.*, 1946; Brett, 1952, 1956; McCauley, 1958; Bishai, 1960; Blaxter, 1960). To what extent an organism is capable of tolerating extreme temperatures by acclimation may vary between different species. With decreasing water temperatures, near the lower limit of tolerance, the survival rate decreases in the form of a sigmoid curve. Furthermore, Brett observed that lowering of the temperature towards the lethal level caused a rapid death of part of the sample. Some larvae, however, survived for several hours, but died then slowly. Brett assumes that lethal temperatures have a shocking effect on the central nervous system for most of the organisms, whereas those surviving the shock will die from an increasing osmotic discrepancy.

Contrary to the results of experiments on species from temperate areas, Kuthaligam (1959) found that larvae of 10 marine tropic species tolerated only a very narrow range of temperature.

Other investigations indicated that young stages of fish tolerated a smaller range of temperature than adult fish, and marine fish smaller than fresh water fish.

1.4 Investigations at Sea

1.4.1 Horizontal and Vertical Distribution

In many species there is a close relation between the abundance of eggs and larvae in the horizontal distribution and the course of isothermal lines. (Literature especially Rapp. Proc. Verb. (150) ICES/ICNAF Redfish Symposium 1961 and this Symposium Section A.)

This distribution may originate from the preference of a certain water temperature by the parent fish during spawning, as it is shown for the larvae of red fish, or from temperature-induced migrations of the larvae. As an example, the behaviour of larvae and young fish of the Baltic Herring may be mentioned here. As elucidated by Lisivnenko (1958), in October, when the temperature in the coastal regions falls to 8° to 9°C., all the fry of the spring spawners migrate to deep waters. Together with the larvae of the autumn spawning herring they return to coastal waters when the temperature has risen to 7° to 8°C. in spring of the following year. With the water temperature rising to 14° to 15°C. in summer, young fish again migrate to deep waters.

In many species the vertical distribution is also strongly correlated with temperature. In this connection, recent investigations by Miller *et al.* (1936) are of special interest. These authors found over 80% of the haddock larvae within the confines of the thermocline.

1.4.2 Limits of Tolerance

Under special circumstances it may be possible that the boundaries of currents will change in such a way that in the mixed water area eggs and larvae are affected by extreme temperature and die.

2. SALINITY

Investigations on the tolerance of eggs and larvae to salinity have been carried out in the following species:

from the Baltic:	*Platichthys flesus* *Pleuronectes platessa* *Limanda limanda* *Scophthalmus maximus* *Gadus morhua* *Clupea sprattus* (Strodtmann, 1918)
from the Canadian Coast:	*Clupea pallasii* (McMynn and Hoar, 1953)
Others:	*Clupea harengus* Population from the Firth of Clyde, (Holliday and Blaxter, 1961) *Osmerus eperlanus eperlanus* (Lillelund, 1961) *Clupea pallasii* Okho Herring (Kurata 1959, Galkina 1962)

2.1 Experiments on the Influence of Salinity on Egg Development

These investigations showed in general that fertilization and development of eggs was possible in a wider salinity range than occurring in nature. However, within the wide limits of tolerance there was a narrower range of salinity with an optimum hatching rate. As pointed out by Strodtmann, pelagic eggs brought into lower salinity will at first sink down. In a medium salinity the eggs may adapt themselves by reducing their specific weight. As experiments by McMynn and Hoar, and those by Lillelund, showed, the salinity tolerance increases during incubation. While early embryological stages of *Osmerus eperlanus* tolerated a salinity of 8 ^{o}/oo, the late stages (eyed stage) could be exposed without danger to a salinity as high as 24 $^{0}/oo$. Only immediately before hatching, the upper lethal tolerance decreased to 8 $^{0}/oo$. This tolerance decrease in the last phase of incubation seems to be a consequence of changing permeability of the egg membrane. As with the temperature, salinity influences the number of myomeres. (Hempel and Blaxter, 1961). The influence on the number of myomeres is not uniform throughout the total range of tolerance. The effect of salinity on the number of myomeres seems to be more marked in especially high and/or low salinity. There are no consistent results on the dependence of the larvae size at hatching on salinity during incubation. While Blaxter and Hempel (1961) and Hempel (1962) found extreme salinity conditions causing smaller larvae, Galkina in her experiments arrived at just opposite results. (Galkina, 1962).

2.2 Experiments on the Influence of Salinity on Larval Development

After hatching, the salinity tolerance of sardine larvae increased rapidly (Lasker and Theilacker, 1962). In a medium salinity range the salinity will have no influence on the life span of non-fed larvae, as is indicated for larvae of *Clupea harengus* by Blaxter and Hempel (1963), and for *Osmerus eperlanus* by Lillelund (1961). The larvae also have a good adaptability to a wide salinity range. Corresponding with the wide range of tolerance to salinity of herring larvae, Bückmann *et al.* (1953) could state no preference for a special salinity by the larvae of this species. There is no conformity in the results of investigations on the question of whether the tolerance to salinity will change during later life history or not. In Shelbourne's (1957) experiments the larvae of *Pleuronectes platessa* were more sensitive to salinity than the adult fish, whereas Holliday and Blaxter came to opposite results with *Clupea harengus*.

3. CONTENT OF DISSOLVED OXYGEN

The O_2 consumption was investigated for eggs and larvae of many species, especially of fresh water fish. (Among others: Juday and Wagner, 1909; Wells, 1913; Lindroth, 1942; Jones, 1952.) Especially thorough studies on the effect of O_2 content of water on fish eggs have been made by Alderdice, Wicket and Brett (1958) with *Oncorhynchus keta*, as well as by Hamdorf (1961) with *Salmo gairdneri*. Experiments of these authors have shown that low O_2 concentrations at the beginning of incubation lead to disturbance in the development of embryos. A low O_2 concentration in early embryological stages causes a longer incubation period and in later stages a shortening of incubation time. Hamdorf also dealt with the special question of the dependence of growth on O_2 content. According to his investigations, the body weight at hatching decreased with decreasing O_2 content (in his experiments from 28 to approximately 5 mg). Moreover, the growth rate of embryos as well as of larvae was influenced by the O_2 concentration. Parallel to the growth of embryos there was a rise in O_2 consumption. Hatching occured as soon as the O_2 concentration in the breeding water became insufficient for covering the minimum O_2 requirements of the embryo. During the growth of larvae, the additional O_2 consumption was proportional to the addition in weight of larvae. It was of interest here that young fish that developed in low O_2 concentrations during embryological and larval stages, and were afterwards brought into normal O_2 conditions, reached -after absorption of yolk sac- the same sizes as the control-fish. The effects of low O_2 concentration on larvae and young fish of some species of salmonids have been studied by Bishai (1962), who found that the sensitivity of the fry to low O_2 content of the water decreased with age. The fry was able to avoid low O_2 concentrations by trial and error. These observations by Bishai are in agreement with results of experiments by Shepard (1955) with fry and fingerlings of *Salvelinus fontinalis*. According to Shepard, larvae and young fish are able to acclimate to low O_2 concentrations, thus reducing the lethal limits.

4. LIGHT

4.1 Experiments on the Effect of Light on Fish Eggs and Larvae

There is little information on the extent to which marine fish eggs and larvae will be affected by light. Blaxter (1956) found in *Clupea harengus* a higher rate of hatching in the dark than in the lighted tank. Corresponding observations were made by Dannevig and Hansen (1952) in breeding experiments with eggs of plaice. However, with cod eggs the best success of hatching was found in tanks near the window. A characteristic example of the sensitivity to light are the eggs of numerous species of salmonides. Recent investigations by Hamdorf (1960) have shown that the different spectral regions have different effects on egg development. The lowest survival rate resulted in the spectral region around 420 mu/. As the degree of sensitivity at this wave-length depends on the intensity of the yellow to red egg pigments, Hamdorf believes that these pigments have the function of protection pigments. As Hamdorf could further show, the sensitivity to light increases until the heart starts beating, after which it decreases rapidly. This process can be understood, as Hamdorf points out, if it is assumed that the radiation destroys the lactoflavin which is of special importance for the respiration of early embryological stages. A sudden lightening of herring eggs ready for hatching after a period in the dark effected spontaneous hatching. In further rearing experiments by Hempel, he found that larvae continuously kept in the dark had a longer life span than those kept at normal day/night conditions.

4.2 Behaviour of Larvae to Light

Immediately after hatching, larvae differ in their reactions to light from species to species. Later they prefer water depths with specific light conditions. Correspondingly, larvae of many species make daily vertical migrations. (Johannsen, 1925; Russel, 1926; Silliman, 1943; and others.) As the larvae of many species take food only in light (Blaxter and Hempel, 1961), it may be assumed that the daily vertical migrations of these larvae are a direct reaction to changing light intensity rather than following the movements of the nutrition horizon. Different quantities of larvae in day and night catches may be caused by the fact that at daylight larvae can better escape plankton nets (Bridger, 1956). Concerning experiments with fish larvae it is of interest that the mortality rate of larvae will be higher in transparent than in opaque tanks, as stated by Bückmann *et al.* (1953) for herring larvae.

5. CURRENTS

5.1 Effect of Currents on Eggs and Larvae

The position of the spawning places of many species of fish is influenced by currents. As an example, investigations by Poulsen (1930) on the spawning intensity of cod in the Belt Sea may be given. The question to what extent current eddies affect the horizontal and vertical distribution of eggs in the marine, also after spawning time, is discussed by Laevastu (1961). By a change of the normal boundaries of currents, eggs and larvae in the mixed area may be exposed to a rapid change in abiotic environmental factors, as Colton (1959) indicated in his investigations in the area of Georges Bank.

More often, however, currents cause a slow drift of eggs and larvae from the original spawning place to other marine areas. In this connection the following observations are of special interest:

The northern drift of cod eggs along the Norwegian coast to the area of the Bear Islands - Spitzbergen Banks and the Barents Sea. (Rollefsen, 1930; Wiborg, 1957).

The inflow of larvae of different species from the North Sea to the Western Baltic (Poulsen, 1934, 1935).

The drift of planktonic stages of many marine species from spawning places to the North-East Atlantic (Fraser, 1958).

The drift of herring larvae by off-coastal winds from the Norwegian coast to deeper areas with poor nutrition (Hjort, 1926).

The drift of haddock larvae from Georges Bank seawards over the edge of the Shelf (Walford, 1938; Chase, 1955; Colton and Temple, 1961).

Consequent to driftings, a change in biotic and abiotic environmental factors will occur for eggs and larvae, offering more or less favourable conditions for development.

5.2 Behaviour of Larvae to Currents

The respective results for fresh water fish do not apply to marine fish because of the completely different current conditions in fresh water areas. Of interest in relation to the behaviour of larvae of marine fish are the observations of Creutzberg (1958, 1959), as well as experiments by Bishai (1960). According to Creutzberg it is possible that elvers (*Anguilla vulgaris*) use the tides for coastward transportation. Bishai found positive rheotaxis in larvae of *Clupea harengus* and *Cyclopterus lumpus*. Larvae of herring began to drift in the tanks only at current speeds higher than 0.58 m/sec.

6. WAVES

It is well known for many species of fresh water fish that eggs are very sensitive to vibration during the first 24 hr of incubation. According to investigations on pressure resistance of eggs of cod and plaice, Rollefsen (1930) and Devold (1935) pointed out that it seems to be probable that eggs of marine fish will be destroyed and burst mechanically by breakers during rough weather. Galkina (1957) investigated the dependence of mechanical resistance of different egg stages of the Okhotsk herring on salinity. The experiments indicated that with increasing salinity also the resistance to mechanical pressure increased. The effect of wave action on fish eggs in coastal waters may therefore be lower than in the open sea.

7. CONCLUSION

7.1 In the foregoing some important results of experimental research on the effect of some abiotic factors on fish eggs and larvae have been summarized. It was not so much intended to give a complete bibliographic review, but to present a large number of different forms of effect. In order to avoid false interpretation, the following points of view should be taken into account:

(a) Special environmental conditions in the experiments.
(b) The isolated consideration of single factors.

ad (a): One of the special environmental factors in the experiments is the limited size of aquariums. This factor might be of more significance in experiments with fish larvae than with eggs. While studying the effect of the biotop volume on metabolism and growth of young trout, Willer and Schnigenberg (1927) coined the term "Raumfaktor" (factor of biotop volume). Also the distance of the test animals from each other has to be taken into account. Two further "artificial" conditions in many experiments are the insufficient depth of water and the unnatural gas content (Henley, 1951). Also the currents produced in experiments are never as laminar as the great marine currents.

ad (b): The character of an experiment requires to limit investigations to the variation of one factor only, leaving the others as constant as possible. In the majority of experiments — also in the aforementioned ones — only the effect of one factor has been studied at a time. In nature, the observed effects mostly result from a combination of several variable factors. The effect of each of these factors may, by parallel actions of other abiotic factors, be intensified, or weakened or, in special cases, even neutralized. There are little experimental investigations on the effects of such combined factors. Kinne (1956, 1960) investigated the 'Temperature/Salinity' relation on *Cyprinodon maculatus*. At relatively low temperatures (15°, 20°C.) the growth of young fish is best in fresh water, whereas at higher temperatures (25°, 30°, 33°C.) best results were found in water of 35 to 55 ‰. Moreover, the intensity of food intake and of conversion efficiency depends on the temperature/salinity relation. Kinne supposes that in the temperature/salinity relation the density of the water—as a function of temperature and salinity—plays a role.

7.2 Investigations on the effects of abiotic factors on fish eggs and larvae may contribute to a better understanding of the following three problems which, during the last years, have become of increasing interest:

(a) Long-term changes in the abundance of fish populations;
(b) Critical periods during the first months of life;
(c) Dependence of annual fluctuations on the environmental conditions of the 0-group.

ad (a): A phenomenon frequently studied during the last decades is the rapid reduction in the stocks of some species of marine food fish, as
the Norwegian herring,
the Plymouth herring,
the sardine Sardinops melanostica in the Japan Sea,
the *Sardinops caerula* of the American West Coast.

Parallel to the reduction in stocks, a more or less obvious change in the reproduction behaviour was observed, as indicated by an alteration in spawning dates as well as spawning places. There was good reason to assume that these long-term changes in the stocks were caused by long-term changes of hydrographical conditions. As investigations in the Baltic have shown, there is a remarkable increase in the stocks of sprat, plaice and, especially, cod. According to Kändler (1949) it may be assumed that the long-term change in abundance may be due to an increasing inflow of water with relatively high salinity into the Baltic during the last three decades. The better hydrographical conditions have led to an increase in the plankton and, thus, to better conditions for the fry. The example of the Baltic indicates that long-term changes in the abundance of fish stocks most probably are part of a complex in which a great number of abiotic and biotic factors are working together, influencing the life cycle of the species concerned.

ad (b): For several species there is evidence for an especially high mortality rate (critical phase) in certain developmental stages from the incubation of the egg to the end of the first months of life. Such high mortality periods have been found, among others,
— in egg stages III and IV of the Baltic herring (Toom, 1962);
— from hatching of larvae to absorption of yolk sac in the Californian sardine (Ahlström, 1954; Farris, 1960) and in the Japanese sardine (Nikai *et al.*, 1955);
— for the span immediately after absorption of the yolk sac and after reaching a length of 16-20 mm in herring larvae (Blaxter and Hempel, 1961);
— 30 to 40 days after hatching in the Atlantic mackerel (Marr, 1956);
— and in the same species for the total first months of life (Sette, 1943).

The given examples have shown that the model of Hjort (1926), who postulated a critical phase immediately after hatching, is not always realized. It is more evident that critical phases may occur in several species and, possibly, in the same species in different developmental stages. The aforementioned results on wide tolerance to abiotic factors in young stages of fish — with the exception of some egg stages with special sensitivity — do not give any hint to critical phases being caused by direct effects of abiotic environmental factors. It is more probable, as pointed out especially by Shelbourne (1957) and Harris (1960), that periods of high mortality are chiefly due to biotic factors, as predators and lack of nourishment. Thus, the effect of the abiotic factors has to be seen more as an indirect one in connection with critical phases.

ad (c): There are many indications that the abundance of a year-class is determined by the combined effects of biotic and abiotic factors during the first months of life. As, in the end, the biotic factors — especially the food supply for the fry — depend to a high degree on the abiotic conditions, the key for the fluctuations of year-classes may well be seen in abiotic conditions from fertilization of the eggs to the end of the "fry stage". As hydrographical conditions before the spawning time influence the begin, position and intensity of spawning, the span during which the abundance of the year-class is determined by abiotic factors may start even before spawning. Some scientists have made attempts to find correlations between the abundance of year-classes and abiotic factors (especially temperature and wind) in the respective breeding area. (Veley, 1950, 1951; Carruthers and Parrish, 1951; Carruthers, Lawford and Veley, 1951; Rae, 1957). Although the correlations represented were not always obvious, it was suggested that the studied abiotic factors play an important part in the determination of the abundance of a year-class. It seems to be possible, however, that in some years their effect may be neutralized by other factors.

In order to examine the coaction of several factors, Wiborg gathered and tabulated for a number of years certain factors that might have been of influence on the abundance of year-class of the Norwegian cod. Wiborg assumed that the following factors caused a rich year-class:

long spawning period;
late hatching or late spawning;
northern drift of eggs and larvae;
northward shifting of the spawning center.

While Wiborg marked the factors by plus or minus only, Lillelund (1961) has gone a step farther. He found in smelt that the abundance of year-class of the population concerned is influenced by the following four factors:

mean volume of water of the river Elbe during spawning time;
mean water temperature
(a) 0. to 13. day after mean date of hatching,
(b) 14. to 27. day after mean date of hatching;
duration of spawning time.

Furthermore there had been indications that the effect of one factor in some year was neutralized by the effect of one of the other factors. In order to quantify the effect of abiotic factors on the abundance of year-classes in relation to the different intensity of the factors concerned, Lillelund set up a graduated scheme of valuation for each of these factors as demonstrated in Table 1.

The table shows that Lillelund assumed a non-straight correlation between temperature and its effect on larvae. This hypothesis based on the fact that, on one hand, plankton development in the

TABLE 1. SCHEME OF VALUATION OF SOME ENVIRONMENTAL FACTORS ON THE ABUNDANCE OF YEAR-CLASSES

		$10\ m^3$/sec	Valuation
I.	Mean outflow of water during spawning time (at water gauge Darsau/ Elbe)	50- 59	— (= minus 2)
		60- 69	-
		70- 79	+
		80- 89	++
		90- 99	+++
		100-109	++++
		110-119	+++++
		120-129	++++++
		130	+++++++
		°C	Valuation
II.	Mean water temperature 0.-13. day after mean date of hatching	9.5	—
		9.5-10.4	-
		10.5-11.4	+
		11.5-12.4	++
		12.5-13.4	++++
		13.5-14.4	++++++++
		14.5-15.4	++++
		15.5-16.4	++
		16.5-17.4	+
		°C	Valuation
III.	Mean water temperature 14.-27. day after mean date of hatching	10.5	-
		10.5-11.4	+
		11.5-12.4	++
		12.5-13.4	+++
		13.5-14.4	+++
		14.5-15.4	+++
		15.5-16.4	+++
		16.5-17.4	++
		17.5-18.4	+
IV.	Duration of spawning time/less than 22 days		-

river Elbe does not start at temperatures lower than 10°C, on the other hand, as indicated by experiments at high temperatures the duration of the yolk sac stage is extremely short. There is a good correlation between the abundance of year-classes of smelt and the scopes calculated on the basis of the scheme and the hydrographical and biological data available for 12 years.

Of course this can only be regarded as an attempt to quantify the effects of combined factors on the abundance of year-class. As it was necessary for the mathematically formulated population dynamics to start with a number of assumptions and to approach the individual parameters only gradually in later years, it will be necessary to correct the scoring of environmental effects by and by on the basis of latest data available. I would not fail to state that, similar to the population dynamics, there will be required a good deal of optimism to come to an evaluation - by using either the above way or another - of the complex effect of abiotic factors on fish eggs and larvae.

REFERENCES

AHLSTROM, E.H. 1954. Distribution and abundance of egg and larval populations of the Pacific sardine. *Fish. Bull. U.S.*, 56 (93): 83-140.

ALDERDICE, D.F., W.P. WICKETT and J.R. BRETT, 1958. Some effects of temporary exposure to low dissolved oxygen levels on Pacific salmon eggs. *J. Fish. Res. Bd. Canada*, 15 (2): 229-249.

BARLOW, G.W. 1961. Causes and significance of morphological variation in fishes. *Syst. Zool.*, 10: 105-117.

BISHAI, H.M. 1959. Upper lethal temperatures for larval salmonides. *J. Cons.*, 25 (2): 129-132.

1959. The effect of water currents on the survival and distribution of fish larvae. *J. Cons.*, 25 (2): 134-145.

1960. The effect of salinity on the survival and distribution of larval and young fish. *J. Cons.*, 26 (2): 166-177.

1962. Reactions of larvae and young salmonids to different hydrogen ion concentration. *J. Cons.*, 27 (2): 167-178.

BLAXTER, J.H.S. 1956. Herring rearing - II, The effect of temperature and other factors on development. *Mar. Res.*, No. 5.

1957. Herring rearing - III, The effects of temperature and other factors on myotome counts. *Mar. Res.*, No. 1.

1960. The effect of extremes of temperature on herring larvae. *J. Mar. biol. Ass. U.K.*, 39: 605-608.

BLAXTER, J.H.S., and G. HEMPEL. 1961. Biologische Beobachtungen bei der Aufzucht von Heringsbrut. *Helgoländ wiss. Meeresunters.*, 7 (5): 260-283.

1963. The influence of egg size on herring larvae (*Clupea harengus* L.). *J. Cons.*, 28 (2): 211-240.

BLAXTER, J.H.S., and F.G.T. HOLLIDAY. 1963. The behaviour and physiology of herring and other clupeids. *Advances in Mar. Biol.*, (1): 262-405, Academic Press London-New York.

BRETT, J.R. 1952. Temperature tolerance in young Pacific salmon, genus Oncorhynchus. *J. Fish. Res. Bd. Canada*, 9 (6): 265-323.

1956. Some principles in the thermal requirements of fishes. *Quart. Rev. Biol.*, 31 (2): 75-87.

BRIDGER, J.P. 1956. On day and night variation in catches of fish larvae. *J. Cons.*, 22 (1): 42-57.

BUCKMANN, A., W. HARDER, and G. HEMPEL. 1953. Unsere Beobachtungen am Hering. *Kurze Mitteil. Fischereibiol. Abteil.*, No. 3: 22-42.

CARRUTHERS, J.N., A.L. LAWFORD, and V.F.C. VELEY. 1951. Fishery Hydrography: Brood-Strength Fluctuations in various North Sea fish, with suggest methods of Prediction. *Kieler Meeresforsch.* 8 (1): 5-15.

CARRUTHERS, J.N., and B.B. PARRISH, 1951. Variations in brood strength in the North Sea haddock, in the light of relevant wind conditions. *Nature, Lond.*, 168: 317.

CHASE, J, 1955. Winds and temperatures in relation to the brood-strength of Georges Bank haddock. *J. Cons.*, 21 (1): 17-24.

COLTON, J.B. 1959. A field observation of mortality of marine fish larvae due to warming. *Limnol. and Oceanogr.*, 4: 219-222.

COLTON, J.B., and R.F. TEMPLE. 1961. The enigma of Georges Bank spawning. *Limnol. and Oceanogr.*, 6: 280-291.

CREUTZBERG, F. 1958. Use of tidal streams by migrating elvers (*Anguilla vulgaris* Turt.). *Nature, Lond.*, 181: 857-858.

1959. Discrimination between ebb and flood tide in migrating elvers (*Anguilla vulgaris* Turt.) by means of olfactory perception. *Nature, Lond.*, 184: 1961-1962.

DANNEVIG, A. and S. HANSEN. 1952. Faktorer av betydning for fiskeeggenes og fiskeyngelens opp vekst. *Fiskeridir. Skr.*, 10 (1).

DEMENTJEVA, T.F. 1957. Some data on the life history of cod in the Central Baltic.

DEVOLD, F. 1935. The susceptibility of plaice eggs to shock. *Det Kongelige Norske Videnskabers selskab.*, 8 (22): 71-74.

DOUDOROFF, P. 1945. The resistance and acclimatization of marine fishes to temperature changes II. Experiments with Fundulus and Atherinops. *Biol. Bull., Woods Hole*, 88: 194-206.

FARRIS, D.A. 1960. The effect of three different types of growth curves on estimates of larval fish survival. *J. Cons.*, 25 (3): 294-305.

FRASER, J.H. 1958. The drift of the planktonic stages of fish in the northeast Atlantic and its possible significance to the stocks of commercial fish. *Spec. Publ. int. Comm. Northw. Atlant. Fish.*, No. 1., . 289-310.

FRY, F.E.J., J.R. BRETT, and G.H. CLAWSON. 1942. Lethal limits of temperature for young goldfish. *Rev. Can. de Biol.*, 1: 50-56.

FRY, F.E.J., J.S. HART and K.F. WALKER, 1946. Lethal temperature relations for a sample of young speckled trout, *Salvelinus fontinalis*. *Univ. Toronto Stud., Biol. Ser.*, 54: 9-35.

GALKINA, L.A. 1962. Effect of salinity on the sperm, eggs, and larvae of the okhotsk herring. *Izv. tikhookean. nauch.-issled. Inst. ryb. Khoz.*, 45: 37-50.

GRAY, J. 1928. The growth of fish. II. The growth-rate of the embryo of Salmo fario. III. The effect of temperature on the eggs of Salmo fario. *Brit. J. Exp. Biol.*, 6: 110-130.

HAMDORF, K. 1960. Die Beeinflussung der Embryonal- und Larvalentwicklung der Regenbogenforelle (*Salmo irideus* Gibb.) durch Strahlung im sichtbaren Bereich. *Vergleich. Physiologie*, 42: 525-565.

1961. Die Beeinflussung der Embryonal- und Larvalentwicklung der Regenbogenforelle (*Salmo irideus* Gibb.) durch die Umweltfaktoren O_2-Partialdruck und Temperatur. *Vergleich. Physiologie*, 44: 532-549.

HANSEN, K., and K.P. ANDERSEN, 1961. Recent Danish Investigations of the distributions of larvae of *Sebastes marinus* in the North Atlantic. *Rapp. Cons. Explor. Mer*, 150: 201-215.

HEMPEL, G. 1953. Die Temperaturabhängigkeit der Myomerenzahl beim Hering (*Clupea harengus*). *Naturwissenschaften,* 40: 467-468.

1962. Über die biologische Bedeutung der Eigrösse beim Hering (*Clupea harengus*). *Habilitationsschrift Math. nat. Fak. Univ. Hamburg.*

HEMPEL, G., and J.H.S. BLAXTER. 1961. Einfluss von Temperatur und Salzgehalt auf Myomerenzahl und Körpergrösse von Herings-larven. Z. *Naturf.* (B). 16 (3): 227-228.

HENLEY, E. 1951. The influence of the gas content of sea water on fish and fish larvae. *Rapp. Proc. Verb.,* 131: 24-27.

HJORT, J. 1926. Fluctuations in the year classes of important food fishes. *J. Cons.,* 1: 1-54.

HOLLIDAY, F.G.T., and J.H.S. BLAXTER. 1960. The effects of salinity on the developing eggs and larvae of the herring. *J. Mar. biol. Ass.,* 39: 591-603.

JOHANSEN, A.C. 1925. On the diurnal vertical movements of young of some fishes in Danish waters. *Medd. Komm. Havunders. Ser. Fisk.,* 8 (2).

JONES, J.R.E. 1952. The reactions of fish to water of low oxygen concentration. *J. exp. Biol.,* 29: 403-415.

JUDAY, C., and G. WAGNER. 1909. Dissolved oxygen as a factor of the distribution of fishes. *Trans. Wis. Acad. Sci. Arts Lett.,* 16: 17-22.

KÄNDLER, R. 1949. Die Häufigkeit pelagischer Fischeier in der Ostsee als Massstab für die Zu- und Abnahme der Fischbestände. *Kieler Meeresforsch.,* 6: 73-89.

KINNE, O. 1956. Über Temperatur und Salzgehalt und ihre physiologisch-biologische Bedeutung. *Biol. Zbl.,* 75 (5/6): 314-327.

1960. Growth, food intake, and food conversion in a eury-plastic fish exposed to different temperatures and salinities. *Physiol. Zool.,* 33 (4): 288-315.

KRÜGER, F. 1961. Über den Exponenten der Temperaturfunktion biologischer Vorgänge und deren Grössenabhängigkeit. *Biol. Zbl.,* 80: 721-750.

KURATA, H. 1959. Preliminary report on the rearing of the herring larvae. *Bull. Hokkaido Fish. Res. Lab.,* (20): 117-138.

KUTHALINGAM, M.D.K., 1959. Temperature tolerance of the larvae of ten species of marine fishes. *Curr. Sci.,* 28: 75-76.

LAEVASTU, T. 1961. The effect of current eddies of the distribution of plaice eggs. Workingpaper No. 89, ICES, C.M. 1961.

LASKER, R. and G.H. Theilacker. 1962. Oxygen consumption and osmoregulation by single Pacific sardine eggs and larvae (*Sardinops caerula* Girard). *J. Cons.,* 27 (1): 25-33.

LASSLEBEN, P. 1952. Fisch und Licht, Belichtung und Gesundheitszustand. *Allg. Fisch. Ztg.* (7, 8).

LILLELUND, K. 1961. Untersuchungen über die Biologie und Populations-dynamik des Stintes. *Arch. Fischereiwiss.,* 12 (Beiheft 1): 1-128.

LINDROTH, A. 1942. Sauerstoffverbrauch der Fische. II. Verschiedene Altersstadien von Lachs und Hecht. *Z. vergl. Physiol.,* 28: 575-583.

1946. Zur Biologie der Befruchtung und Entwicklung beim Hecht. *Rep. Inst. Freshw. Res. Drottning,* 24: 1-173.

LISIVNENKO, L.N. 1958. Distribution and behaviour of Salaka (Baltic Herring) larvae and fry in the Gulf of Riga. *Intern. Counc. Explor. Sea,* No. 78.

MARR, J.C. 1956. The "critical period" in the early life history of marine fishes. *J. Cons.,* 21, (2): 160-169.

MCCAULEY, R.W. 1958. Thermal relations of geographic races of salvelinus. *Canad. J. Zool.,* 36: 655-662.

MCMYNN, R.G., and W.S. HOAR, 1953. Effects of salinity on the development of the Pacific herring. *Canad. J. Zool.,* 31: 417-431.

NIKAI, Z., S. USAMI, S. HATTORI, *et al.* 1955. Progress report of the cooperative iwashi resources investigations, April 1949 - December 1951. *Fish Agency Tokai Reg. Fish Res. Lab. Tokyo,* p. 116.

POULSEN, E.M. 1930. On the fluctuations in the abundance of cod fry in the Kattegatt and the Belt Sea. *Rapp. Proc. Verb.,* 65: 26-30.

1934. On the remarkable inflow of Coal fish larvae into the Kattegatt in 1932. *Rapp. Proc. Verb.,* 89 (3): 81-83.

1935. Fluctuations in the regional distribution of certain fish-stocks within the transition area during recent years. *Rapp. Proc. Verb.,* 102 (3): 3-16.

1936. Yearly variations in the number of larvae of autumn spawning herrings in the southern part of the transition area. *Rapp. Proc. Verb.,* 100 (2): 22-24.

QASIM, S.Z. 1956. Time and duration of the spawning season in some marine teleosts in relation to their distribution. *J. Cons.,* 21 (2): 144-153.

RAE, K.M. 1957. Relationship between wind, plankton distribution and haddock brood. *Bull. Marine Ecology,* 4 (38): 247-269.

ROLLEFSEN, G. 1930. Observation on cod eggs. *Rapp. Proc. Verb.,* 65: 31-34.

1932. The susceptibility of cod eggs to external influences. *Cons. perm. intern. Explor. Mer,* 7: 367-378.

RUSSEL, F.S. 1926. The vertical distribution of marine macro-plankton.
3. Diurnal observations of the pelagic young of teleostean fishes in the Plymouth area. *J. Mar. biol. Ass. U.K.,* 14 (N.S.) (2): 387-414.

1928. The vertical distribution of marine macro-plankton.
8. Further observations on the diurnal behaviour of the pelagic young of teleostean fishes in the Plymouth area. *J. Mar. biol. Ass., U.K.,* 15 (N.S.) (3): 829-850.

SETTE, O.E. 1943. Biology of the Atlantik mackerel (*Scomber scombrus*) of North America Part 1: Early life history, including the growth, drift, and mortality of the egg and larval population. *Fish. Bull. U.S.,* 50 (38): 149-237.

SHELBOURNE, J.E. 1957. New evidence for a "critical period" in the life of larval plaice. *Int. Counc. Explor. Sea, Near North. Seas Comm.,* No. 50.

SHEPARD, M.P. 1955. Resistance and tolerance of young speckled trout (*Salvelinus fontinalis*) to oxygen lack, with special reference to low oxygen acclimation. *J. Fish. Res. Bd. Canada,* 12 (3): 387-446.

SILLIMAN, R.P. 1943. Thermal and diurnal changes in the vertical distribution of eggs and larvae of the pilchard (*Sardinops caerulea*). *J. Mar. Res.,* 5 (2): 118-129.

STRODTMANN, S. 1918. Weitere Untersuchungen über Ostseefische. III. *Bericht Wiss. Meeresunters. Neue Folge.*, 14 (1): 34-94.

TÅNING, Å.V.,1952. Experimental study of meristoc characters in fishes. *Biol. Rev.*, (27): 169.

TESTER, A.L. 1938. Variation in the mean vertebral count of herring (*Clupea pallasii*) with water temperature. *J. Cons.*, 13: 71.

TOOM, M.M. 1962. Experiments in the incubation of Baltic herring eggs. *Trud. vsesoiuz. nauch.-issled. Inst. morsk. ryb. Khoz.*, 34: 19-29.

VELEY, V.F.C. 1950. Fishery hydrography: brood-strength fluctuations in the hake with a suggested method of prediction. *Ann. Biol.*, 7: 44-46.

1951. Brood strength fluctuations in the sprat. *Rapp. Proc. Verb.*, 131: 71-73.

WALFORD, L.A. 1938. Effects of currents on the distribution and survival of eggs and larvae of haddock (*Melanogrammus aeglefinus*) on Georges Bank. *Bull. U.S. Bur. Fish.*, 49 (29): 1-73.

WELLS, M.M. 1913. The resistance of fishes to different concentrations and combinations of oxygen and carbon dioxide. *Biol. Bull., Woods Hole*, 25: 323-347.

WIBORG, K.F. 1957. Factors influencing the size of the year-classes in the Arcto-Norwegian tribe of cod. *Fiskeridir. Skr.*, 11 (8): 5-22.

WILLER, A. and E. SCHNIGENBERG. 1927. Untersuchungen über das Wachstum bei Fischen. I. Über den Einfluss des Raumfaktors auf das Wachstum der Bachforellenbrut. *Fisch.*, 25.

WILLER, A., 1928. Der Raumfaktorenkomplex in der Forellenzucht. Mitt. d. Fisch. Vereine f.d. Prov. Brandenburg, Ostpreussen, Pommern u.d. Grenzmark.

F-5

FECUNDITY AND EGG SIZE IN RELATION TO THE ENVIRONMENT *

By

G. Hempel[1]

ABSTRACT

Information about how fish react in their reproduction to changes in the environment is rather scarce. Some possible direct and indirect environmental effects are discussed, mainly by using data on herring. Direct effects on the number and the weight of eggs at spawning seem to be restricted. Indirect influences of food supply and temperature will affect the reproduction by changes in growth rate, in maturation rate, migratory pattern, mixing of neighbouring populations and the resulting time and place of spawning. This may have considerable effect on the total number of eggs produced by the population and on the average yolk-content of the egg. The dry-weight of the eggs affects the duration of the yolk-sac stage, the size of the young larvae and their searching effort. This will be positively related to survival rate.

INTRODUCTION

Until now not much is known about the influence of the environment on the reproduction of marine fish. The main purpose of this paper is to stress the need for more extensive and detailed studies in this field. Both the number and the size of the eggs produced by a female of a given age may vary with the environmental conditions. The absolute number of recruits for the fishable stock will depend on the number of eggs spawned as long as no density-dependent compensatory mortality occurs. The egg size has a direct influence on the early life history and the survival rate of the larvae, as recently shown for herring (Blaxter and Hempel, 1963).

TERMS

The term number of eggs refers to the total number of eggs spawned by a female within a season. Usually it is estimated from the number of ripening eggs in a female under the assumption that no eggs are resorbed or additionally produced afterwards until spawning. "Egg weight" is the average dry weight of the ripe, transparent eggs. "Total egg mass" is the term for the product of the average number and weight of eggs for a given age and size group of fish at spawning. At stage VI, weighings of the total egg mass are not reliable, some eggs may be shed beforehand and others may not have finished the intake of organic matter.

DIFFERENCES IN NUMBER OF EGGS

Information on the number of eggs is available for several species of marine fish, but with special emphasis on plaice and herring. In herring the number of eggs per female normally increases faster than the weight of the fish. This is most pronounced for the increase in number of eggs produced at the second spawning compared with the low number at the first spawning. A direct influence of age (or related to this the number of spawning seasons) on the number of eggs in herring was noticed by several authors (Antipova, 1928; Liamin, 1956; Probatov and Friedland, 1957; Baxter, 1959; Anokhina, 1963; Polder and Zijlstra, 1959; Krivobok, 1961). In fish of the same size and age, the number of eggs is higher in those which spawn for the second time compared with first time spawners. Exceptions to this rule may be found in those herring which live under unfavourable feeding conditions. The first time spawners amongst the herring of the Onega Bay of the White Sea produce more eggs than the second-time spawners of the same size. Here the feeding period after the first spawning is not long enough (part of the short season of unfavourable feeding conditions is used for spawning), for a high egg production to take place.

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* This paper is dedicated to Prof. Dr R. Kändler on the occasion of his 65th birthday.

Direct influences of the environment on the number of eggs in a female seem to exist in a number of species. Scott (1962) showed for rainbow trout that egg number but not egg size varies with the physiological condition and the feeding of the mother fish. Bagenal (1957) described changes from year to year in the number of eggs produced by a female of a given size in *Hippoglossoides platessoides*. According to Polder and Zijlstra (1959) the Doggerbank herring produced about 20% more eggs in 1957 than herring of similar size and age in the period 1954 to 1956. No attempt was made by the authors to attribute the high production of eggs in 1957 to any specific environmental factor or to an admixture of herring with higher egg numbers (*e.g.* Buchan herring). Anokhina (1960) related the number of eggs produced by Baltic herring to the fat content of the mother. She reported higher egg numbers in fat fish than in lean fish. This held for comparison between fish of different fat content caught within one season, as well as for a comparison between different seasons where the average fat content differed from year to year. The differences in fat content were attributed to differences in food supply and overwintering conditions. Hodder (this symposium) tried to explain the low fecundity of Grand Bank haddock in 1959 by environmental effects as temperature and especially feeding conditions. Unfavourable conditions two years in advance and/or during the few months immediately preceding spawning may reduce fecundity, the same may hold for good feeding conditions about one year before spawning, *i.e.* during a period while they grow and occupy the surface area of the lamellae.

Indirect effects of the environment on the number of eggs might be expected because of the relationship of the number of eggs to total age, weight and age at first maturity. The effect by changing the growth rate in fish (and so affecting the age at first maturity) has been described for herring by various authors. Anokhina (1963) ascribed changes in the egg number in 4- and 5-year-old herring of the White Sea to changes in growth rate which were related to feeding conditions, *e.g.* in 1958 the food supply and the overwintering conditions were better than in 1957, in consequence the fish grew faster and produced more eggs relative to their age (but not to their body size). The most striking indirect effect of this kind was described by Bibov (1960) as a result of the very fast growth shown by Baltic herring which were transplanted as fry into the Aral Sea. Bridger (1959) analysed the changes in egg number in relation to age which took place in Downs herring in 1950-55. He attributed the higher average number of eggs in herring of the age-groups 4 to 7 to both the increase in growth and in maturation. As suggested by Cushing and Burd (1956) these fish "speeded up" growth and first maturity by one year due to unfavourable feeding conditions. Similar indirect effects of the environment on the spawning potential of the stock are to be expected in other marine fish.

THE WEIGHT OF EGGS

Data of the size of eggs in relation to age, size and condition factor of the mother are scarcer than those on the number of eggs. In the course of their work on the number of eggs in different herring populations, Farran (1938), Baxter (1958), Bridger (1959) and others, refer to racial differences in the size of eggs. This has been carried further in more detailed studies by Hempel and Blaxter (1963) with special emphasis to changes of egg size during the life history of the fish.

Recruit spawners produce eggs which are about 10% lighter than those of the older fish. From the second spawning onwards the egg weight does not depend on the age of the fish, except possibly in very old fish. In Norwegian herring of 12 years of age and more, some indications of a decrease in egg size were found.

The variability in egg volume (calculated from the diameter of the fixed ripe egg) is considerable in some groups of herring. The ratio between the smallest and the largest egg in a sample of 100 eggs was in most cases from 1:1.3 to 1:2.0. In samples of Baltic and Doggerbank herring higher variability was found. Whether this variability in volume reflects a variability in the content of organic matter or just differences in the water content must be checked by weighings of individual eggs.

Anokhina (1960) found higher coefficients of variance in the diameter of eggs in lean herring than in fat herring. Nikolski (1962) tried to explain this finding as due to insufficient nourishment of those eggs in lean herring, which were distant from the main blood vessels. Only in well fed herring are the nutrients sufficient to reach all eggs. Anokhina (1960) assumed that high variability in egg size permitted at least some larvae (those from the biggest eggs) to survive in poor years. Preliminary investigations on 50 North Sea (Downs) herring (Hempel, unpublished) failed to show a relationship between the fat content of the mother and the mean value and variance of egg size. The average fat content of the eggs was also found to be independent of the maternal fat content. Further investigations in this field are urgently needed in order to get an understanding of the effect of the condition of the mother on the quality of the eggs. In this connection, two facts should be considered: The eggs of most species of marine fish have very low fat contents. Protein rather than fat is the main constituent of the yolk and seems to be used both for conversion into larval substance and for metabolism. High "condition" of the mother taken as the relative fat content or the weight/length relationship does not necessarily mean that the female is in her prime for reproduction, especially the storage of fat, which might be due to unbalanced feeding.

TIME OF SPAWNING

Shifts in spawning time due to changes in the temperature regime are often described but they are rarely related to changes in fecundity. Only Krivobok (1961) made a careful study on the changes in number of eggs in coastal herring spawning in summer in the White Sea. He compared herring of uniform length (17 cm) which, however, differed considerably in age. In the course of the six week's season, he found a shift in the average age of the fish from 4.9 to 5.4 years, fast growing young fish with low fecundity arriving first on the spawning ground, followed by older fish. The number of ripe eggs increased in each age-group by 45 to 65%. The gutted weight of the fish caught at the end of the season (end of June) was almost the same as in the early spawners, although the average weight of the gonads was 14.8 g instead of 4.2 g. The number of eggs differs from female to female but it is fixed before feeding starts in spring. The rate of maturation depends on the number of eggs laid down (and their final size?) and on the supply of food. Temperature affecting the ratio between growth and basic metabolism will have a very strong influence on the survival rate of the larvae. It would therefore be worthwhile to check how far differences in food supply may affect the time of spawning. The relationship between the number and size of the eggs and spawning time and its dependence upon the environment require extensive and careful studies.

DISCUSSION

Direct effects of environmental factors on egg number and egg size seem to be rather limited compared with effects on growth. When considering the effect of changes in the environment on reproduction we are mainly left with the indirect influences which affect the reproduction of the stock by changes in the growth rate, the rate of maturation, age structure and possibly by shifts in spawning time and spawning place. Changes in the total fecundity of the population and the average fecundity of individual fish may also be caused by mixing of different groups of herring, which differ in their total egg mass at a given age or in the ratio between egg size and egg number. Racial differences in number of eggs are described for various species of fish. Sometimes differences are quite striking between neighbouring populations; in North Sea herring the egg weight of Downs herring is three to four times as high as that of Buchan herring (Hempel and Blaxter, 1963).

As shown by Baxter (1957), however, the number of eggs in Buchan herring is far higher than in Downs herring. The total mass of eggs produced by a female 27 cm is, however, higher in Downs herring than in Buchan herring (7.3 g dry-matter against 5.0 g). This difference in total production per season might be interpreted as a result of differences in spawning time, giving the Downs herring the opportunity of using the whole season of high plankton abundance for feeding, while in Buchan herring the feeding period is cut down by early spawning. Dogger herring whose time and place of spawning occurs between the spawning of Buchan and Downs herring show intermediate values.

If the migratory pattern or the spawning time of one of these groups shifts due to environmental factors, a considerable mixing of the populations may take place, causing changes in the reproduction and in the fitness of the larvae which are originally pre-adapted to other areas and seasons.

REFERENCES

ANOKHINA, L.E. 1960. Interrelations between fecundity variability of the size of the eggs and fatness of mother fish in Onega herring. *C.R.Acad. Sci. USSR*, 133 (4): 960-963.

1963. Some aspects of the fecundity of herring in the White Sea. *Rapp. Cons. Explor. Mer*, 154 (in press).

ANTIPOVA, O.P. 1928. Data on the fecundity of the White Sea herring. *Ann. State Institute Exper. Agr.*, 6 (3-4): 113-114.

BAGENAL, T.B. 1957. Annual variations in fish fecundity. *J. Mar. Biol. Ass. U.K.*, 36: 377-382.

BAXTER, I.D. 1959. Fecundities of winter-spring and summer-autumn herring spawners. *J.Cons.*, 25: 73-80.

BIBOV, N.E. 1960. Acclimatization of Salaka (Baltic herring) *Clupea harengus membras* L. in the Aral Sea. *Int. Council Explor. Sea, Annual Meeting*, Paper No. 135.

BLAXTER, J.H.S., and G. HEMPEL. 1963. The influence of egg size on herring larvae. *J. Cons.*, 28: 211-240.

BRIDGER, J.P. 1961. On fecundity and larval abundance of Downs herring. *Fish. Invest. Lond.*, (2), 23 (3): 30 p.

CUSHING, D.H., and A.C. BURD. 1957. On the herring of the Southern North Sea. *Fish. Invest. Lond.*, (2), 20 (11): 31 p.

FARRAN, G.P. 1938. On the size and the number of ova in the Irish herring. *J. Cons.*, 13: 91-100.

HEMPEL, G., and J.H.S. BLAXTER. 1963. On the condition of herring larvae. *Rapp. Cons. Explor. Mer.*, 154: 35-40.

KRIVOBOK, M.N. 1961. The relationship between the spawning time and the fecundity of *Clupea harengus membras*. *Trudy VNIRO*, 44: 160-163.

LIAMIN, K.A. 1956. Investigation into the life-cycle of summer-spawning herring of Iceland. *Trudy PINRO*, 9. Transl. in *U.S. Fish Wildl. Serv. Spec. Sci. Rep.* 327: 166-202 (1959).

NIKOLSKI, G.V. 1962. On some adaptations to the regulation of population density in fish species with different types of stock structure. *In* E.D. LeCren and M.W. Holdgate (*eds.*) The exploitation of natural animal populations. New York. p. 265-282.

POLDER, J. and J.J. ZIJLSTRA. 1959. Fecundity in the North Sea herring. *Int. Council Explor. Sea, Annual Meeting*, Paper No. 84: 10 p.

PROBATOV, A.N. and I.G. FRIEDLAND. 1957. Some regularities in the change of the Pacific herring fecundity. *Uchen Zapiski, Rostov-on-the-Don State University*, 28: Ser. 5.

SCOTT, D.D. 1962. Effect of food quality on the fecundity of Rainbow trout, *Salmo gairdneri*. *J. Fish. Res. Bd. Canada*, 19 (4): 715-734.

F-6A

SEASONAL CHANGES IN THE PHYSIOLOGY OF THE BARENTS SEA COD, *GADUS MORHUA* L., IN RELATION TO ITS ENVIRONMENT

I. ENDOCRINE CHANGES PARTICULARLY AFFECTING MIGRATION AND MATURATION

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CONTENTS

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ABSTRACT

Changes in their internal environment directly affect the reactions of fish to the external environment; the activities of the system of endocrine glands co-ordinate many of these internal changes. This paper considers quantitative changes in the activity of three glands in the Barents Sea cod, the thyroid, gonads and interrenals, and attempts to assess their physiological role in maturation and migration.

A seasonal cycle of thyroid activity was demonstrated in adult and in immature cod. In adults, the thyroid became active at the start of the spawning migration, and activity continued until the fish reached the spawning grounds; the duration of thyroid activity coincided with migration. In immature cod the gland was active throughout the period of their overwintering migration. Adult cod were ripening during their spawning migration, so that the activities of the gonadal and thyroid hormones could not be separated, but there was no gonadal activity in immature fish, and it appeared that the activity of the thyroid gland alone would support a lengthy migration.

The southerly overwintering migration of some large immature cod extends to within a short distance of the adult spawning grounds. Thyroid activity in these fish continued over a longer period than in immature fish overwintering around Bear Island, corresponding to the increased duration of their winter migration. It is suggested that in immature cod migration continued as long as the thyroid remained active.

Histological changes in the cod ovary during maturation are described, and a dual mechanism to relate fecundity closely to the growth achieved by the fish is discussed. Problems of oestrogen secretion in the ovary are outlined and reasons given for considering that oestrogen secretion occurs in the latter part of the maturation cycle, during the period of vitellogenesis. The histology of the maturing testis, and seasonal variations in the activity of the interstitial cells, secreting male hormone, are also described. The interstitial tissue became active in November-December, reaching maximum activity just prior to spawning. It appears that in the cod gonadal hormones are secreted in the latter part of the migration period, several weeks after the onset of migratory activity. Though thyroid hormones appear to play the dominant role in migration, their effects may later be augmented by sex steroids.

Activity in the interrenal gland began in November, continuing until June; by July the interrenal had returned to the summer resting condition. The role of adrenal cortical hormones in fish is discussed, and from the present results it is concluded that interrenal activity in adult and immature cod may be associated with the winter period of poor feeding, and, in the adults, with the physiological demands of gonadal maturation during this time.

The external factors regulating maturation and migration in the Barents Sea cod are considered. These cycles are initiated at the autumnal equinox and it is suggested that photoperiod may be critical; it seems unlikely that they are initiated by temperature changes.

INTRODUCTION

Fish must continually adjust and acclimatize their metabolic processes and their activity in relation to changes in environmental conditions. Seasonal variations in environmental factors may be great; thus, in the Arctic seas, food may only be available in quantity for a limited period of rapid growth and development, and conditions for good larval survival may only be achieved by reproduction in a restricted area and over a relatively short period of time in each year. It is reasonable to expect that in such circumstances the physiological responses of the fish would be of a highly adaptive character.

While this Environmental Symposium was largely devoted to considering some of the results of these internal reactions to external environmental variables, seasonal changes in the response of the fish itself were discussed; in this context it is not out of place to draw attention to the reactions of the fish to changes occurring within its own "internal environment". Thus, although successful spawning may depend on the correct behavioural reactions to environmental stimuli in the vicinity of the spawning area, it is also dependent upon precisely timed physiological changes controlling growth, maturation and migration, which may have occurred over several months prior to the spawning event. The activities of the system of endocrine glands are intimately concerned in the regulation and co-ordination of these physiological reactions, but relatively little detailed information is available concerning these alterations of the internal environment in even the commonest demersal fishes.

This paper considers some results of a study of the physiological reactions of the Arcto-Norwegian cod to its environment, and the nature of seasonal changes in these reactions; in particular we have tried to make quantitative measurements of the activity of different glands of the endocrine system in order to assess their role in modifying the reactions of this fish. This study is still far from complete but some aspects concerning migration and maturation are discussed below, and the reactions of cod to low temperatures are considered separately in Part II of the paper.

THYROID ACTIVITY AND MIGRATION

1. Introduction

In many species of migratory fish, gonadal maturation and migration occur simultaneously and initially it was thought that gonadal hormones might be essential for the induction of migration. However, amongst juvenile salmon migrating seawards, were fish with quiescent and with developing gonads, while others had regressing gonads after participating in the adult spawning (Fontaine, 1954, 1956). Migratory behaviour has been observed in sterile male hybrid Anabantid fish (Forselius, 1957) and in sterile male salmonids (Fabricius, quoted in Forselius, 1957) indicating that gonadal activity was not an essential requisite for migration. In these fish, and in adult migrating salmon, *Salmo salar* L. and *Oncorhynchus* spp., and in eels, *Anguilla vulgaris*, evidence of increased thyroid activity at the time of migration has been obtained (Fontaine, 1954; Hoar, 1953, 1955; Olivereau, 1954). These observations, and the more recent studies of Honma and his associates on other salmonid fishes (Honma, 1959*a*, *b*; Honma and Tamura, 1963) have suggested that it is probable that the thyroid gland has an important role in controlling migration. However, the evidence obtained from these studies was not conclusive since these species encounter changes in the salinity of their environment during migration, and salinity changes alone have been shown to stimulate thyroid activity in non-migratory fish (Olivereau, 1954).

The Barents Sea cod appeared to be a particularly suitable species for a study of the hormonal factors regulating migration, because of the great length of its spawning migration, the adults often travelling distances of up to 800 miles to their spawning grounds, without the complication of a change in osmotic medium. The migrations of the Barents Sea cod have been described in detail (Maslov, 1944, 1960; Saetersdal, 1956; Konstantinov, 1957; Trout, 1957). Throughout the summer months the cod are found on shallow-water feeding grounds in the north-eastern and central areas of the Barents Sea. In late September, as the gonads begin to ripen, the adult fish leave the feeding areas and migrate to their spawning grounds inside the Lofoten Islands on the north Norwegian coast. The main spawning season is from mid-February to the end of March. After spawning, the spent cod return again to the Barents Sea feeding areas.

The immature cod are found on the shallow-water feeding grounds during the summer months, June to September. In autumn these fish migrate into deeper waters around the edges of the shelf, where they remain throughout the winter until, in the late spring, they return to the feeding areas. This migration is repeated each year until the fish mature.

2. Thyroid activity in the Barents Sea cod

Changes in thyroid activity have been studied in adult cod migrating to their spawning grounds, and in immature cod moving to overwintering areas.

In the cod, as in the majority of teleosts, the thyroid gland consists of numerous discrete thyroid follicles, lying in the connective tissue around the ventral aorta (Fig. 1). The thyroid tissue was removed, fixed in Bouin's fluid, embedded, sectioned and stained with Heidenhain's Azan stain. A quantitative estimate of thyroid activity was obtained from measurements of the follicular cell height, and the results of these readings were confirmed by the staining reaction of the colloid. In resting glands the follicular cells were low, and stretched around the stored colloid, which had a dense laminated appearance and stained deep red. The follicular cells in active glands were high and columnar, whilst the colloid stained blue, and appeared granular.

Using these criteria, the thyroid gland of adult cod was found to be inactive throughout the spring and summer months, from April to September, when the follicular cell height was low and the follicles were packed with stored colloid. Secretory activity commenced in late September, and

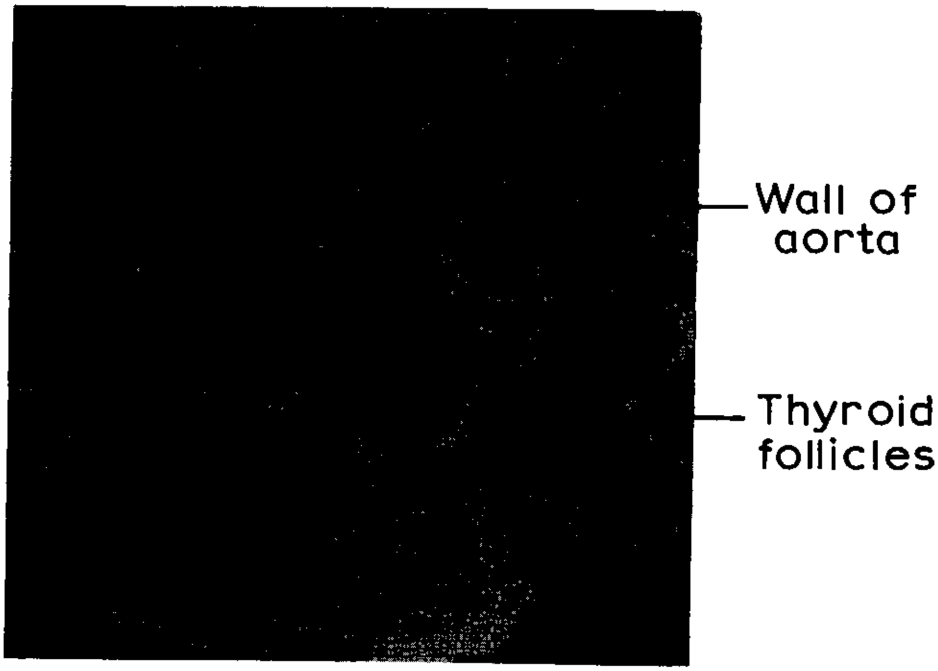

Fig. 1. Photomicrograph of distribution of thyroid follicles around aorta in cod.

increased throughout the winter months; the colloid appeared granular, was rapidly resorbed, and was often invaded by leucocytes. Maximum cell height was reached in January, prior to spawning. The activity of the gland was less in fish caught in March at spawning time. In spent fish, the gland had re-entered the resting condition (Fig. 2).

There was also a seasonal cycle of thyroid activity in the immature cod migrating to their overwintering areas. The thyroid became active in late September, as in the adult fish, but the maximum cell height was reached in December, after which follicular cell height decreased, returning to the resting stage by March (Fig. 2). The magnitude of the seasonal changes in thyroid activity in immature cod was less than in the adults (Woodhead, 1959*a*).

These results suggested that thyroid activity might be related to migration in the Barents Sea cod, since the gland became active at the start of the migration in both the adult and immature fish; in the adults, the thyroid remained active until March, when the fish reached the Lofoten Island spawning grounds, but in immature cod thyroid activity had begun to fall by January, when most of the fish were completing their migration to the overwintering grounds. The period of thyroid activity therefore coincided with the duration of the spawning migration of the adult fish, and with the overwintering migration of the immature fish.

In the adult cod the gonads were also ripening throughout the spawning migration, so that activities of gonadal and thyroid hormones could not be separated, but gonads were inactive, of course, in the migrating immature fish, suggesting that the activity of the thyroid alone might stimulate and support an extensive migration.

3. The prolonged migration of large immature cod

It has been shown that the extent of the overwintering migration of the immature cod tends to increase as the fish become older, so that some of the largest immature cod may migrate to the Norwegian coast, within a short distance of the adult spawning grounds; this extended winter migration has been called a "dummy run" (Trout, 1957). The relationship between thyroid activity and migration was further demonstrated from a study of the thyroids of immature cod collected at stations near Bear Island and on the Norwegian coast, during early spring. In comparing thyroid activity in immature

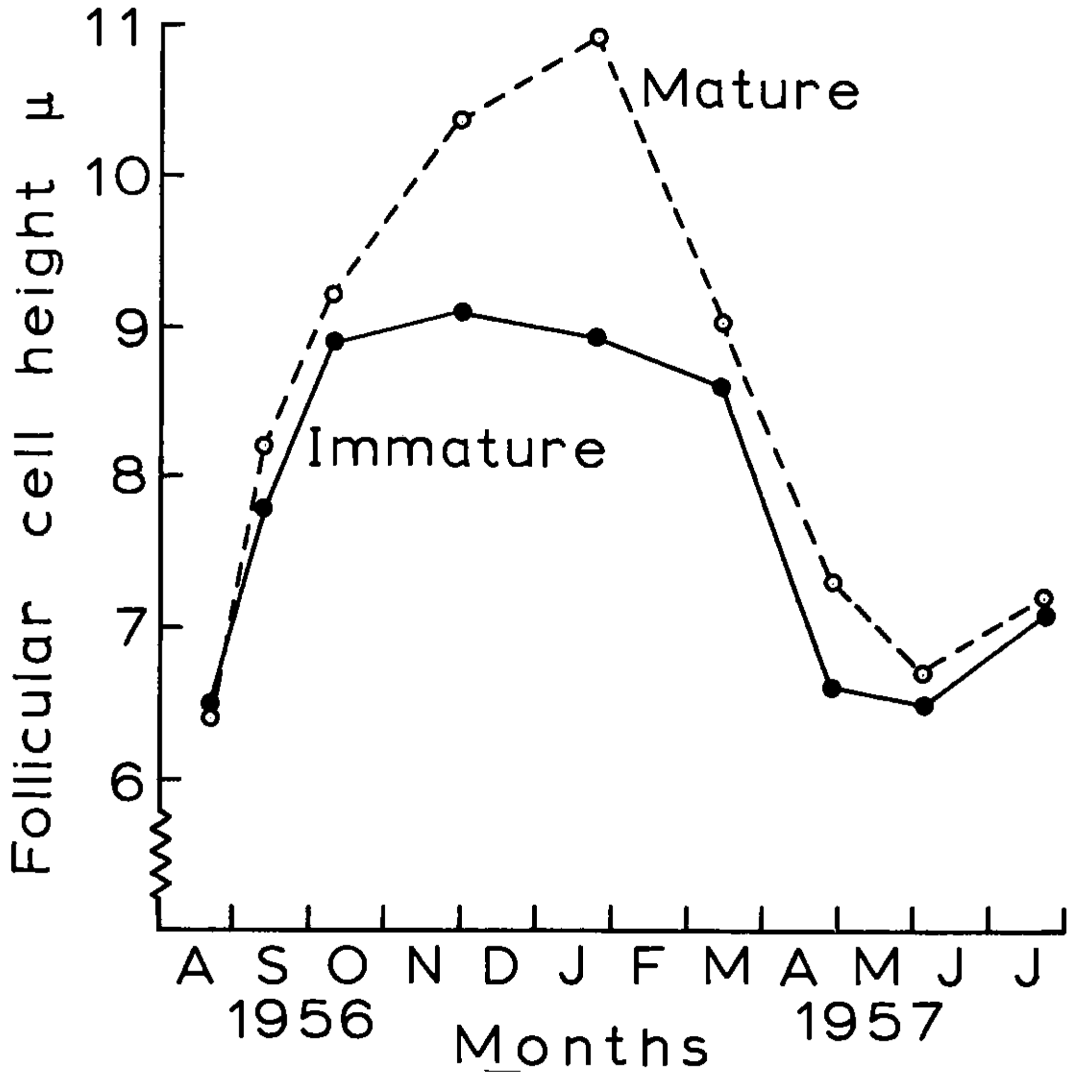

Fig. 2. Seasonal cycle of thyroid activity in Barents Sea cod, expressed in terms of follicular cell height.
N.B. An *increase* in follicular cell height indicates increasing activity.

Svalbard cod which had moved to their overwintering grounds around Bear Island with those of "dummy run" immature fish caught on the Norway coast, the otoliths of the cod were read to ensure that only fish which had migrated from the Svalbard region were used. (The cod from the north-western and south-eastern parts of the Barents Sea, and from the Norwegian coastal stock, can be distinguished by characteristic otolith types (Trout, 1957; Mankevich, 1960).) Generally, the "dummy run" immatures migrating to the Norway coast are large fish, so that it might be objected that any differences in thyroid activity were due to differences in size; there was no evidence of a direct relationship between size and thyroid activity in the cod, but to meet this objection fish of the same size range from each area were used in the comparison.

It was found that the thyroid glands of immature cod caught on the Norway coast in March were in a more active condition than those of immature fish taken around Bear Island. In the latter, follicular cell height had declined from a January level of 8.6µ to a level of 7.2µ by March. However, the fish caught on the Norway coast had a follicular cell height of 8.6µ, and the glands were still as active as the January thyroids (Table 1). In immature cod the thyroid cycle did not rise

TABLE 1. MEAN FOLLICULAR CELL HEIGHT OF IMMATURE COD CAUGHT IN MARCH

Sample area		Number of fish	Mean follicular cell height μ ± S.D.
Around Bear Island	1956	10	7.3 ± 0.4
	1957	10	7.2 ± 0.6
"Dummy run" immatures:			
Norwegian coast *c.* 270 miles south of Bear Island	1956	3	9.2 ± 0.9
	1957	10	8.6 ± 0.7
Norwegian coast *c.* 410 miles south of Bear Island	1957	10	8.8 ± 0.5

to a peak as in adult cod, but once the gland had become active, activity continued at a steady level. Thyroid activity continued for a longer time in the "dummy run" cod caught off the Norwegian coast than in fish caught around Bear Island, and this coincided with the increased length and duration of their overwintering migration (Woodhead, 1959*b*). It seemed that in these "dummy run" cod the migration continued as long as the thyroid remained active. This evidence lends further support to the suggestion that the activity of the thyroid gland may initiate and sustain active and lengthy migrations.

4. Thyroid and migration in the spurdog

In view of these findings in the cod, it is of considerable interest that a correlation between thyroid activity and migration has also been found in the spurdog, *Squalus acanthias* (Woodhead, 1963, 1964). Spurdogs are ovoviviparous elasmobranchs and their reproductive cycle lasts for two years, but they migrate annually between Scotland and the southern Norwegian coast (Aasen, 1963; Holden, in press); reproduction and migration could therefore conveniently be studied in relation to thyroid activity. A marked annual cycle of thyroid activity was found in female spurdogs, the gland becoming active at the beginning of migration, and activity increasing throughout the migration. Although some thyroid activity was also related to reproduction, the primary association appeared to be with the annual migration.

5. Thyroid hormones and the migratory mechanism

Although thyroid activity has been related to migration in the Barents Sea cod, the problem of its mode of action remains. Thyroid hormones have numerous diverse metabolic and morphogenic functions in vertebrates. However, their effects upon motor activity and upon the nervous system are strikingly consistent in all animals; these hormones increase locomotory activity and heighten excitability and the sensitivity of the animal to external stimuli (Gorbman and Bern, 1962).

There is some experimental evidence to show that thyroid hormones produce similar effects in fish. Young salmon and goldfish, kept in solutions of thyroxine, were considerably more active than the controls (Hoar *et al.*, 1955). Thyroxine treatment increased the excitability of the fish, so that they responded to electrical stimulation at lower voltages than the untreated fish; also the experimental fish swam more vigorously against water currents than the control fish. Conversely, Vilter (1944) and Fontaine (1948) working with the elvers of the eel, *Anguilla anguilla*, found a decrease in rheotactic behaviour when the elvers were treated with drugs inhibiting thyroid activity.

Trout (1957) suggested that the spawning migration of adult cod, and the overwintering migration of the immatures, were active contranatant movements; in contrast the return of the spent cod to the feeding areas took place by passive carriage of the fish within the water mass. Although such a hypothesis is not without difficulties, it appears to fit many of the known facts, and it is therefore of interest to consider theoretically what might be the effects of thyroid hormones in inducing an active contranatant migration of this type. A simple theory, and one which would be in keeping with the experimental results, would be that thyroid hormones could cause a general increase in swimming activity and an increased tendency to swim against water currents. Many fish readily orientate against a strong water current, if provided with adequate sensory clues, and it seems likely that a change in reaction to current would be in the nature of a lowered threshold for initiation of the swimming response, rather than a completely new response. The passive denatant return of spent fish to the feeding grounds might similarly be achieved by an increase in the threshold for the reaction to current, probably accompanied by a fall in the general level of activity, the fish swimming randomly within the northward-moving waters of the Norwegian current. In this manner, thyroid hormones could act upon the fish to potentiate certain characteristic activities which lead to migration, rather than to produce specific new orientations or complately new behaviour patterns - modes of activity which would fit well with the known functions of these hormones.

THYROID ACTIVITY AND GONADAL MATURATION

There is a considerable body of evidence to suggest that thyroid activity may be associated with reproductive cycles (reviewed in Pickford, 1957; Barrington, 1963). Hyperactivity of the thyroid coincident with spawning has been reported in several species of fish (Buchmann, 1940; Olivereau, 1954; Fortune, 1955), while treatment of fish with thyroxine or with antithyroid drugs may accelerate or retard the onset of maturation (Hopper, 1952; Gaiser, 1952; Barrington and Matty, 1952; Smith, Sladek and Kellner, 1953).

Although the thyroid gland of the large "dummy run" immature cod migrating to the vicinity of the adult spawning grounds remained active over a similar length of time to that of the adult cod, the degree of activity attained was significantly lower than in the ripe adults. The thyroid of the immature cod was equally as active as that of adult fish in September and October, but by November the adult thyroid had become significantly more active, while thyroid activity in the immature cod remained at a fairly steady level throughout most of the winter (Table 2). This difference between the adults and immatures had become even more pronounced by January, when the adult thyroid was maximally active.

Pickford (1957) has suggested that some thyroid activity is necessary for gonadal maturation in fishes, and in many non-migratory species increased thyroid function has been found during the reproductive cycle (Koch and Heuts, 1942; Heuts, 1943, Ivanova, 1954*a*, *b*; Zaitsev, 1955*a*, *b*). It seems likely that in the Barents Sea cod this may be represented by the differences in the degree of activity between the immature and mature thyroid cycles, which became noticeable in November, coinciding with the period of rapid gonad growth.

TABLE 2. COMPARISON OF THYROID ACTIVITY IN ADULT AND IMMATURE COD

	Adult	Immature	
	Mean value of follicular cell height μ	Mean value of follicular cell height μ	Significance of difference p
August	6.4	6.5	0.75
September	8.2	7.8	0.30
October	9.2	8.9	0.40
November-December	10.3	9.1	< 0.01
January	10.9	8.6	< 0.001
March (pre-spawning)	9.0	8.6*	< 0.001
April	7.3	6.6	0.01
June	6.7	6.5	0.30
July	7.2	7.1	0.80

*Value for "dummy run" immature cod which had migrated to the Norwegian coast with the adult fish

l. Thyroid activity and reproduction in the spurdog

There was evidence that some thyroid activity in the spurdog might be associated with reproductive events. Maximum thyroid activity occurred during the winter, both in spawning females and in non-spawning females which had reached the middle of the gestation period, but the magnitude of the observed changes was invariably greater in the spawning females.

THYROID CYCLES AND TEMPERATURE

Seasonal changes in the activity of the thyroid gland of yearling trout have been inversely related to environmental temperatures by Swift (1959, 1960), who considered that temperature was a major controlling factor in influencing the cycle of activity. He suggested that thyroid activity acts as a temperature-compensating mechanism (Swift, 1959). Swift's results were re-investigated by Hoffert and Fromm (1959) who questioned the value of his data and doubted that the trout thyroid was involved in temperature compensation. Our investigations showed no obvious relationship between thyroid activity in cod and temperature; highest water temperatures of about 6°C. were encountered by adult cod on the Norwegian coast in winter when the gland was fully active, and the gland was inactive at lowest summer temperatures of 0°C. The comparison of thyroids taken from fish caught at different temperatures on the same cruise failed to show any significant differences either in the summer or during winter, suggesting that, in the cod, the thyroid cycle was not associated with temperature compensation (Woodhead, 1959*b*).

GONAD CYCLES IN THE BARENTS SEA COD

The Barents Sea cod matures for the first time between 5 and 15 years of age, the average age at first maturity being about 8 or 9 years. The distribution of spawning zones on otoliths suggests that once maturity has been attained reproduction occurs annually (Rollefsen, 1933).

1. The ovary

1.1 Ovarian maturation

During the summer months of May to early September there was little ovarian activity, although some slow growth of the gonad took place. Histological sections of ovaries collected during the summer showed that they contained oocytes in three phases of development: oogonia, small cells which had recently differentiated from the germinal epithelium; primary oocytes, which had undergone a period of minor growth; and larger oocytes in the "circumnuclear ring" phase. Circumnuclear ring oocytes are large, round cells, with a central, well defined reticular nucleus. Characteristically these cells have a ring of coarse, deep-staining granulations within the lightly-staining and finely granular cytoplasm, which initially appears within the cytoplasm close to the nucleus, but, as the oocyte increases in size, the ring moves outwards until eventually it lies close to the periphery of the egg. Only cells which achieve the circumnuclear ring phase by the late autumn complete their growth and maturation within the subsequent reproductive cycle. Rapid ovarian growth was resumed in late September, when the growth of the circumnuclear ring phase oocytes began. Initially, the eggs increased in volume, and the follicle membranes surrounding them became distinct. In November, some time after this phase, vacuoles appeared in the periphery of the oocyte, in the region of the circumnuclear ring. (These vacuoles may represent areas of oil deposition which are removed during routine fixation (Sorokin, 1957).) Following the formation of the vacuoles, the first yolk droplets appeared amongst them; initially the yolk granules are small and separate, but as growth continues and increasing amounts of yolk are incorporated into the oocytes, the droplets coalesce and yolk extends towards the nucleus. In the circumnuclear ring oocytes, the nucleus contains numerous small nucleoli which closely adhere to the nuclear membrane; in the ripening egg, the nucleus undergoes transformation, its outer membrane becomes indistinct and irregular, while the nucleoli become detached from the nuclear membrane and scattered throughout the nucleus. In sections the average diameter of the oocytes at the beginning of ripening in September was 140μ; by December the oocytes had reached a diameter of 300μ (Fig. 3).

Vitellogenesis continued throughout the winter months, until the cod reached the spawning areas in February and March. In January the oocytes measured about 400μ; by late February-March the eggs were completely filled with large spherical yolk granules, and were about 580μ in diameter. The outer membrane of the egg had thickened considerably and showed radial striations, while the egg nucleus had frequently become eccentrically displaced and its membrane was very indistinct. The final stages of ripening occur rapidly and may be completed within a comparatively short time (possibly only a few days (Sorokin, 1957)). Fluid is taken up by the ovaries, the eggs increase in size and their yolk becomes homogenous throughout. The follicular membranes surrounding the eggs are ruptured as the eggs swell, the lobule walls are broken and the eggs pass into the centre of the ovary for spawning.

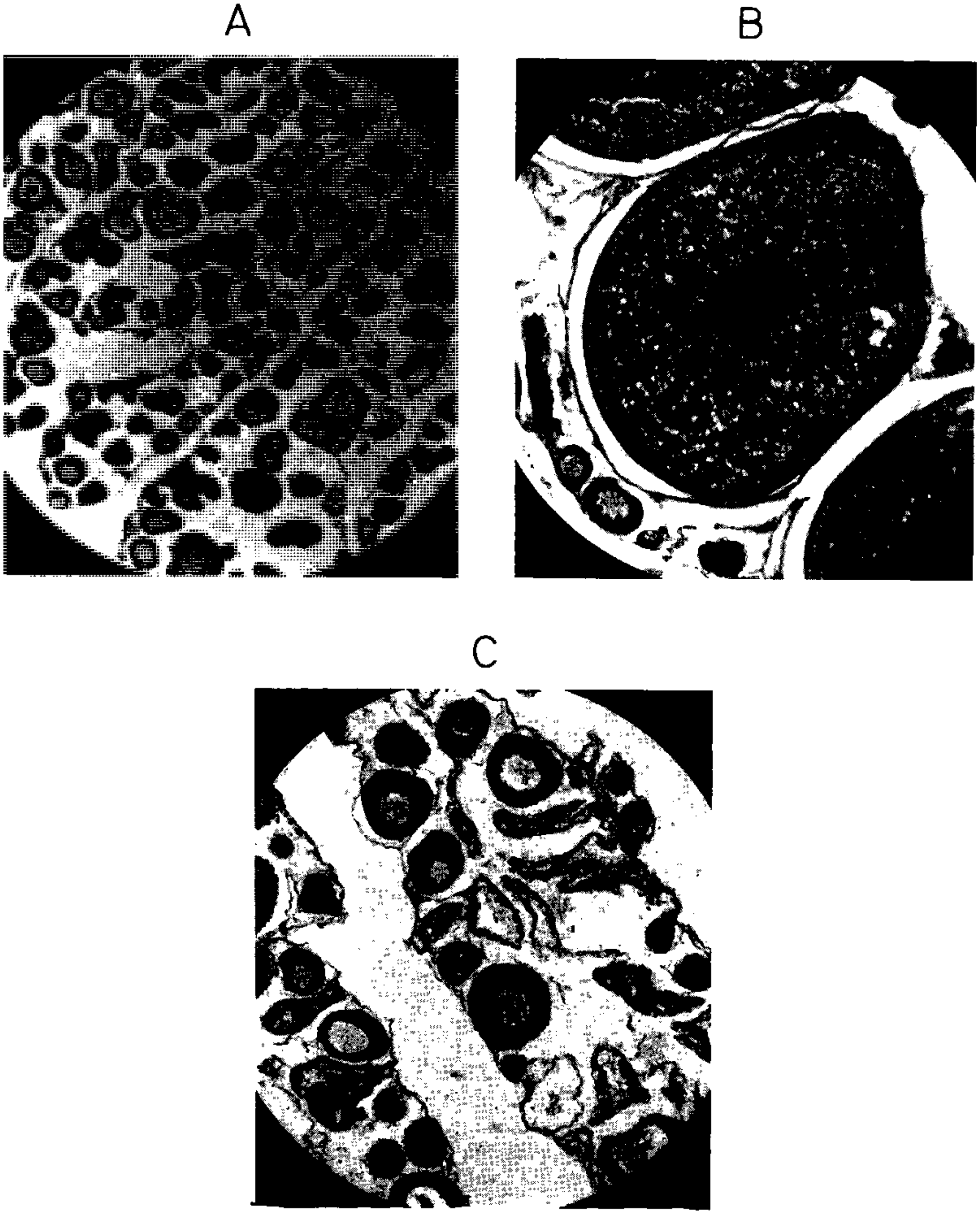

Fig. 3. A. Resting ovary showing small oogonia, oocytes which have undergone a phase of minor growth, and "circumnuclear ring" phase oocytes.
B. Ovary collected in January-February showing ripe eggs filled with yolk.
C. Ovary from spent female, showing large number of empty follicle membranes. Oocytes which had been present throughout the previous maturation cycle can be seen.

Ovarian regeneration and reorganisation starts soon after spawning. The ruptured follicular membranes shrink, any remaining unshed eggs are broken down and resorbed, and the lobule walls reform. Oocytes which had been present throughout the previous spawning grew rapidly to reach the circumnuclear ring phase. Simultaneously, a new generation of oogonia were produced from undifferentiated germ cells. The regeneration of the ovary appeared to be accomplished by May, but the remains of follicle membranes were found in the ovary for some four or even five months after spawning.

Quantitative changes in biochemical components accompanying the maturation cycle in the ovary of the cod have been described in recent years (Braekkan, 1958; Plack, Woodhead and Woodhead, 1961; Braekkan and Boge, 1962).

1.2 The effect of feeding conditions upon fecundity

It has been established that feeding conditions can have considerable effects upon the fecundity of fish, affecting the rate of maturation, the numbers and size of eggs, and the frequency of reproduction; various effects of nutrition on reproductive capacities of fish have been reviewed by Woodhead (1960*a*). Studies of the seasonal changes in the cod ovary revealed a mechanism whereby fecundity could be related to the conditions which had prevailed during the previous feeding season.

The numbers of oocytes in each phase of development in the ovaries of spent fish were compared with those collected at the end of the summer and during maturation; eggs were classified as minor growth phase oocytes, circumnuclear ring phase oocytes, and ripening eggs (those containing oil or yolk). The spent ovaries contained small oocytes which had not developed during the previous maturation cycle. By May, regeneration had taken place, and the numbers of eggs in the minor growth phase had increased by the development of further oocytes; growth of the oocytes had occurred and eggs in the circumnuclear ring phase were abundant. Comparison of the May ovaries with those collected in August showed no significant differences in the number of eggs in each of these phases, suggesting that there had been little ovarian activity during the summer months.

Ovarian growth was resumed in late September when oocytes in the circumnuclear ring phase began to increase in size. Simultaneously, some oocytes in the minor growth phase began to increase in size, and a circumnuclear ring appeared in the cytoplasm close to the nucleus. In October and November there were further increases in the numbers of small oocytes reaching this phase; these newly formed circumnuclear ring oocytes could be distinguished by their size, and by the position of the cytoplasmic ring close to the nucleus. Thus, before the start of the maturation cycle in autumn, the number of eggs which would start to ripen was already partly determined. The numbers of these eggs were then further increased by growth of some of the minor growth phase oocytes, and this growth process continued until November when vitellogenesis became well established. The November ovaries could be divided into two groups; those in which yolk deposition was just beginning, and those in which vitellogenesis was established; a comparison of ovaries at the initiation of vitellogenesis with those at the stage where vitellogenesis had become well established showed that there was no further increase in numbers of eggs which would ripen, and very few small circumnuclear ring phase oocytes could be found in ovaries at the latter stage (Table 3).

These results suggest that the fecundity of the cod is partly determined after spawning, when the new generation of circumnuclear ring phase oocytes is produced, and is probably related directly to the size of the fish. However, the number of oocytes which will ripen during the maturation season is increased during the period of ovarian growth in the autumn, before vitellogenesis is well established. The growth achieved by the fish during the summer feeding period could therefore be reflected in the numbers of extra eggs which develop to the circumnuclear ring phase in autumn.

In some species of fish, fecundity appears to be adjusted by atresia of the developing oocytes. Thus, in the rainbow trout, *Salmo gairdneri*, during the summer months atresia reduces the numbers of developing eggs and this has been associated with a decrease in feeding; experimentally restricting the intake of food in this species increased the numbers of atretic eggs (Scott, 1962). In the carp, *Cyprinus carpio*, a considerable number of eggs do not ripen fully but are resorbed after spawning, and Vasnetzov (quoted by Nikolsky, 1950) has suggested that when there is a marked improvement in feeding conditions these eggs may develop completely, increasing fecundity.

Atretic eggs were found in the majority of the cod ovaries examined, but their numbers were few, and they rarely formed more than one per cent of the ripening eggs in the ovary. In the present study there was no evidence of wholesale atresia of eggs, nor did it appear likely, from

TABLE 3. THE NUMBERS OF OOCYTES IN DIFFERENT PHASES OF DEVELOPMENT THROUGHOUT THE YEAR

Month	Percentage of eggs in minor growth phase	Percentage of circumnuclear ring eggs	Percentage of eggs with yolk
May	68	32	0
August	64	36	0
September	62	38	0
October	46	44	10
	(Vitellogenesis (beginning		
November-December	(43	40	17
	(Vitellogenesis (established		
	(44	23	33
January	45	4	51
March (spawning)	45	2	53

their infrequent occurrence, that oocyte atresia was an important factor in regulating fecundity in the cod under normal conditions. This dual mechanism of fecundity determination in spring and autumn has obvious advantages, since it involves minimum oocyte atresia, while probably closely relating the fecundity of the female to size and growth.

1.3 Oestrogen secretion

1.3.1 Control of vitellogenesis

There is considerable evidence that during gonadal maturation in lower vertebrates, including fish, the transport in the blood of yolk phospholipid-glycolipoprotein to the developing eggs is associated with an increase in the level of plasma calcium, the calcium being bound to the yolk protein complex (Bailey, 1957; Simkiss, 1961; Urist and Schjeide, 1961). These conditions have been produced in laboratory animals in a non-reproductive condition with a single dose of exogenous oestrogen and it would seem that they are under estrogenic-control. It was thought likely that similar changes in the calcium-protein complex would occur in the blood of adult cod during maturation, and that they might be used as an index of oestrogenic activity. Plasma samples were collected from Barents Sea cod throughout the year to see whether such variations occurred.

The analyses showed a marked seasonal cycle in plasma calcium in adult cod, the magnitude of the changes being greater in females than in males. During the spring and summer, plasma calcium remained at a resting level in both sexes, but in October the level had begun to rise slowly, reaching maximum values in the period January to March; these increases coincided with the period of gonadal maturation and were highest when the gonads were ripe. Immediately after spawning, plasma calcium levels fell to their minima in both sexes, later returning to the summer resting values. No significant changes in calcium were observed in the plasma of immature fish of either sex throughout the year (Woodhead, P.M.J., in preparation).

The increased levels of calcium observed in adult cod during the autumn and winter were associated with gonad maturation; plasma calciums had increased significantly by the onset of vitellogenesis and achieved their greatest height when vitellogenesis was well established; it seemed that in the female cod, at least, hyper-calcaemia was associated with vitellogenesis. That these changes were oestrogen-controlled in cod, as had been shown for other fish (Bailey, 1957; Urist and Schjeide, 1961; Fleming and Meier, 1961), was given some support by laboratory experiments in which cod were injected with oestradiol and with oestrone. The hormone injections caused an increase in plasma calcium, which was directly proportional to the dose of hormone given; oestradiol was more effective than oestrone in producing this response (P.M.J. Woodhead, unpublished experiments). It therefore seemed probable that the calcium changes in the cod were in response to changes in oestrogen secretion by the ovary. Increased oestrogen secretion during the period of vitellogenesis suggested that the two were related, the oestrogens perhaps controlling, or being involved in, the elaboration of yolk proteins in the liver for transport to the ripening ovaries. Recent studies on vitamin A aldehyde in the cod lend support to this conclusion; vitamin A aldehyde only appeared in the ovary after the onset of vitellogenesis (Plack, *et al.*, 1961) and analyses showed that it was also present in the blood of female cod during vitellogenesis; it was absent from the blood or present only at a low level when the gonad was resting, but, as for plasma calcium, a high level can be produced experimentally by injecting non-reproducing cod with exogenous oestrogens (P.M.J. Woodhead and P.A. Plack, unpublished).

From the seasonal changes in blood calcium it is inferred that in the cod, oestrogen secretion occurs during the latter part of the maturation cycle, from November onwards, achieving its highest level during January to March.

The seasonal changes observed in the plasma calcium of adult male cod are less easy to explain, since androgens have not been shown to cause such changes in any lower vertebrates. Although oestrogens have been demonstrated in the blood of some maturing male teleosts (at a lower level than in females; Cedard and Nomura, 1961) and it seemed possible that oestrogens might also produce the hypercalcaemia observed in male cod, Gottfried *et al.* (1962) have failed to find any substantial quantities of oestrogens in mature cod testes.

1.3.2 The secretion of hormones from the fish ovary

Oestrogens have been isolated from fish ovaries (Donahue, 1941) and recently oestradiol-17 β and oestrone have been found in the mature ova of the cod, at concentrations of 4.8 μg/kg and 1 μg/kg respectively (Gottfried *et al.*, 1962); some oestradiol, but no oestrone, was also contained in the ovarian sac. However, there is considerable uncertainty about the site of oestrogen production. The ripening ovary of fish usually contains a number of degenerating eggs or corpora atretica, and a hormonal function has been ascribed to these by several workers, notably Bretschneider and De Wit (1947), D'Ancona (1950), Hoar (1955) and Ball (1960), although as yet there is no critical evidence to show that these atretic eggs have a secretory function, or, indeed, any function at all.

Corpora atretica are present in cod ovaries, and they appear similar in many respects to those described previously in other teleosts (Bretschneider and De Wit, 1947). In September, at the beginning of gonadal maturation, very few atretic eggs were found; in October about a quarter of the ovaries examined contained atretic eggs, but by November-December more than 90% of the ovaries examined contained a few atretic eggs. Their appearance coincided with the start of vitellogenesis in the ovary, and they were rarely formed outside this period.

Histological results from the study of the Barents Sea cod ovaries did not provide further evidence to show whether corpora atretica had a secretory function, or if they were simply degenerating eggs in the process of resorption. A finding apposite to this problem was obtained from the analyses of plasma calcium levels (described above).

The hypercalcaemia found in adult female cod during the winter months was associated with oestrogen production and vitellogenesis in the maturing ovary. Corpora atretica were formed at the onset of vitellogenesis and persisted throughout ripening. If the size and complexity of the resorbing corpora atretica corresponded to secretory activity, they would appear to have been most active at the onset of vitellogenesis, their activity declining in the later phases of yolk deposition. Their occurrence in the ovary corresponded with the period of increased plasma calcium levels, and if hypercalcaemia reflected increased levels of oestrogen in the blood, these results could suggest that the corpora atretica had a secretory function.

Surprisingly, a few "apparently immature" females had ovaries in which all the eggs which had begun to mature had become atretic. Plasma calcium analyses showed that these fish had values above the usual immature range, suggesting that oestrogens were being secreted by the ovaries, possibly associated with the presence of atretic eggs. However, the relationship was by no means so simple and direct. These "immature" cod had much greater numbers of atretic eggs than normally ripening females, and accordingly it might have been expected that they would have proportionately higher levels of calcium in the plasma; in fact, the levels of their plasma calcium fell within the normal range for maturing females.

2. The testis

2.1. The maturation of the testis

The summer "resting" testis consisted almost entirely of cysts containing large, faintly staining spermatogonia, with large, round, central, lightly staining nuclei. There was little gametogenic activity during this period; occasionally the cells within a cyst divided and produced groups of secondary spermatogonia, distinguishable by their dense nuclei and indistinct cell boundaries. Secondary spermatogonia appeared in large numbers in late September, as maturation of the testis began; probably the existing spermatogonia divide to produce more spermatogonia, while groups of these give rise to secondary spermatogonia, the two processes occurring simultaneously. Primary spermatocytes, secondary spermatocytes and spermatids, representing the following three stages of spermatogenesis, predominated in the testis from mid-November to early January. The primary spermatocyte is largest, and usually has a nucleus in which the chromatin threads appear as a tangled mass, or are aggregated at one side. Secondary spermatocytes are smaller, with evenly dispersed chromatin; spermatids are smaller still, and have an elliptically shaped nucleus, and a very small cytoplasmic rim, so that the cells appear kidney-shaped.

Spermatozoa began to appear in the ripening testis from December. Initially the sperm were localized in bundles amongst the other cells, but, as more were produced, the cyst walls ruptured, the orientation of the bundles was lost and the testis became filled with ripe sperm. Almost immediately after spawning regeneration of the testis began; unshed sperm was resorbed, and the testis filled with primary spermatogonia (Fig. 4).

2.2. Seasonal changes in the interstitital cells of the testis

Lipid positive cells, analogous to the mammalian Leydig cells, which secrete male sex hormones, have been demonstrated in the testes of fish (Marshall and Lofts, 1956). Similar interstitial cells occur in the cod testes; they were readily distinguished in sections stained with Masson's trichrome stain, and their activity has been assessed on the basis of cytological characteristics. Four stages of activity were adopted. Inactive cells were small, with a central, heavily staining, dense nucleus and a thin rim of faintly staining cytoplasm. Cells classified as slightly active were larger, with increased cytoplasmic area; occasional faint granules were seen in the cytoplasm, and the nucleus showed chromatin threads aggregated at one side. Active cells were larger, and the cytoplasmic granules were coarse, conspicuous and more closely packed, whilst in maximally active cells there had been a further increase in cytoplasmic area, so that the cells were now approximately three times as large in diameter as the inactive cells, and the cytoplasm contained numerous coarse granules. There was little change in nuclear volume as the cells became active.

Testes collected throughout the spring and summer contained inactive cells, and in September the tissue still showed few signs of activity. Secretory activity appeared to begin about November-December when about one third of the interstitial cells were ascribed to the "slightly active" category (although less than 10% were characterised as "active" or "maximally active"). By January, activity had increased and was well established; cells in all four stages of activity were present, but "active" and "maximally active" cells predominated (about 60% of all cells). The testes of fish caught in early March, probably some three weeks before spawning, contained large numbers of maximally active cells. Samples from "running ripe" males, very kindly collected inside the Lofoten Island spawning grounds by Dr F.R. Harden Jones, showed that interstitial cell activity had begun to decline, and, after spawning, the activity of the gland had returned to its summer level (Fig. 5).

The interstitial cells of the cod testis show well marked seasonal variations in activity. Secretory activity became apparent in November-December, reaching a maximum just prior to spawning (as appeared to occur for oestrogens in the female). Testes collected from spawning fish showed that activity had begun to decline, and in spent cod the gland had become inactive.

It is assumed that the interstitial cell changes in the maturing testis are associated with sex hormone secretion in cod. Androgens have been shown to be present in the testes of mature sockeye salmon, *Oncorhynchus nerka*, and chum salmon, *O. keta* (Potter and Hoar, 1954; Idler and Tsuyuki, 1959), but no analysis has been described for the cod testis.

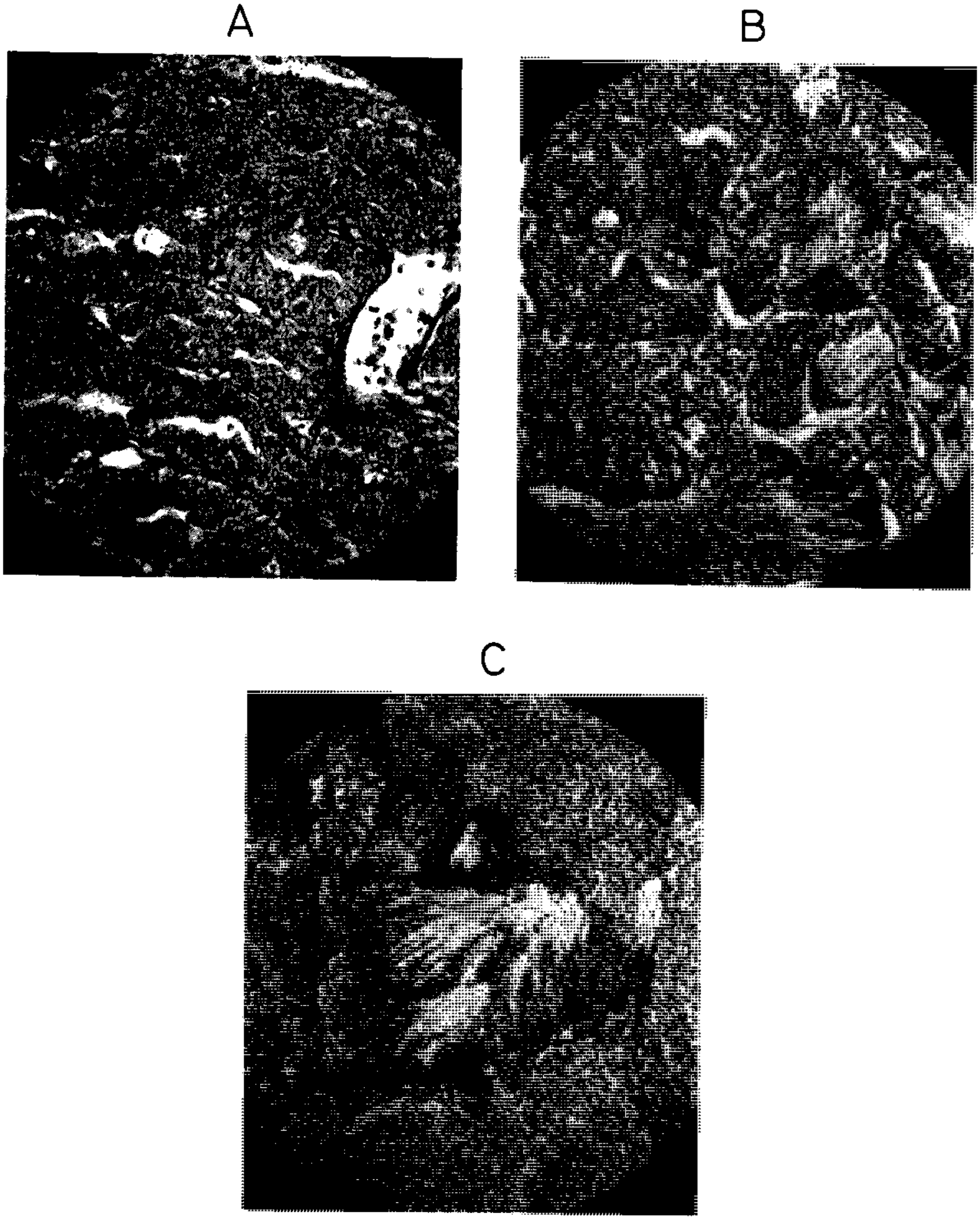

Fig. 4. Photomicrographs of the cod testis during maturation.
A. Resting testis, completely filled with large primary spermatogonia.
B. Ripening testis collected in December showing all later stages of spermatogenesis. Bundles of sperm can be seen.
C. Testis collected in February, almost completely filled with spermatozoa.

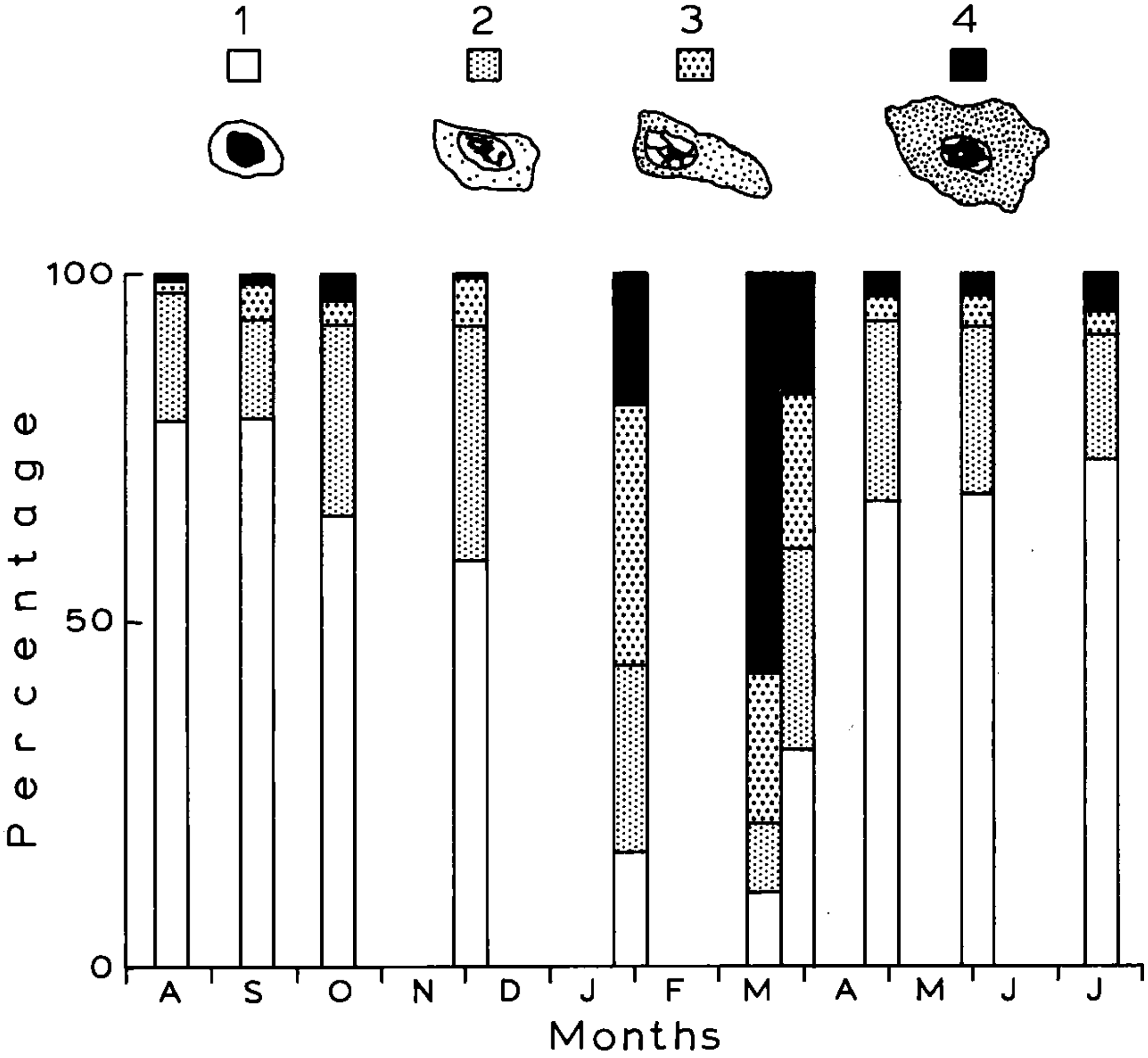

Fig. 5. Interstitial cell cycle in the testis, shown as percentage occurrence of cells of different activity, estimated histologically.

2.3. Gonadal hormones and the spawning migration

While the migration of the Barents Sea cod has been primarily associated with thyroid activity, the functions of gonadal hormones in this behaviour may also be of considerable importance. Hoar and his co-workers (1955) showed that sex steroids had similar effects to thyroxine upon the activity of fish, and on their sensitivity to stimulation. Goldfish and juvenile salmon kept in solutions of testosterone or stilboestrol were more active than untreated fish; they had a lower threshold for the response to electrical stimulation, and showed increased rheotaxis. Sex steroids had greater effects on this behaviour than thyroxine, and their maximum influence was generally seen sooner after treatment (after ten days, in contrast to fifteen days for thyroxine). Goldfish fed with beef testes have been found to show a 400% increase in locomotory activity (Stanley and Tescher, 1931) and Woodhead (1956) observed that the mean swimming speed of minnows, *Phoxinus phoxinus*, was 159% higher in April, prior to spawning, than during the winter months; these experiments have since been confirmed by Aminul Haque (in Barrington, 1960). In prespawning minnows, the thyroid has been found to be active (Barrington and Matty, 1954), but the gonads were apparently also secreting hormones, since the fish were in breeding dress. Both thyroid and gonadal hormones may therefore have contributed to the increased swimming activity.

In the adult cod, the effect of thyroid and gonadal hormones on migratory behaviour is probably additive. However, the cycle of secretory activity in the gonads of both males and females did not begin until November-December, about two months after migration had begun; as discussed above, thyroid hormones would appear to play a dominant rule in controlling migration, but their effects may be augmented by sex steroids secreted during the later stages of the migration.

THE INTERRENAL GLAND OF THE COD (ADRENAL CORTICAL TISSUE)

The interrenal tissue in fish does not form a discrete gland, but lies scattered amongst the head kidney, in close proximity to the cardinal veins and their branches. The anatomical position of the gland makes surgical removal impracticable, and hence data on its functions, and on the roles of the adrenal cortical hormones in fish, are often inconclusive.

In the present context it is particularly interesting to find that there is evidence of variations in interrenal activity during the spawning migrations of some fish. Changes in the histological appearance of the gland have been found during the spawning migration of Pacific salmon, accompanied by a progressive rise in the level of blood corticosteroids (Idler, Ronald and Schmidt, 1959; Robertson, *et al.*, 1961). In Atlantic salmon, blood corticosteroids also rose during the spawning migration but later fell at spawning (Fontaine and Hatey, 1954).

1. Seasonal changes in the interrenal gland of cod

A study was made of the histological changes in the interrenal gland of adult Barents Sea cod during their spawning migration. Changes in the cytological characteristics of the interrenal cells were studied, in particular the size and shape of individual cells and their staining properties with Masson's trichrome stain, the arrangement of the tissue into chords, or groups of cells, and the degree of vascularisation of the gland.

From July to October, the interrenal gland was composed of chords of cells, uniform in appearance, extending from the branches of the cardinal veins into the kidney tissue. Individual cells were large and columnar, with a round reticular nucleus, and faintly granular cytoplasm. Within each chord, the cells tended to be orientated in the same direction, with the nuclei of adjacent cells in alignment. Small blood vessels were present between the chords (Fig. 6A). The histological appearance of the gland suggested a resting condition, with little secretory activity.

Changes indicating the onset of secretory activity, were apparent in the late November sample. Whilst considerable areas of the interrenal tissue were still disposed in regular chords, some cells had formed into clumps; within these clumps two new types of interrenal cells had appeared. The most conspicuous and numerous of these were small, shrunken, intensely staining cells, in some of which degenerative changes were apparent; the cytoplasmic area had become very reduced, consisting in some cases simply of a thin rim of cytoplasm, slightly elongated at one side, surrounding the dense nucleus (Fig. 6B,C). The second type of cell was large, round, lightly staining, and approximately twice the diameter of the columnar interrenal cells. Both the cytoplasmic and nuclear areas had increased, and the cytoplasm showed a few faint granulations; sometimes vacuoles were present in the cytoplasm. Interrenal cells of this second type are characteristic of a hyperplastic gland (Robertson and Wexler, 1959; Mahon *et al.*, 1962). Histologically, the interrenal gland showed signs of increasing activity.

The interrenal glands collected from cod in January showed greater degenerative changes. The majority of chords had broken down and the cells had become grouped together, while the numbers of small degenerating cells had increased considerably (Fig. 6D). Large interrenal cells were present in the groups of cells. Interrenal glands collected in March had a very similar appearance, but the vascularisation of the gland was more pronounced than in the January sample, and the gland appeared to be extremely active.

Interrenals collected from spent cod in May-June showed some evidence of recovery. Many of the cells were grouped together, but chords had begun to reform. A striking feature of these chords was the occurrence of numerous thin elongated closely packed cells, which stained lightly. Mitoses were seen occasionally in these cells, and it appeared that regeneration of the interrenal tissue

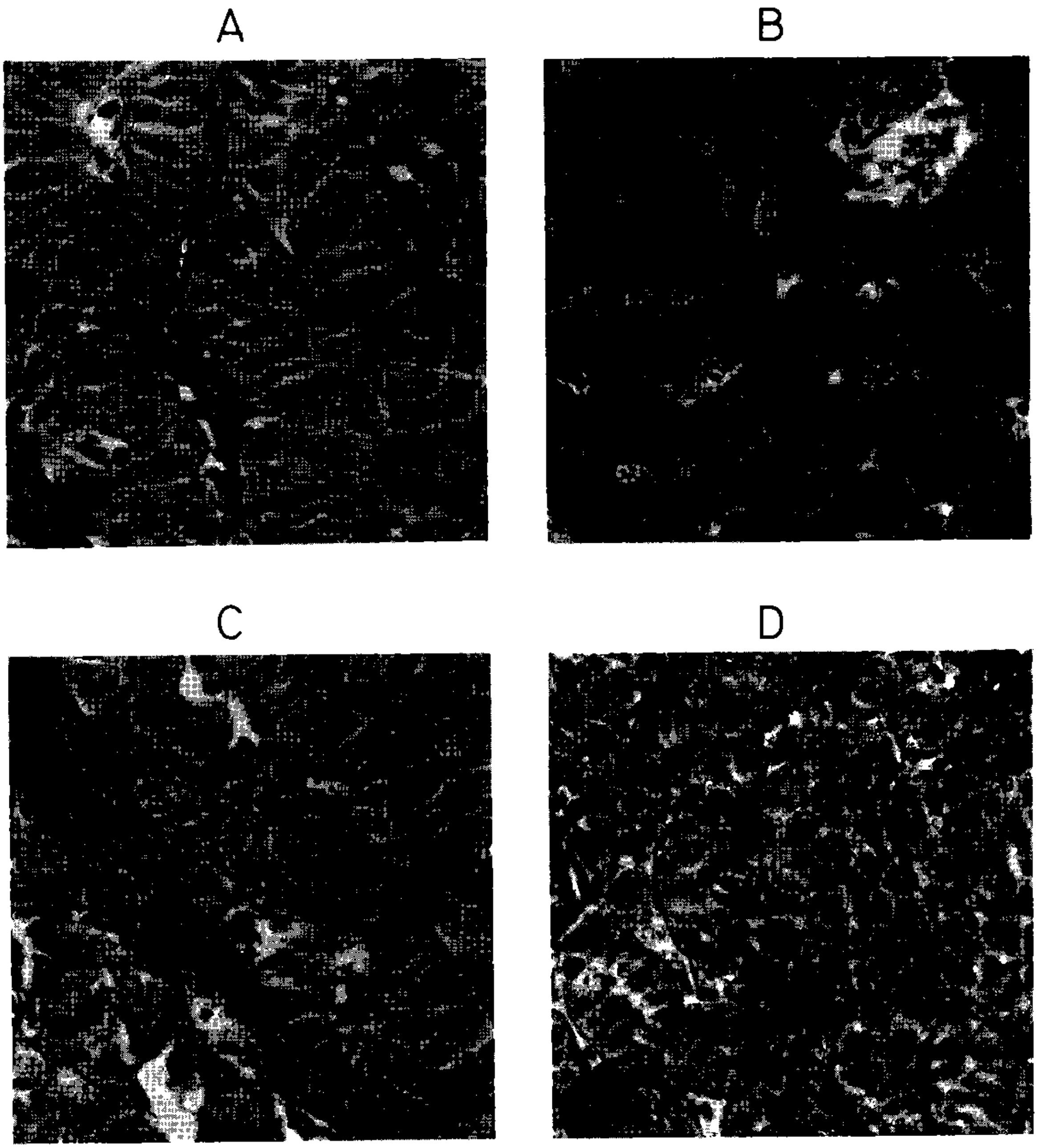

Fig. 6. Photomicrographs of the interrenal gland of the cod.

A. Inactive gland, showing large, lightly staining, regular, interrenal cells.

B. Initial stages of secretory activity. Occasional large, rounded, hypertrophic interrenal cells, and small, shrunken, degenerate cells are present. Blood vessels are abundant between the chords.

C. Active interrenal, with the cells grouped together. Within the groups are numerous small, shrunken degenerate cells and large, pale staining, hypertrophic cells.

D. Interrenal gland collected from cod in March, showing considerable degenerative changes.

was taking place. Degenerate interrenal cells were also present, although numbers had diminished considerably, and there were few large rounded interrenal cells. Histologically the interrenal gland appeared to be regenerating, but whilst secretory activity had declined considerably, the gland had not re-entered the resting condition, and it seemed likely that some secretory activity was still taking place. The changes described appeared to be the same in male and female cod.

2. The role of adrenal cortical hormones

It seems likely that the interrenal tissue in fish secretes corticosteroids which are similar or identical to some of those found in higher vertebrates. The presence of steroids concerned with carbohydrate metabolism and with salt and water balance has been demonstrated in fish blood (Phillips, *et al.*, 1959; Idler, *et al.*, 1959). However, the functions of these hormones in regulating mineral metabolism in fish are not fully understood. Experimental evidence has shown that corticosteroids can influence osmoregulation in freshwater fish (Secton, 1955; Holmes, 1959), but there is as yet little evidence to show whether they have a similar function in marine teleosts, and Chester Jones, Phillips and Holmes (1959) concluded that the adrenal cortical hormones are relatively inactive in osmoregulation in marine teleosts.

However, experiments in which freshwater fish were transferred to sea water resulted in an augmentation of plasma corticosteroids (Leloup-Hatey, 1959; Faure, 1960), while there is histological evidence of increased interrenal activity in salmon smolt transferred from fresh water to sea water, which has been interpreted as a feature of osmoregulation incident to the migration of the fish from fresh water to the sea (Olivereau, 1962); such experiments suggest that corticosteroids may indeed have a role in mineral metabolism in the marine environment. In this respect the changes in the interrenal of the cod are of particular interest, since the preliminary examination of their annual cycle of activity showed some evidence of coincidence between the duration of the low temperature limit to the cod in the winter and spring (which appears to influence the osmoregulatory mechanism - discussed in Part II of this paper) and activity of the interrenal gland.

Corticosteroids in fishes may be involved in the stimulation of metabolic processes, and it has been suggested that the increased activity of the gland during spawning migrations may be correlated with heightened carbohydrate metabolism and muscular activity (Fontaine and Hatey, 1954; Chester Jones, *et al.*, 1959). Robertson *et al.* (1961) found a marked hyperglycaemia during the spawning migration of Pacific salmon, which they associated with gluconeogenesis, when the interrenal glands were hyperactive. However, the causes of adrenal hyperplasia in salmon are difficult to determine, and the situation is complex, since migration and gonadal maturation occur whilst the fish are starving. Further, the fish encounter marked salinity changes during their migration. All these factors have been shown to affect adrenal cortical activity in either fish or mammals. Robertson and Wexler (1959) examined this problem in detail, and they suggested that neither osmoregulation nor the stress of migration is the dominant factor causing interrenal hyperplasia, but that the interrenal activity might be related to the stress of the development of gonads whilst the fish were starving.

The hypertrophy of the interrenal gland during the spawning migration of the Barents Sea cod might reflect an intrinsic cycle of activity, mobilizing carbohydrate reserves in relation to migration. However, if this was the case, activity would have been expected to start earlier, but there was no evidence of any secretory activity coincident with the onset of migration. Hypertrophy and degenerative changes became apparent in late November, when the fish are often feeding poorly (due to lesser availability of food in winter); this was the period of most rapid gonad growth and vitellogenesis in the female, so that the degenerative changes might equally have been the result of the increased demands of gonad maturation during a period when the fish were in poor nutritional condition.

A preliminary consideration of interrenal changes in immature cod indicated a similar, although lesser, cycle of activity. Hypertrophy of the gland was seen from late November, but extensive degenerative changes, such as occurred in the adult maturing cod, were infrequent. The interrenal gland in the immature cod remained active after their migration had ceased; this is in contrast to the cycle of activity in the thyroid gland, which declined as migration was completed. On the basis of these results it would appear that interrenal activity in immature and mature cod may be related to the winter period of poor feeding, and that the greater activity in adult fish is associated with the pronounced physiological demands of gonadal maturation.

Nevertheless, the possibility that the activity of the interrenal gland does play a part in migration cannot be precluded, even though it had not become active at the initiation of migration; it is hoped that these factors will be separated in a more detailed study now in progress.

EXTERNAL FACTORS REGULATING MATURATION AND MIGRATION

Marshall (1936) emphasised that breeding seasons were dependent upon external environmental factors, and suggested that their influence was exerted by nervous stimulation of gonadotrophic hormone released from the pituitary gland; this concept has been supported by later work, and the pathway linking external variables to internal physiological rhythms has been well established in higher vertebrates. The mode of regulation appears to be similar in fish (Olivereau, 1954; Zaitsev, 1955*a*, *b*). Changes in the physical, chemical or biological environment of the animal affect nervous receptors communicating with the hypothalamus, which, in turn, stimulates the pituitary gland to release hormones initiating activity in the endocrine target organs.

There seems little doubt that internal rhythmical changes may occur in the absence of external stimuli, and evidence of endogenous rhythms of breeding activity have been found in fish kept under constant experimental conditions (Bullough, 1939; Scrimshaw, 1944). However, the regular coordination of sexual cycles tends to break down under such constant conditions; thus Bullough (1939) found that in the minnow certain phases of gametogenesis were unduly lengthened, and Robinson and Rugh (1943) observed that the regularity of the 24-hourly spawning cycle in *Oryzias latipes* disappeared under constant illumination. The results from experiments with fish and other vertebrates suggest that seasonal rhythms in physiological activity are innate, but the role of external environmental factors is to precisely time these rhythms.

Two of the most important physical factors which have been shown experimentally to affect the timing of breeding cycles in fish are light and temperature. The relative importance of each varies with the ecological environment of the particular species, but in many marine fish photoperiod appears to be critical, provided that temperature does not deviate too far from the normal seasonal range.

Discussing the importance of external factors Bullough (1939) concluded that temperature would probably be important in the marine environment, since temperature variations over wide areas of the ocean were slow and changed in a regular manner throughout the year. But in many offshore regions this is not the case and if the temperatures are considered in detail over the range of a species, or from year to year, the changes do not seem to be sufficiently precise to form a basis for control, or even for temperature to be a dominant regulating factor. On the Svalbard Shelf of the Barents Sea the cod encounter only a small temperature range, from about -1°C to 5 or 6°C, and during most of the summer feeding period abundant catches may be made over most of this range (see Part II of this paper, Fig. 2). There is no sudden fluctuation in the autumn; indeed in September when migration and maturation commence the temperatures are about the same as in August and it seems unlikely that these physiological changes are initiated by temperature.

It seems probable that changes in the light regime, varying steadily from season to season, might initiate the spawning migration, and gonad maturation, in the Barents Sea cod. The initiation of these reactions occurs at the time of the autumnal equinox, when diurnal periods of light and darkness are equal throughout the northern hemisphere; we suggest that at this time, when diurnal periods of light and darkness are equal, the internal physiological rhythms resulting in migration and maturation are "triggered off". This change would be a common environmental factor throughout the range of the Barents Sea cod, so that characteristic changes would occur on all grounds; although theoretically photoperiod would vary with depth according to the penetration of light, these variations would not be great since at this time the cod in the Barents Sea are mainly found in shallow water (Trout, 1957) where light would be easily detected throughout most of the daytime period (Woodhead, 1964, this symposium). It appears less likely that other light factors such as intensity, rate of change of intensity, daily absorption of radiation, or rate of change of photoperiod would be the principal controlling factors, since they all vary with the latitude and water transparency and more critically with the depth at which the fish occur, and it is more difficult to see how such factors might synchronize the widespread behaviour change. To be able to detect daily changes in photoperiod the fish must be able to measure the relative length of day and night with reasonable accuracy; the fish would therefore need a 24-hour "clock" on which to make the comparison. There is abundant evidence to show that many animals do have such "clocks"; fish are no exception, and show well defined diurnal rhythms in behaviour and physiology (Woodhead, 1964, this symposium). Recent data have suggested that in some species "internal clocks" of individual animals may not be synchronous, but that there is a basic precision within a population. Webb and Brown (1959) have suggested that this would ensure that the population as a whole was maintained, rather than individuals. Single fish might show some variation in the time at which they began their spawning migration, but the movement of the population as a whole would be co-ordinated and synchronized.

At the time of the equinox marked changes may also occur in the biological environment, both in the plankton and to a lesser extent in the benthos. Such changes could act secondarily as "triggers" for the physiological rhythms of the fish. However this would seem a less likely mechanism than the direct influence of photoperiod, since due to the discontinuous nature of the biological environment much precision of timing would probably be lost.

Using trawler catch per unit effort data Trout (1962, 1963) has demonstrated a regular seasonal cycle of changes in catch, not only for the Barents Sea stock, but also for cod of several other stocks in the North Atlantic; these catch changes were interpreted as indicating a specific pattern of seasonal behaviour for the cod. It is of interest to speculate whether the coincidence of the equinox throughout the range of the cod might account for the similar timing of the patterns in widely separated stocks.

CONCLUSIONS

It is now generally accepted that many of the seasonal changes in the distribution, density and availability of fish stem from fundamental behavioural changes which are internally induced. This is especially the case in such species as the Barents Sea cod, which remain within a rather narrow range of temperature and salinity throughout the year. In these fish there are regular and well defined seasonal changes in distribution, direction and speed of movements, concentration and availability, depth change and reactions to low temperatures; evidence is accumulating which suggests that environmental changes are superimposed upon, and modify, many of these basic patterns, rather than the reverse. The basic behavioural patterns appear to be characteristic of the species and are probably controlled largely by internal physiological changes releasing different levels, or patterns, of metabolic activity, locomotion, sensory perception, or shifts in the control of homeostasis. In order to interpret the reactions of the fish to their external environment, it is therefore necessary to understand the internal changes which are also occurring; thus although seasonal migration is essentially a problem of fish behaviour in relation to environmental stimuli, it can only be understood in relation to the endocrine changes which initiate, maintain and possibly also terminate this complex of behaviour patterns.

In this paper we have attempted to describe in semi-quantitative terms the annual changes in three of the most important endocrine organs of the cod of the Barents Sea— the thyroid, gonads and interrenal glands. These are the glands whose activities are most likely to bring about annual changes in the reactions of the cod to the external environment; the pituitary would also be involved in such changes, but has not been discussed here, although one of us has previously described the presence of gonadotrophic, thyrotrophic and adreno-corticotrophic hormones in the cod pituitary (Woodhead, A.D. and Fontaine, 1959; Woodhead, A.D., 1960*b*, 1961), and Heller (1963) has suggested that the neurohypophysical lobe also contains arginine vasotocin and another active peptide ichthyotocin. Although the present descriptions refer to only three glands, and we are aware that they are incomplete, they are presented here as parts of the essential framework within which the detailed analysis of the seasonal changes in the physiological reactions of the cod must be made. The technique of studying changes in single endocrine organs in respect to the reactions of the fish is limited, since the endocrine glands tend to work in an integrated manner and their interrelationships may be complex; nevertheless it may be claimed that this study of the cod has already yielded several results of apparent importance to the investigation and understanding of the behaviour of commercial fish stocks.

At present very little work has been done in this field. Thus, despite the remarkable plasticity of the reproductive processes in fish, it has been said that our knowledge of reproduction in the classes of fishes is based mainly on about fifty species out of some 20,000 available, and very few of these have been marine fish of commercial importance. Considering other endocrine glands, much less information is available; indeed, the present descriptions of thyroid activity in the cod and spurdog are the only quantitative analyses of the seasonal changes in this gland made for any marine fishes; this would also seem to apply to the interrenal gland. Studies in the field of freshwater fisheries research are based upon far more detailed work.

We consider that similar physiological studies of the reactions and capacities of marine fish would provide data of fundamental importance to fisheries biology. To take one relevant example, although many investigations have been made concerning the relationships between cod and temperature, it has often been impossible to disentangle the critical features of the ecological complex, so that the results have been largely inferential. Approaching this problem from a physiological viewpoint (second part of this paper) has yielded apparent evidence of direct effects of low temperature on cod, even though the study has so far been of limited scope. The application of this physiological approach to some of the complex problems of fisheries biology should provide rewarding additions to the results of the better established fisheries disciplines related to the study of the environment and its influences upon the fish.

REFERENCES

AASEN, O. 1963. Norske pigghåmerkninger 1962. *Fiskets Gang.* 49: 455-460.

D'ANCONA, U. 1950. Follicoli atresici e corpi lutei nei Teleostei. *Arch. Anatomia,* 54: 413-419.

ARONSON, L.R. 1959. Hormones and reproductive behaviour: some phylogenetic considerations. *In Comparative endocrinology.* 98-120. New York: John Wiley and Sons.

BAILEY, R.E. 1957. The effect of estradiol on serum calcium, phosphorus and protein of goldfish. *J. exp. Zool.,* 136: 455-470.

BALL, J.N. 1960. Reproduction in female bony fishes. *Symp. zool. Soc. Lond.,* No. 1: 105-135.

BARRINGTON, E.J.W. 1960. Some problems of adenohypophysial relationships in cyclostomes and fish. *Symp. zool. Soc. Lond.,* No. 2: 69-85.

1963. *An introduction to general and comparative endocrinology.* Oxford: Clarendon Press.

BARRINGTON, E.J.W., and A.J. MATTY. 1952. Influence of thiourea on reproduction in the minnow. *Nature,* Lond., 170: 105-106.

1954. Seasonal variation in the thyroid gland of the minnow, *Phoxinus phoxinus* L., with some observations on the effect of temperature. *Proc. zool. Soc. Lond.,* 124: 89-95.

BRAEKKAN, O.R. 1958. Vitamins and the reproductive cycle of ovaries in cod (*Gadus morhua*). *Fiskeridirek. Skr., teknol. Undersøk.* 3: 1-9.

BRAEKKAN, O.R., and G. BOGE. 1962. Further studies on vitamins and the reproductive cycle of ovaries in the cod. *Fiskeridirek. Skr., teknol. Undersøk.,* 4: 1-15.

BRETSCHNEIDER, L.H., and J.J. DUYVENE DE WIT. 1947. *Sexual endocrinology of non-mammalian vertebrates.* Monographs on the progress of research in Holland during the war. Amsterdam. Elsevier Publishing Co. Inc.

BUCHMANN, H. 1940. Hypophyse und Thyreoidea im Individualzyklus des Herings. *Zool. Jb.,* 66: 191-262.

BULLOUGH, W.S. 1939. A study of the reproductive cycle of the minnow in relation to the environment. *Proc. zool. Soc. Lond., A.* 109: 79-102.

CEDARD, L., and T. NOMURA. 1961. Dosage fluorimétrique après chromatographie de partage des oestrogènes dans le sang de certain Téléostéens. *Bull. Inst. Oceanogr. Monaco,* 51: (1196).

CHESTER JONES, I., J.G. PHILLIPS, and W.N. HOLMES. 1959. Comparative physiology of the Adrenal Cortex. *In "Comparative Endocrinology",* 582-612. New York: John Wiley and Sons.

DONAHUE, J.K. 1941. Occurrence of estrogens in the ovaries of the winter flounder. *Endocrinology,* 28: 519-520.

FAURE, L.C. 1960. Recherches sur l'adaptation de Cyprins dorés à des milieux de salinité diverse et sur son déterminisme endocrinien. *Diplôme d'Etudes Supérieures, Univ. Paris. Fac. Sci.*

FLEMING, W.R. and A.H. MEIER, 1961. Further studies of the effect of mammalian parathyroid extract on the serum calcium levels of two closely related teleosts. *Comp. Biochem. Physiol.* 3: 17-26.

FONTAINE, M. 1948. Du rôle joué par les facteurs internes dans certaines migrations de poissons: Etude critique de diverse méthodes d'investigation. *J. Cons.,* 15: 284-294.

1954. Du déterminisms physiologique des migrations. *Biol. Revs.,* 29: 390-418.

1956. Analyse expérimentale de l'instinct migrateur des poissons. *In "L'instinct dans le comportement des animaux et de l'homme".* 151-175. Paris, Masson et Cie.

FONTAINE, M., and J. HATEY. 1954. Teneur en acide ascorbique de l'interrenal des poissons (Selaciens et Teleosteens). *Bull. Inst. Oceanogr. Monaco,* 58: 1037.

FORSELIUS, S. 1957. Studies of anabantid fishes. *Zoologiska Bidrag från Uppsala,* 32: 93-597.

FORTUNE, P.Y. 1955. Comparative studies of the thyroid function in teleosts of tropical and temperate habitats. *J. exp. Biol.,* 32: 504-513.

GAISER, M.L. 1952. Effets produits par l'administration prolongée de thiourée et de thyroxine chez *Lebistes reticulatus.* *C.R. Soc. Biol., Paris,* 146: 496-498.

GORBMAN, A., and H.A. BERN. 1962. *A textbook of comparative endocrinology.* New York: John Wiley and Sons.

GOTTFRIED, H., S.V. HUNT., T.H. SIMPSON, and R.S. WRIGHT. 1962. Sex hormones in fish. The oestrogens of cod (*Gadus callarias*). *J. Endocrin.,* 24: 425-430.

HELLER, H. 1963. Comparative aspects of neurohypophysial morphology and function. *Symp. zool. Soc. Lond.,*: No. 9.

HEUTS, M.J. 1943. La régulation osmotique chez l'épinochette (*Pygosteus pungitius* L.). *Ann. Soc. zool. Belg.,* 74: 99-105.

HOAR, W.S. 1953. Control and timing of fish migration. *Biol. Revs.,* 28: 437-452.

1955. Reproduction in teleost fish. *Mem. Soc. Endocrin.* No. 4: 5-24.

HOAR, W.S., M.H.A. KEENLEYSIDE, and R.G. GOODALL. 1955. The effects of thyroxine and gonadal steroids on the activity of salmon and goldfish. *Canad. J. Zool.,* 33: 428-439.

HOFFERT, J.R., and P.O. FROMM. 1959. Estimation of thyroid secretion rate of rainbow trout using radioactive iodine. *J. cell. comp. Psychol.,* 54: 163-169.

HOLMES, W.N. 1959. Studies on the hormonal control of sodium metabolism in the rainbow trout (*Salmo gairdneri*). *Acta. endocrinol. Kbh.,* 31: 487-602.

HONMA, Y. 1959*a*. Studies on the endocrine glands of a salmonoid fish, Ayu, *Plecoglossus altivelis,* Temminck and Schlegel. I. Seasonal variations in the endocrines of the annual fish. *J. Fac. Sci., Niigata Univ.,* Ser. II. 2: 225-233.

1959*b*. Studies on the endocrine glands of a salmonoid fish, Ayu, *Plecoglossus altivelis,* Temminck and Schlegel. II. Endocrines of the spent fish or Otu-nen Ayu. *J. Fac. Sci., Niigata Univ.,* Ser. II. 2: 235-242.

HONMA, Y., and E. TAMURA, 1963. Studies on the endocrine glands of the salmonoid fish, the Ayu, *Plecoglossus altivelis*, Temminck and Schlegel. V. Seasonal changes in the endocrines of the land-locked form, the Koayu. *Zoologica*, N.Y., 48: 25-32.

HOPPER, A.F. 1952. Growth and maturation response of *Lebistes reticulatus* to treatment with mammalian tyroid powder and thiouracil. *J. exp. Zool.*, 119: 205-217.

IDLER, D.R., and H. TSUYUKI. 1959. Biochemical studies on sockeye salmon during spawning migration. VIII. Androgen content of testes. *J. Fish. Res. Bd. Canada*, 16: 559-560.

IDLER, D.R., A.P. RONALD, and P.S. SCHMIDT. 1959. Biochemical studies on sockeye salmon during spawning migration. VII. Steroid hormones in plasma. *Canad. J. Biochem. Physiol.*, 37: 1227-1238.

IVANOVA, A.D. 1954*a*. The thyroid gland of osetr and sevriuga in the period of spawning migration and spawning. *Dokl. Akad. Nauk.SSSR*, 98: 693-696. (In Russian).

1954*b*. The thyreotropic effect in hypophysis injections of acipenserines. *Dokl. Akad. Nauk. SSSR*, 99: 333-336. (In Russian).

KOCH, H.J. and M.J. HEUTS. 1942. Influence de l'hormone thyroidienne sur le régulation osmotique chez *Gasterosteus aculeatus* L., form *gymnurus* Cuv. *Ann. Soc. zool. Belg.*, 73: 165-172.

KONSTANTINOV, K.C. 1957. Results of the marking of the bottom fishes of the Barents Sea in 1945-1955. *Trans. Knipovich Polar Sci. Inst. Sea Fish and Oceanogr.*, 10: 78-87. (In Russian).

LELOUP-HATEY, J. 1959. Influence du passage direct de l'eau douce à une solution saline équilibrée isotonique à l'eau de mer (Δ = -2°) sur la teneur en 17-hydroxycorticostéroides du plasma d'un Téléostéen stéreohalin: la Carpe (*Cyprinus carpio* L.). *Compt. rend. Soc. biol.*, 153: 206-211.

MAHON, E.F., W.S. HOAR, and S. TABATA. 1962. Histophysiological studies of the adrenal tissues of the goldfish. *Canad. J. Zool.*, 40: 449-464.

MANKEVICH, E.M. 1960. Biological peculiarities in some groups of the Barents Sea cod. *In Soviet Fish. Invest. in North European Seas. PINRO*, 253-266. (In Russian).

MARSHALL, F.H.A. 1936. The Croonian lecture: Sexual periodicity and the causes which determine it. *Philos. Trans.* B. 226: 423.

MARSHALL, A.J. and B. LOFTS. 1956. The Leydig-cell homologue in certain teleost fishes. *Nature*, Lond., 177: 704-705.

MASLOV, N.A. 1944. The bottom-fish of the Barents Sea and their fisheries. *Trans. Knipovich Polar. Sci. Inst. Sea-Fish. and Oceanogr.* 8: 3-186. (In Russian).

1960. Soviet investigation on the biology of cod and other demersal fish in the Barents Sea. *In Soviet Fish. Invest. North European Seas, PINRO*, 185-231. (In Russian).

NIKOLSKY, G.V. 1950. On certain laws governing the dynamics of the fecundity of fishes. *Zool. Zh.* 29: 489-500. (In Russian).

OLIVEREAU, M. 1954. Hypophyse et glande thyroide chez les poissons. Étude histophysiologique de quelques corrélations encodriniennes, en particulier chez *Salmo salar* L. *Ann. Inst. océanogr. Monaco.*, 29: 95-296.

1962. Modifications de l'interrénal du smolt (*Salmo salar* L.) au cours du passage d'eau douce en eau de mer. *Gen. Comp. Endocrin.*, 2: 565-573.

PHILLIPS, J.G., W.N. HOLMES, and P.K. BONDY. 1959. Adrenocorticosteroids in salmon plasma (*Oncorhynchus nerka*). *Endocrinology*, 65: 811-818.

PICKFORD, G.E. 1957. The thyroid and thyrotrophin. In: Pickford, G.E. and Atz, J.W. *The physiology of the Pituitary Gland of Fishes*. New York Zool. Soc.

PLACK, P.A., A.D. WOODHEAD, and P.M.J. WOODHEAD. 1961. Vitamin A compounds in the ovaries of the cod, *Gadus morhua* L., from the Arctic. *J. Mar. biol. Ass. U.K.*, 41: 617-630.

POTTER, G.D. and W.S. HOAR. 1954. The presence of androgens in chum salmon (*Oncorhynchus keta* Walbaum). *J. Fish. Res. Bd. Canada*, 11: 63-68.

ROBERTSON, O.H., and B.C. WEXLER. 1959. Hyperplasia of the adrenal cortical tissue in Pacific salmon (genus *Oncorhynchus*) and rainbow trout (*Salmo gairdnerii*) accompanying sexual maturation and spawning. *Endocrinology*, 65: 225-238.

ROBERTSON, O.H., M.A. KRUPP, C.B. FAVOUR, S. HANE, and S.F. THOMAS. 1961. Physiological changes occurring in the blood of the Pacific salmon (*Oncorhynchus tshawytscha*) accompanying sexual maturation and spawning. *Endocrinology*, 68: 733-746.

ROBINSON, E.J. and R. RUGH. 1943. The reproductive processes of the fish, *Oryzias latipes*. *Biol. Bull., Woods Hole*, 84: 115-125.

ROLLEFSEN, G. 1933. The otoliths of the cod. *Fiskeridir. Skr. Havundersøk.*, 4 (3): 1-14.

SAETERSDAL, G. 1956. Fisheries research in northern waters - study items and results. *Forskning og Fiske* Nr. 1.

SCOTT, D.P. 1962. Effect of food quantity on fecundity of rainbow trout, *Salmo gairdneri*. *J. Fish. Res. Bd. Canada*, 19: 715-731.

SCRIMSHAW, N.S. 1944. Superfetation in poeciliid fishes. *Copeia*, 3: 180-183.

SECTON, A.W. 1955. Factors influencing the uptake of sodium against a diffusion gradient in the goldfish gill. Ph.D. Thesis. Univ. of Missouri.

SIMKISS, K. 1961. Calcium metabolism and avian reproduction. *Biol. Rev.*, 36: 321-367.

SMITH, D.C., S.A. SLADEK, and A.W. KELLNER. 1953. The effect of mammalian thyroid extract on the growth rate and sexual differentiation in the fish, *Lebistes reticulatus*, treated with thiourea. *Physiol., Zoöl.*, 26: 117-124.

SOROKIN, V.P. 1957. Ovogenesis and the annual development of the ovaries of cod (*Gadus morhua morhua* L.). *Trudy PINRO*, 10: 125-144. (In Russian).

STANLEY, L.L., and G.L. TESCHER. 1931. Activity of goldfish on testicular substance diet. *Endocrinology*, 15: 55-56.

SWIFT, D.R. 1959. Seasonal variations in the activity of the thyroid gland of yearling brown trout (*Salmo trutta* Linn.). *J. exp. Biol.*, 36: 120-125.

1960. Cyclical activity of the thyroid gland of fish in relation to environmental changes. *Symp. zool. Soc. Lond.*, No. 2: 17-27.

TROUT, G.C. 1957. The Bear Island cod: migrations and movements. *Fish. Invest. Lond.*, Ser. 2, 21 (6): 1-51.

1962. Specific seasonal density changes in cod and haddock populations. *I.C.E.S. 1962.Comp. Fish. Comm.* No. 24, 1-5.

1963. Availability - facts from the fishermen, Pts. 1 and 2. *World Fishing*, 12: 10 and 11.

URIST, M.R. and A.O. SCHJEIDE. 1961. The partition of calcium and protein in the blood of oviparous vertebrates during estrus. *J. Gen. Physiol.*, 44: 743-756.

VILTER, V. 1944. Rhéotropisme de la civelle et activité thyroidienne. *C.R. Soc. Biol.*, Paris, 138: 668-669.

WEBB, H.M., and F.A. BROWN, Jr., 1959. Timing long-cycle physiological rhythms. *Physiol. Rev.* 39: 127-161.

WOODHEAD, A.D. 1959*a*. Variations in the activity of the thyroid gland of the cod, *Gadus callarias* L., in relation to its migrations in the Barents Sea. I. Seasonal changes. *J. Mar. biol. Ass. U.K.*, 38: 407-415.

1959*b*. Variations in the activity of the thyroid gland of the cod, *Gadus callarias* L., in relation to its migrations in the Barents Sea. II. The "dummy run" of the immature fish. *J. Mar. biol. Ass., U.K.*, 38: 417-422.

1960*a*. Nutrition and reproductive capacity in fish. *Proc. Nutr. Soc.*, 19: 23-28.

1960*b*. The presence of adrenocorticotrophic hormone in the pituitary of the Arctic cod, *Gadus morhua* L. *J. Endocrin.*, 21: 295-301.

1961. Assays for gonadotrophins in the pituitary gland of the Arctic cod, *Gadus morhua* L., and the presence of a gonadotrophic antagonist. *J. Endocrin.*, 22: 421-432.

1963. Thyroid cycles and their relation to reproduction and migration in *Acanthias vulgaris* L., an ovoviviparous elasmobranch. Abstract in *Gen. Comp. Endocrin.* Dec. 1963.

1964. Variations de l'activité thyroidienne et sa relation avec la reproduction et les migrations de *Squalus acanthias* sélacien ovovivipare. *Ann. d'Endocrin.* In press.

WOODHEAD, A.D., and Y.A. FONTAINE. 1959. Quelques données sur le pouvoir thyréotrope de l'hypophyse de la Morue (*Gadus morhua* L.) *Bull. Inst. Océanogr. Monaco*, 56: (1137) 1-6.

WOODHEAD, P.M.J. 1964. Effects of light upon behaviour and distribution of demersal fishes of the North Atlantic. *This symposium Contribution No. A-15.*

ZAITSEV, A.V. 1955*a*. Questions of neurosecretory activity of the ganglion cells of the hypothalamic nuclei of pike and carp in connection with seasonal manifestation of the gonadotrophic function of the hypophysis. *Dokl. Akad. Nauk SSSR.*, 101: 351-354.(In Russian).

1955*b*. A histological investigation of the annual changes of the thyroid gland of the pike, and the neurosecretory activity of the hypothalamic nuclei in the seasonal change of the thyreotropic function of the hypophysis. *Dokl. Akad. Nauk SSSR.*, 104: 315-318. (In Russian).

F-6B

SEASONAL CHANGES IN THE PHYSIOLOGY OF THE BARENTS SEA COD *GADUS MORHUA* L., IN RELATION TO ITS ENVIRONMENT

II. PHYSIOLOGICAL REACTIONS TO LOW TEMPERATURES

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and

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ABSTRACT

Studies on cod distribution in relation to temperature in the Barents Sea are discussed and data on 1,451 trawl hauls at various temperatures and times of year are presented. Abundant cod catches were not made below about 1.7°C from October to June, although during the summer feeding period large catches were made to at least 0°C.

Cod caught below 2°C between October and June were shown to have elevated blood salt contents, although this did not occur during the summer. Very similar changes were found in North Sea cod in the severe winter of 1963; cod from below 2°C had increasingly high blood sodium contents.

There are many records of cod being killed by low temperatures; to investigate their thermal tolerance cod were tagged and released at different low temperatures in the Barents Sea; recaptures clearly showed that many cod survived but also suggested that low temperatures may have reduced the survival rate.

Histological examination of gill epithelium in cod caught below 2°C (with elevated blood salts) showed signs of increased secretory activity in the so-called chloride secretory cells, suggesting a compensatory response to establish homeostasis. Mucous secretion appeared to have broken down in the gills of these fish. These changes did not occur in cod from low temperatures in the summer.

From the close correspondence of the details of seasonal temperature distribution, and of the physiological changes in Barents Sea cod, it was concluded tbat these fish encounter a limit to normal physiology at about 2°C between October and June, but that this limit changes in summer, perhaps to 0°C. Considering the causes of seasonal changes it seems likely that both feeding and encocrine changes are involved, but the relationships are not yet clear.

Laboratory experiments have shown that cod may survive supercooling for some weeks; such thermal tolerance, even temporarily, would have obvious survival value for Arctic cod, but need not conflict with our view that cod undergo an essential change in normal physiology at low temperatures.

Preliminary investigations of the effects of low temperatures on 0-group and I-group cod suggested that young stages may not be so critically effected as the adult fish.

INTRODUCTION

In an earlier paper (Woodhead and Woodhead, 1959) we considered the effects of low temperatures (below 2°C) upon the physiology of the Barents Sea cod, and found a close association between these effects and seasonal changes in the distribution of the cod with respect to temperature, which have been described by other authors. These studies on the Barents Sea cod have now been taken further, and related investigations were also made on the cod of the North Sea during the severe winter of 1963 when temperatures fell to abnormally low levels. This paper presents these new results and goes on to reconsider our previous conclusions in relation to them. Eliassen *et al.* (1960) repeated

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our observations in the Barents Sea, obtaining similar results but applying an interpretation different from our own, and Leivestad (1964) has further shown experimentally that cod can tolerate very low temperatures; their views are discussed.

DISTRIBUTION AND TEMPERATURE IN THE BARENTS SEA

When considering the details of the distribution of the cod with reference to changes in the marine environment, there have been frequent investigations into the relationships between the catches of cod and sea temperatures, an obvious choice since many of the cod stocks in northern seas live in regions where Arctic waters form cold fronts with warmer waters of Atlantic origin and temperature gradients may be steep. But since the cycle of temperature in the seas tends to follow a regular pattern, in many cod fisheries — just as for other fish which make well defined and regular migrations — there are sure to be apparent relationships between the distribution of the fish and temperature, which may be no more than coincidence. Thus, although cod have been caught over a wide range of temperature from about 17°C to -1°C there would be little significance in the statement that on the Svalbard Shelf (Spitsbergen, Bear Island, Hope Island) of the Barents Sea the best catches of cod are made at between 0° and 5°C, since the temperature range available on the Shelf covers only about seven degrees, from -1°C to 6°C.

There have been several detailed reports of low temperature limiting the distribution of the cod in the Barents Sea. Maslov (1944, 1960) and Mironova (1958) showed that the cod catches of the Russian trawler fleets were related to the position of the 2°C isotherm, few cod being caught below that temperature, and they showed that the fishable area could vary from year to year with changes in hydrographic conditions. Over ten years, from 1949 to 1958, the R/V *Ernest Holt* made many trawling surveys in the north-western Barents Sea on the cod of the Svalbard Shelf, and the fish were frequently found to be limited at a temperature of about 2°C (Graham *et al.*, 1954), and for perhaps the most detailed of these surveys it was suggested that the critical limit lay at 1.75°C (Lee, 1952). Extensive echo-sounder surveys both in the north-western and south-eastern Barents Sea have also shown the fish to be limited by low temperatures (Saetersdal, 1956; Cushing, 1959; Midttun, 1959; Beverton and Lee, 1964), although from the surveys of both Cushing and Saetersdal it appeared that 1.5°C was probably nearer the limiting temperature. There has therefore been considerable agreement between the results of these independent surveys, that the low temperature limit to the distribution of the cod lay between 1.5 and 2.0°C. An exception to this general picture was found during the summer months of July to September, when some cod may enter colder waters, down to about 0°C, to feed heavily upon planktonic krill and on the capelin (*Mallotus villosus*) or herring (*Clupea harengus*) (Lee, 1952, 1956).

Although these surveys reported apparently critical situations in a given area at a particular season, it was difficult to assess the temperature relationships throughout the year. For this purpose results have been provided from the cruises of the R/V *Ernest Holt* fishing on the Svalbard Shelf over the ten years from 1949 to 1958; temperatures at the sea-bed were observed at the beginning and end of the trawl hauls, and the cod catches could therefore be compared directly with temperatures throughout the seasons of the year. The catch of cod, in baskets per hour (a basket of cod weighs about 38 kgm), was compared with the mean of the temperatures recorded at each end of the trawl haul. (Catches made when the temperature differences between the beginning and end of the trawl hauls exceeded one degree have been excluded as too inaccurate.) It was found that the same relationship generally held for the whole of the period October to June, and that, as previously reported by Lee (1956), large catches of cod were not taken in water below 2°C in this period. These results for 1109 trawl hauls are shown in Fig. 1. From this figure it appears that temperatures between 1.7°C and 2.0°C were critical in limiting the distribution of abundant cod (although it is also apparent that small catches of cod were frequently made at lower temperatures). There were a few exceptions where high catches had occasionally been made at 1°C, or even lower; these were usually made at the edge of the bank south of Bear Island in February-March; it is not uncommon for water cooled on the banks to cascade off the shelf in this region (Lee, 1963), and these fish may well have been surrounded or trapped by such cold cascading waters, as happened in March 1955 (Beverton and Lee, 1964). During October in both 1957 and 1958, however, some fairly high catches were made on cod which were feeding heavily in cold waters (see also the discussion of conditions in October 1960 later in this paper), and it appears that the temperature distribution of cod, when feeding heavily on fish, is not so precisely defined at this time.

The observations of Lee (1956) that the limiting effects of low temperatures were not apparent during the summer months of July, August and September are in accord with the results of the present

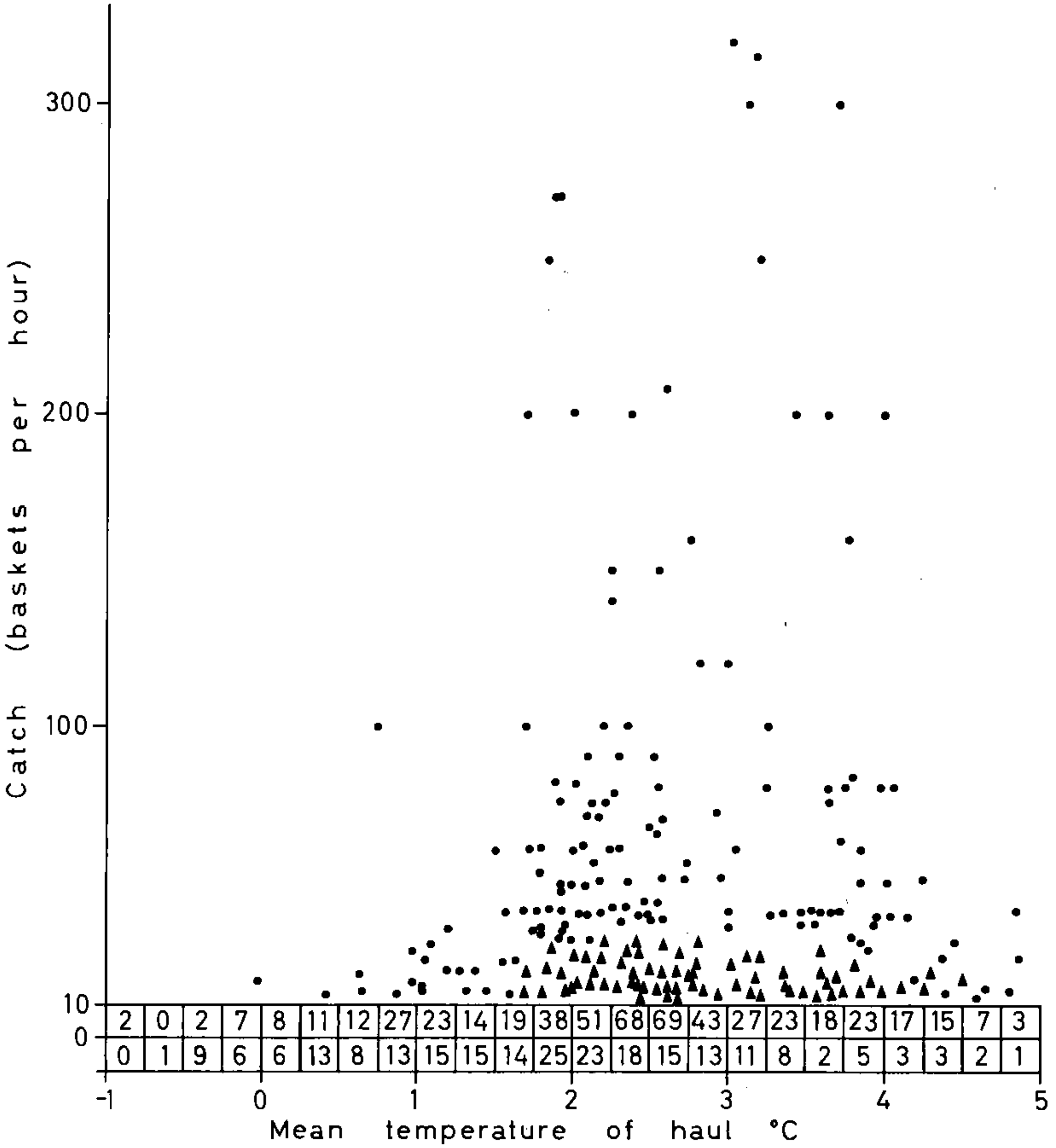

Fig. 1. Catches of cod in relation to temperature in the Barents Sea, October to June; for 1,109 trawl hauls between 1949 and 1958. The number of empty hauls for each quarter degree of temperature is shown below the zero-catch line; similarly the number of catches of cod of between 1 and 10 baskets per hour are shown above the zero-catch line. Higher catches are generally given as single points except at some of the lower levels, where it was necessary to combine similar trawl hauls in groups of three for illustration purposes; these groups are shown as small triangles.

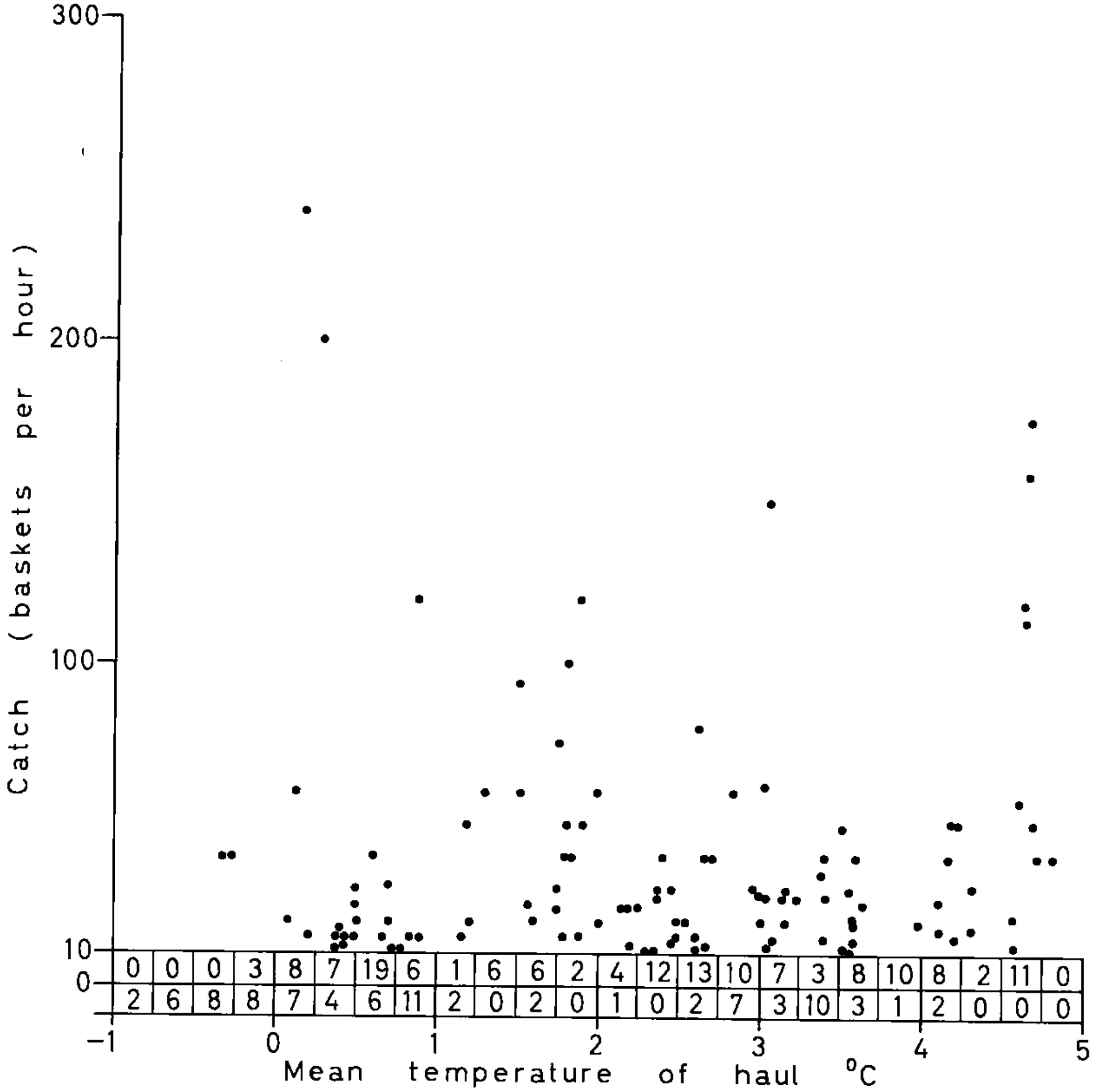

Fig. 2. Catches of cod in relation to temperature in the Barents Sea, July to September; for 342 trawl hauls between 1949 and 1958. Empty catches, and catches of 1 to 10 baskets per hour are given as numbers below and above the zero-catch line, as in Fig. 1.

analysis, shown for 342 trawl hauls in Fig. 2, in which there was no evidence of a temperature limit to catches of cod during those months, at least down to 0°C.

Although these observations on the distribution of the cod suggested a close relationship to temperature and emphasized the apparently limiting effect of temperatures below 2°C for much of the year, they did not necessarily imply active avoidance by the fish, because if the cod were associated with currents rather than with temperatures, those cod living in the waters of Atlantic origin would be found in warm waters (*i.e.* temperatures greater than 2°C), and would therefore appear to avoid the cold Arctic waters. However, in this case it might be more difficult to account for the concentration of cod at hydrographic boundaries, and for the occasional finding of very large numbers of cod in pockets of warm water almost surrounded by colder water which contained few cod (Lee, 1952; Beverton and Lee, 1964). The problem was therefore whether low temperatures exerted a direct effect upon the behaviour or physiology of the cod.

PHYSIOLOGICAL EFFECTS OF LOW TEMPERATURES IN THE BARENTS SEA

We have previously considered the problem from a physiological point of view (Woodhead and Woodhead, 1959). It seemed unlikely that the cod were aggregating about a preferred temperature of 2°C since they were frequently also caught in large numbers at higher temperatures, but not at lower ones. It appeared that the cod had reached a limit at about 2°C and it was postulated that this might be the temperature limit for some physiological process. Relatively little is known of the effects of prolonged exposure to low temperatures upon the physiological reactions of teleosts, but at an incipient lower lethal temperature death of both marine and freshwater fish appears to be associated with osmotic imbalance in the blood (Doudoroff, 1942, 1945; Brett, 1952; Wikgren, 1953), and in some species the time to death may be significantly prolonged by immersing them in a solution approximately isotonic with the blood.

If the temperature limit to the distribution of the cod in the Barents Sea acted through a similar physiological mechamism, blood taken from cod caught below the limiting temperature of 2°C would be expected to show an increased salt content. Analyses for sodium, potassium and chloride, and total salt content (estimated by freezing-point depression) were all higher, on the average, in cod caught in cold water - sometimes as much as 25% higher than in fish caught at above 2°C. Typical results for plasma analyses are shown in Fig. 3. It was considered that the values for cod caught at temperatures above 2°C represented the range for fish in a normal condition of salt balance, since no differences were found between the salt content of the blood of fish caught at 2°C and at 4° or 5°C; similar levels of sodium and potassium have also been obtained for North Sea cod at 5°C and at 12°C. But for fish caught below 2°C the high values obtained suggested that many were in a state of salt imbalance, even though many of these cod were caught at only about half a degree below 2°C and only 10% of the "cold water" fish were caught below 1°C.

Similar results were obtained on a number of cruises made between October and June. However, this did not apply during the summer months, when analyses showed that there was no difference in the salt content of the plasma taken from cod caught at above and below 2°C in July and in September, even though some of these summer fish were caught at 0°C. Typical results are shown in Fig. 4 (see note for Fig. 3).

We interpreted these results as showing that during the winter and spring temperatures below 2°C exert direct effects upon the physiology of the cod, which are reflected in the disturbance of the normal levels of salts in the blood; during the summer months of July to September low temperatures do not have these effects and the cod are able to regulate their blood salt contents normally. It is suggested that these observations on the physiology of the cod afford evidence that the apparent relationship between the distribution of the cod and low temperatures is not coincidental, and it seems likely that cod avoid water below 2°C (except during the summer months), although nothing is known of the behavioural mechanisms involved.

Our view that cod caught at below 2°C, and having a high blood salt content, were in a state of salt imbalance, has been opposed by Eliassen *et al.* (1960) who repeated the observations on the Barents Sea cod, with similar results to our own, showing a higher salt content in blood from fish caught below 2°C than from above 2°C. But they considered that the hypotonicity of the blood was largely maintained, and that the higher salt content in the blood of cod caught at temperatures below 2°C simply indicated a "small shift in osmolarity" in adapting to a lower temperature. In support of their hypothesis, Eliassen *et al.* (1960) presented data from experiments slowly acclimatising *Cottus scorpius* L., to a temperature of -1.5°C, showing that after two or three weeks at this temperature most of the fish had survived, although the plasma freezing point depression had increased by about 25% (compared with plasma from *Cottus* at 4.5°C). They considered that "some new kind of balance must have been acquired". *Cottus* is a Norwegian shore fish and it might be expected to have a greater resistance to low temperatures, but Leivestad (1964, this symposium) has now shown experimentally that cod can also tolerate prolonged exposure to a temperature of -1.4°C, and that they have an elevated blood salt content under these conditions. It is therefore quite possible that the cod in the Barents Sea may adapt to a higher level of blood salts at temperatures below 2°C, although we had previously supposed that prolonged exposure to such low temperature conditions might be lethal.

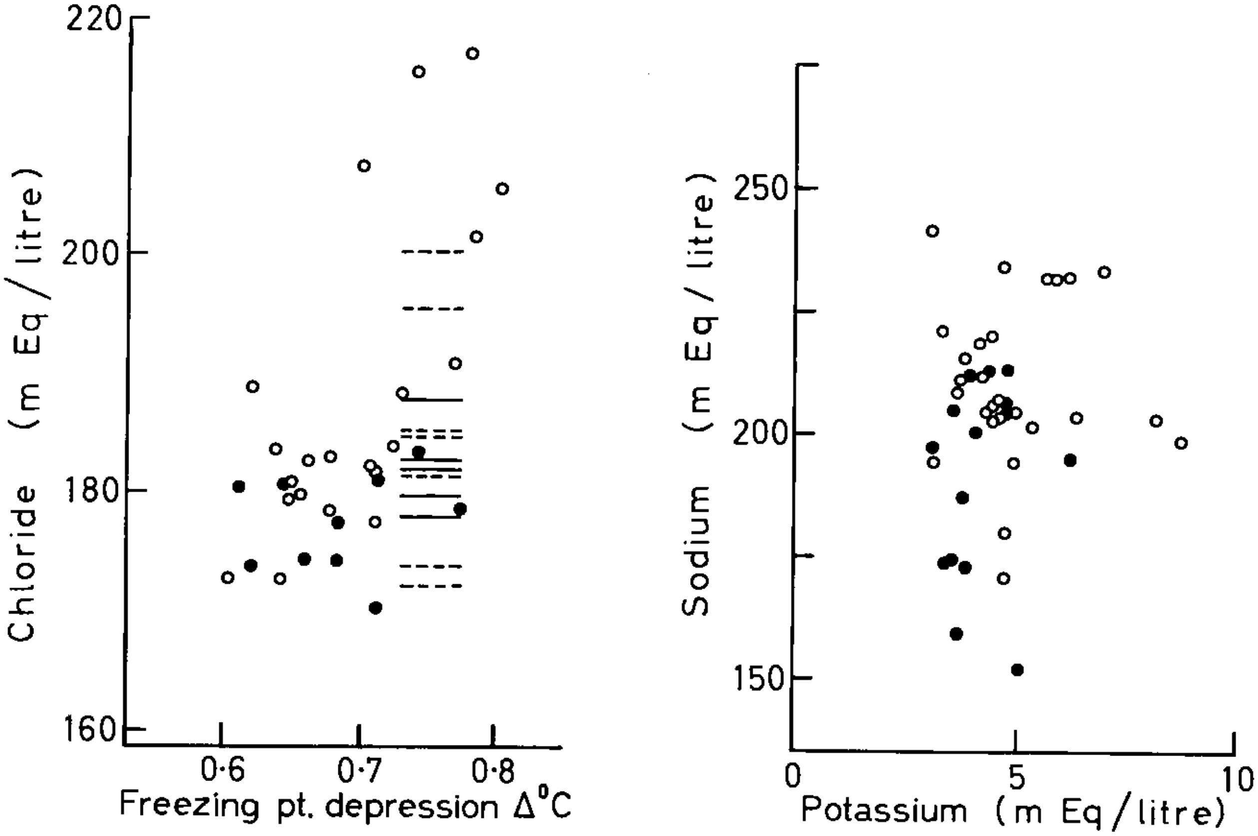

Fig. 3. Plasma salt contents of cod caught above and below 2°C in the Barents Sea, June, with cod distribution limited at 2°C.

● = Cod caught above 2°C
○ = Cod caught below 2°C
—— = Cod caught above 2°C, chloride analysis only
– – – = Cod caught below 2°C, chloride analysis only.

N.B. The values given for plasma chloride and freezing-point depression in Figs. 3 and 4 are different from those previously reported by us (Woodhead and Woodhead, 1959). It was found that the earlier results covered rather different ranges to those reported by other workers. The results were therefore re-checked against new standards and it was discovered both that the freezing point thermometer was inaccurate and that the chloride standardisation has been incorrect; the corrected values are presented here. It must be emphasised that these corrections in no way affect the arguments or conclusions previously drawn, since the discussions were based upon the direct comparison of results from cod caught at different temperatures, and the same methods and equipment were used throughout the investigation. The present corrections will allow the results to be compared with those for other fish.

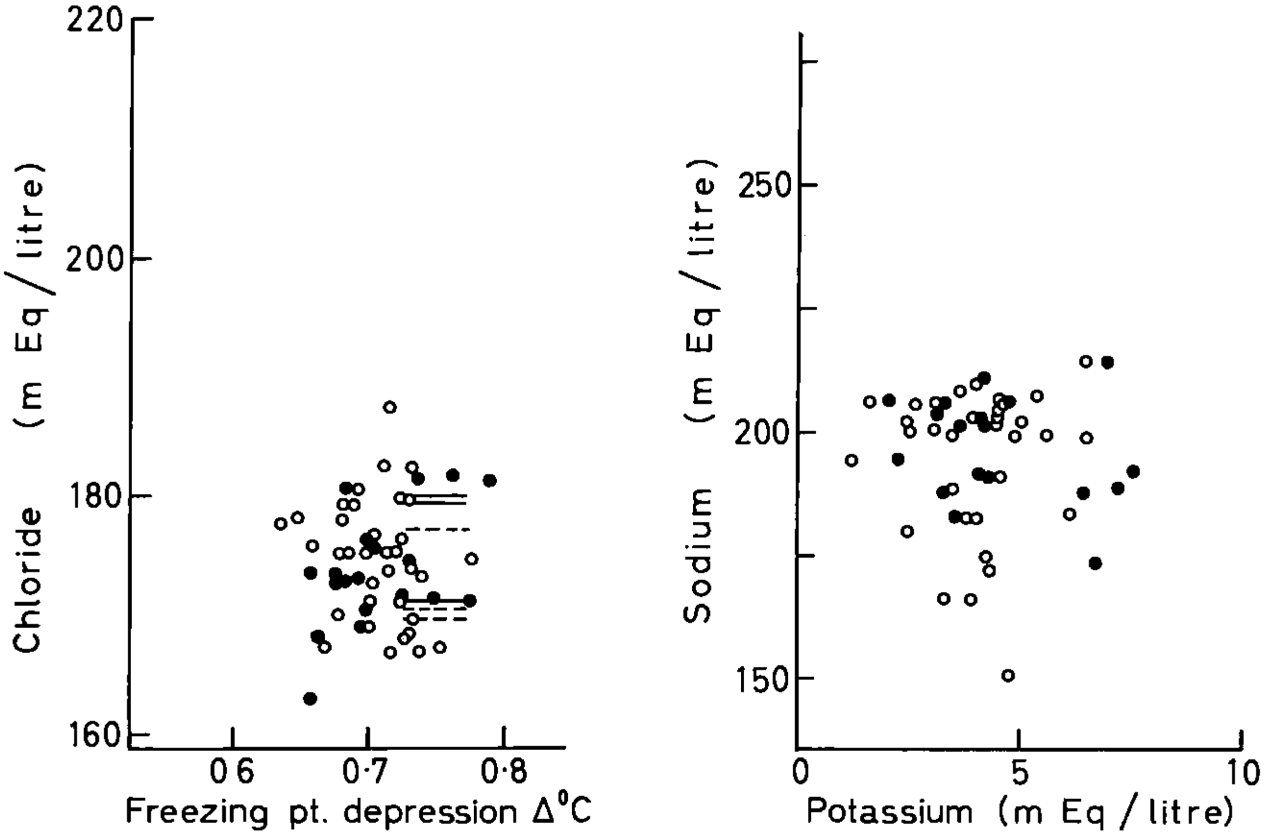

Fig. 4. Plasma salt contents of cod caught above and below 2°C in the Barents Sea, July, with cod distribution not limited at 2°C.

Symbols and note as for Fig. 3.

COD AT LOW TEMPERATURES IN THE NORTH SEA

During the severe winter of 1947 very cold waters extended out from the shallow continental coasts of the North Sea, and cod were concentrated along the edge of the cold water mass and provided large catches for trawlers (Simpson, 1953), thus reproducing conditions regularly encountered at Svalbard. In the cold winter of 1963 temperatures again fell exceptionally low, and a heavy cod fishery developed in the German Bight as the cod were concentrated by the advance of cold waters formed in the coastal areas; Danish fishermen caught about 1,000 tons of cod in this area compared with a normal catch of 200 tons (personal communication, Jørgen Møller-Christensen, Charlottenlund).

In view of our earlier studies it was considered of interest to examine the blood-salt content of cod caught at low temperatures under these exceptional conditions in the North Sea. A series of 89 serum samples was collected in March 1963 from cod caught at temperatures between 4° and -0.3°C, and in Fig. 5 the serum sodium values for these fish have been plotted against the mean temperatures of the trawl hauls.[3] For comparison with these winter serum samples the range, mean, and standard deviation for a further seventeen samples, collected in a similar manner, from North Sea cod caught in the summer at between 12° and 14.5°C have also been included in Fig. 5. It can be seen from this figure that increasing numbers of North Sea cod caught below a temperature of about

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[3] The blood was taken from the caudal artery into a chemically clean plastic tube and allowed to clot. It was intended to decant the serum for frozen storage, but due to some misunderstanding the whole clotted samples were frozen; this treatment later caused considerably haemolysis of fragmented red corpuscles on thawing, and denatured proteins were precipitated (Woodhead, 1964*b*). This regrettable error must have contributed to the wide scatter of results; nevertheless the serum samples from fish caught at different temperatures were directly comparable, since they were all treated in the same manner.

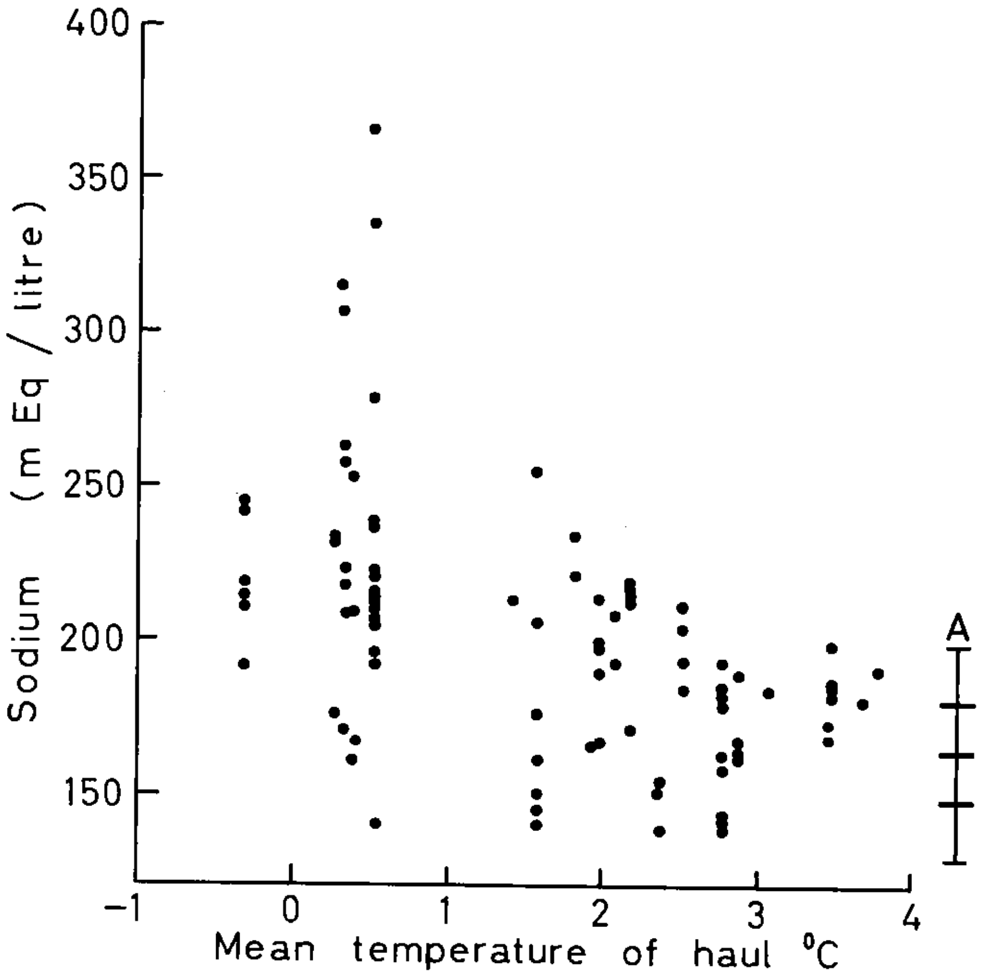

Fig. 5. Serum sodium values of cod in relation to mean temperatures of the trawl haul; North Sea in February-March 1963. The mean standard deviation, and range for 17 cod caught between 12° and 14.5°C are also shown (A).

2°C had a high serum sodium content, although the serum sodium contents of fish caught at above 2°C fell over about the same range as those of summer cod at 12° to 14.5°C. In some samples taken from cod caught at near 0°C, the sodium content of the serum was nearly double the values observed at temperatures above 2°C. These high levels appeared to be much greater than the slight shift in osmolarity suggested by Eliassen *et al.* (1960). It seemed that hypotonicity was not being maintained and that the sodium content of the blood of some of these cod was probably approaching lethal levels.

It was remarkable that during the cold winter of 1963, changes similar to those found in cod occurred in a more accentuated form in the North Sea populations of the sole, *Solea vulgaris*. Soles were heavily concentrated by the very cold waters which moved out from the shallows, and exceptionally high catches were made by trawlers (Woodhead, 1964 *c*); also, large numbers of soles were killed by cold in these areas. Analysis of serum collected from soles caught by trawl at different temperatures had increased levels of serum sodium (Woodhead, 1964 *b*). The temperature limit for normal serum sodium levels in the sole appeared to be between 3° and 4°C.

DEATH OF COD IN COLD WATERS

In our earlier paper we had assumed that if cod remained at low temperatures, below 2°C, they would finally die (except in the summer months), although this might take some time to occur. There is considerable evidence that cod are killed by low temperatures; thus Thompson (1943) reported dead cod over 20 miles in the Gulf of St. Lawrence in 1934 and concluded that the fish had been killed by encountering very cold Arctic water, and Templeman (1964, this symposium) has described similar reports for the Newfoundland area; Dannevig (1930) and Johansen (1929) have also reported the common occurrence of dead cod (and also *Pollachius pollachius* and *P. virens*) on the Scandinavian coasts during severe winters. Similarly during the winters of 1929, 1947 and 1963 large numbers of dead fish, including cod, were reported to have been killed by low temperatures in the North Sea (Lumby and Atkinson, 1929; Simpson, 1953; Woodhead, 1964*a* and *b*); in both 1947 and 1963 some dead cod were reported by trawlers in areas where temperatures did not fall below 1°C. Dannevig (1930) also reported a brief experiment in which five cod from water at 3.5°C were placed in a tank at 0.6°C which was being cooled fairly rapidly; within 20 min of being placed in the tank, when the temperature was -0.4°C, the cod appeared "agitated", and they were dead after 50 min, by which time the temperature had reached -1.0°C; however, this fall in temperature was rapid and would not allow time for acclimation, so that the results cannot be compared directly with most observations at sea.

Live cod have been frequently caught in smaller numbers many miles inside the cold water masses of the Barents Sea; often they have been in very poor condition when caught (and unfit for tagging experiments), but on other occasions they have been lively, and it is obvious that they must be able to withstand the physiological effects of low temperatures for a period of some days at least. This was investigated by an experiment in October 1957 when cod were caught and tagged in low temperatures between Hope Island and Bear Island; these fish were feeding heavily on capelin. Recaptures of the cod were all made more than one month after release and analysis of the total returns over the following six years, for fish released at different temperatures, suggested that low temperatures significantly reduced the survival rate of the cod, particularly for those fish released at 0.5°C, or less (Table 1). From this result it was thought that the tolerance of low temperatures by cod might be rather limited. In order to verify this, an experiment was made at Bear Island in October 1960 when 382 tagged cod were released at temperatures above 2°C and another 450 cod were released in areas where the bottom temperatures were about 0°C (189 of these cod were transplanted from warmer water areas before being released). The returns of tagged cod from these experiments have not been high, and the marked differences in recaptures observed in the 1957 experiment were not repeated, the recaptures of fish released above 2°C being only 26% better than for those released at 0°C (Table 2). The cod were all recaptured more than one month after release and clearly many had survived their sojourn in cold waters. However, all cod in the area were feeding heavily on small herring at that time and there was no evidence that low temperatures were limiting their distribution; many fish were feeding within the cold water masses and chemical analyses made on their blood showed only small increases in their blood salt contents. (This is discussed in more detail below). Since the cod did not appear to be critically limited by low temperatures on these occasions, the tagging experiments were perhaps not as definitive as would at first appear, and the question of prolonged survival of the cod in cold water remains open.

TABLE 1. TOTAL RECAPTURES OVER SIX YEARS FOR TAGGED COD RELEASED IN WATERS OF DIFFERENT TEMPERATURES, BEAR ISLAND AND HOPE ISLAND, OCTOBER 1957.

Temperature °C	Number released	Number recaptured	Percentage recaptured
< 0.5	138	5	3.6
0.5 to 1.0	216	19	8.8
1.0 to 2.0	131	16	12.8
> 2.0	158	21	13.3

HISTOLOGICAL CHANGES IN COD GILLS

It has been established that extrarenal excretion plays a considerable role in osmoregulation in fish (Keys, 1931, 1933; Schlieper, 1935) and that excess ions are excreted by the gills (Smith,

TABLE 2. TOTAL RECAPTURES OVER THREE YEARS FOR TAGGED COD RELEASED IN WATERS ABOVE AND BELOW 2°C, BEAR ISLAND, OCTOBER 1960.

Number released	Number recaptured	Bottom temperature (capture and release)	Distance from 2° isotherm
15	3	+ 2.45	All caught
104	11	+ 2.30	and released
97	6	+ 2.42	at temperatures
76	4	<u>c</u>. + 2.45	above 2°C
Total released above 2°C, 382; total recaptures, 24; = 6.3%			
189[a]	8	+ 0.05[a]	16 miles
131	8	0.00[b]	17 miles
24	2	-0.25 to -0.66[b]	> 14 miles
106	4	-0.40[b]	> 16 miles
Total released below 2°C, 450; total recaptures, 22; = 5.0%			

[a] Fish caught at 2.4°C and transplanted to cold water before release.

[b] Fish caught and released in water about 0°C.

1930; Keys, 1931). Specialized large acidophilic cells, the "chloride-secretory cells", located in the gills close to the afferent branchial blood vessels, were first described by Keys and Willmer (1932), who believed that these cells were responsible for salt excretion. This classical hypothesis was first challenged by Bevelander (1935, 1936) who considered these cells as mucous cells, and more recently other authors have questioned whether they have a salt-excretory function (Parry, *et al.*, 1959; Holliday and Parry, 1962; Dayle and Gorecki, 1961). Despite these objections to the "chloride-secretory cell" being a site of ionic regulation in fish, there is considerable evidence showing adaptive changes in these cells when fish are subjected to salt loading (Liu, 1942; Copeland, 1948, 1950; Getman, 1950; Morris, 1957, 1960; Colombo, 1961; Vickers, 1961), suggesting that if these cells are not the actual site of salt extraction in the gills, it is probable that they have at least associated functions.

The high salt content found in the blood of cod caught below 2°C from October to July could have been due to the primary effect of low temperatures on the mechanism of osmotic regulation, or to the secondary effect of a primary lesion elsewhere. A study was therefore made of the gills of fish from warm and cold waters, in order to ascertain whether histological differences could be observed (Woodhead and Woodhead, 1959). Examination of the gills of such cod caught at temperatures below 2°C, which were known to have abnormally high blood salt contents, showed that the numbers of "chloride-secretory cells" had increased by about four to seven times above normal. Individual "chloride-secretory cells" were almost twice as large as in cod caught at above 2°C, the cells stained more deeply and showed increased cytoplasmic granulation. From their histological appearance the chloride cells appeared to be in a state of increased secretory activity, and together with their increased numbers, these changes were interpreted as being a compensatory response to the abnormally high salt content of the blood. Since there was no evidence of breakdown or exhaustion of these cells, the primary site for the effect of low temperatures would appear to be elsewhere.

Examination of the gills of cod caught in waters above and below 2°C in the summer months of July to September did not show any increased activity of the "chloride-secretory cells" in cold-water fish, except for some fish caught at between 0.26° and -0.14°C. In the latter sample, the "chloride cells" of a few fish showed some evidence of an increase in activity, although this was not marked, and was not found in all the fish; it seemed likely that these cod were beginning to approach their summer limiting temperature just below 0°C, although serum analyses showed that they were not yet in a state of salt imbalance.

The gills of cod caught below 2°C, in a state of salt imbalance, also exhibited a marked depletion of mucus, which was almost absent from the gill leaflets; the numbers of mucous cells were reduced, and those that remained were usually atrophied and discharging their contents. Muscus depletion would permit more rapid entry of salts from the environment into the circulation, and since the gills offer the greatest area of body surface of the fish to the external environment, this increase in the osmotic load on the fish could be considerable. In this way the dislocation of mucus production, either as a primary or a secondary effect of low temperature, might well be the cause of the increased salt content found in the blood.

Marked mucus depletion was not observed in the gills of fish caught in cold water during the summer months, and analyses of the blood of these fish showed no evidence of osmotic imbalance.

DISCUSSION OF THE EFFECTS OF LOW TEMPERATURES

In considering the present data concerning effects of low temperature on the cod we conclude that, on balance, the results suggest that Barents Sea cod approach or encounter a limit to normal physiology at a temperature of about 2°C (between October and June), and that this is reflected in the increased salt content of the blood of fish caught at lower temperatures. Apparently marked increases in salt content were observed in the blood of some cod caught at only 0.5° or 1°C below this limit, whereas no such changes were found in the blood of cod caught at higher temperatures of 4° or 5°C. These effects were perhaps even more clearly shown in the large collection of sera made from North Sea cod during the winter of 1963, in which increasingly high levels of serum sodium were recorded for fish caught below approximately 2°C, but above that temperature serum sodium values fell within the same range as those for summer cod caught at between 12° and 14.5°C. The magnitude of these changes in the blood, in response to only small changes in environmental temperature, suggested to us that there was an essential change in the physiology of the cod below 2°C, rather than the hypothesis of Eliassen *et al.*(1960) that the cod had simply acquired some new level of ionic balance, dependent upon temperature. This view was also supported by the marked histological changes seen in the gills of cod caught below 2°C, suggesting that the increase in blood salts had stimulated compensatory activity in the salt excretory mechanism, presumably in an attempt to regain salt balance; such changes might not have been expected if the cod were already in a new state of ionic balance. Furthermore, the cod were apparently unaffected by the same low temperatures during the summer; there were no signs of increased secretory activity in the gill epithelium, yet the fish were able to maintain a steady level of blood salts at least down to 0°C, although on the hypothesis of Eliassen *et al.* (1960) it might have been expected that some differential in level of blood salts would still have been observed at low temperatures.

The close correspondence between the details of the seasonal distribution of the cod at low temperatures in the Barents Sea and the physiological changes observed in the fish are persuasive; from comparisons of Figs. 1 and 5 it can be seen that at temperatures at which the catches of Barents Sea cod fall rapidly, the sodium content of the blood (of North Sea cod) increases. In some cases very high levels of blood salt have been observed in cod, and we have previously assumed that prolonged exposure to low temperatures might be lethal to them as was observed for North Sea soles in 1963 (Woodhead, 1964*b*). However from the fishing data for the Barents Sea, and the results of the experiments releasing tagged cod in cold water, there can be no doubt that many cod are able to tolerate the effects of low temperatures for some time, though possibly with reduced survival. Indeed, Leivestad's experiments (1964) have demonstrated that cod may even survive supercooling for some weeks in the laboratory.

The ability to tolerate low temperatures, at least temporarily, would have obvious survival advantages for cod living in close proximity to the arctic water masses. Nevertheless the results of the various fish surveys have consistently shown that relatively few cod were normally found at low temperatures, except during the summer feeding period. We consider that the fact that cod have been shown to tolerate very low temperatures after acclimation in the laboratory need not conflict with our view that in the Barents Sea cod undergo a change in their normal physiology at low temperatures, - at about 2°C from October to June and 0°C or lower during the summer. The important questions of how long cod are able to tolerate low temperatures in the sea, and whether some form of acclimation can finally be acquired under these conditions (as occurred in Leivestad's experiments), remain at present unanswered.

SEASONAL CHANGES IN REACTIONS TO LOW TEMPERATURES

The results of the serum analyses showed that the effects of low temperature changed during the year; similar seasonal changes in physiological reactions have frequently been shown in cold-blooded vertebrates (Wells, 1935; Precht, 1955); in particular, changes have been reported in the thermal tolerance and osmoregulatory ability of fish (Koch and Heuts, 1942; Brett, 1946; Hart, 1952; Hoar, 1955; Hoar and Eales, 1963). Such variations can occur independently of seasonal changes in temperature and may be related to activity of the endocrine glands, or to the nutritional history and condition of the fish, or may be part of the growth processes. The experiments of Hoar (1955, 1956) are of some interest in this context; he showed marked seasonal variations in the ability of goldfish to withstand low temperatures although kept under constant nutritional and thermal conditions. He was able to induce similar changes experimentally by keeping goldfish under different conditions of daily illumination, and concluded that the differences in thermal tolerance were due to photoperiodically controlled changes in endocrine physiology. Possible causes of the seasonal variations observed in the Barents Sea cod are considered below.

Nutritional condition

A number of experiments have shown that thermal tolerance in fish may be increased by different diets or decreased by starvation (Ellis, 1947; Hoar and Dorchester, 1949; Hoar and Cottle, 1952; Irvine, *et al.*, 1957) and there is evidence that starvation may also affect the ability of the cod to tolerate low temperatures. On the Svalbard grounds cod frequently have little food available during the winter and spring (Trout, 1957), and are usually in very poor condition by the end of May; they are then thin and weak, the skin is flaccid, the liver small and highly discoloured with bile pigments. With the heavy summer feeding the fish regain condition rapidly; they become firm and smooth to the touch, brightly coloured and very lively when caught, and at the same time high catches of cod may begin to be made also below 2°C. It seems that the cod must begin to feed heavily before they regain the ability to withstand temperatures below 2°C. In the autumn, on the other hand, when the fish lose this ability they are in good condition after the summer feeding and may still be feeding well, so that there does not appear to be a direct link with starvation at that time; it seems likely that changes in endocrine physiology are involved.

However, on a cruise made in October 1960, large numbers of cod were found to the south of Bear Island feeding heavily, their stomachs being packed full of young herring, at temperatures both above and below 2°C. Analyses made on the blood taken from these fish showed that of 32 plasma samples taken from fish caught at 0°C, 21 had plasma sodium values which fell within the range for 12 control cod caught between 4° and 5°C. Although the complete sample of cod caught at 0°C had a significantly higher mean serum sodium content than the 12 control fish (Table 2), the mean difference between these fish and the cod from higher temperatures was less than 4%, a much smaller difference than would have been expected from our previous analyses for Barents Sea cod and for North Sea cod, at 0°C. These results were surprising when compared with similar analyses made on the blood of cod caught in October 1954 and 1955, when the cod were more obviously affected by temperatures just below 2°C, and it would seem that the cod were better able to tolerate low temperatures when feeding heavily on other fish (which would form an iso-osmotic food). If this were generally the case, the possibility would arise that cod might occur in large numbers at temperatures below 2°C at any time of the year when abundant food was available, although this laboratory has not observed this to actually occur during our own work in the Barents Sea; indeed in early spring of 1954 cod were feeding south-east of Bear Island, yet did not enter cold water although this was only a few miles away (Beverton and Lee, 1964, this symposium).

Endocrine changes

The maintenance of a constant internal ionic milieu involves the coordinated activity of many endocrine glands; several of these have been examined in the cod and are described elsewhere at this symposium (Woodhead and Woodhead, 1964). Some changes which may be related to the seasonal changes in temperature tolerance are discussed briefly here.

Gonads:

It seems unlikely that gonadal secretions, or the onset of maturation, were responsible for the seasonal changes, since the effects occurred in both immature, juveniles and maturing adult cod.

Thyroid:

Activity of the thyroid gland, and treatment with thyroid hormones and inhibitors, have been shown to significantly change the tolerance of low temperatures in goldfish (Hoar, 1955; Hoar and Eales, 1962) and it was thought likely that thyroid activity might similarly affect the physiology of the cod. The thyroid became active at the end of September, agreeing well with the development of the 2°C limit in October, but thyroid activity had declined in most immature cod in February, and in adults by the end of March (Woodhead, A.D. 1959), although the cod did not regain their ability to enter cold water until some two or three months later. (However, in the spring starvation may be a complicating factor, as discussed above.) Thyroids from fish caught at above and below 2°C showed no significant differences in histological appearance and we previously concluded that the results "neither prove nor disprove that the thyroid gland itself is directly involved in the changes in the resistance of cod to low temperatures" (Woodhead and Woodhead, 1959).

Interrenals:

Histological evidence of secretory activity became apparent in November, some weeks after the development of the 2°C limit. This would appear to rule out interrenal activity as controlling the seasonal changes. However, the onset of the 2°C limit may be less precisely timed than previously assumed (as shown by the cod feeding at 0°C in October, 1960, discussed above). Interrenal activity continued into the spring and appeared to be associated with poor feeding or starvation, which was certainly a complicating factor in the seasonal changes. Both cortisol and deoxycorticosterone may strongly affect the rate of sodium excretion through the gills of freshwater fish under a sodium load (Holmes, 1959), and the interrenal might therefore be involved in the changes observed in the cod; more critical evidence may be obtained when the interrenal analysis is completed.

From these results it can be seen that we have not found a close correspondence between the period of secretory activity of a particular endocrine gland and the seasonal changes in thermal tolerance in the cod. Perhaps this is not surprising since endocrine regulation of physiological changes is frequently complex and the integrated activity of several glands may be involved. That endocrine changes occur in cod during the autumn, at about the same time as the changes in the effects of low temperatures, is demonstrated by the activity of the thyroid gland (and of the gonads in adult fish), but it seems likely that the final understanding of which gland, or glands, are responsible for such changes can finally only come from experimental studies in the laboratory.

EFFECTS OF LOW TEMPERATURES UPON O-GROUP AND I-GROUP COD

Since low temperatures may have a limiting effect upon immature and adult cod, it seemed quite probable that they may have similar effects upon the cod larvae and O-group fish. Several authors have suggested that the recent climatic warming in northern latitudes has been accompanied by an increase in size of cod stocks, both in the Barents Sea and at Greenland (Tåning, 1953; Lee, 1956; Hill and Lee, 1957), and this might be accounted for in part by there being a greater area of the shelf feeding grounds over which temperatures were above the limiting threshold of the young cod, allowing successful settlement from the pelagic phase to the bottom, and increased survival. Tåning (1953) and Jensen (1939) have reviewed evidence for higher sea temperatures at West Greenland, and Blacker (1957) and Nesis (1960) have produced biological evidence which strongly suggests that warm Atlantic water now covers much greater areas of the banks in the Barents Sea.

The observations of Hermann at Greenland (Hachey, *et al.*, 1954; Hermann, *et al.*, 1964, this symposium) have shown that in years when temperatures fell below 1.8°C on the Fyllas Bank (where cod larvae were found) only poor year-classes survived, but in years of higher temperatures much stronger year-classes resulted. However catches of large numbers of very small cod have been made at sub-zero temperatures off Newfoundland (Templeman and Fleming, 1964, this symposium).

To investigate the temperature tolerance of young cod, blood analyses were made on O-group and I-group cod caught in a shrimp-mesh covered trawl fished south of Bear Island at depths of about 200 m in October 1960. (This heavy gear obviously is poor for capturing small fish for physiological work, since they are easily damaged.) Analyses for sodium content in haemolysed whole-blood samples showed no significant differences in the levels of sodium in the blood of either O-group or I-group fish taken at 0°C, when compared with control fish taken at about 2.5°C (Table 3), suggesting that

TABLE 3. PLASMA SODIUM CONTENT FOR FEEDING COD[a] CAUGHT AT ABOVE AND BELOW 2°C, BEAR ISLAND, OCTOBER 1960.

Temperature	Plasma Sodium (m Eq./litre)	Significance p
12 fish; 4 to 5°C	210.8 ± 5.8	Significant difference p =< 0.01
32 fish; 0°C	217.5 ± 7.2	

[a] All cod (above and below 2°C) were immature fish, 50 to 80 cm long.

TABLE 4. BLOOD SODIUM CONTENT IN 0-GROUP AND I-GROUP COD FROM LOW TEMPERATURES BEAR ISLAND, OCTOBER 1961

Group	Number of fish	Blood Sodium m Equivs	Significance p
0-group, 2.5°C	26	211.2± 28.7	Not significant
0-group, 0°C	23	216.3± 24.5	p= approx. 0.5
I-group, 2.5°C	14	195.6± 27.3	Not significant
I-group, 0°C	18	192.4± 25.1	p= approx. 0.5

the small cod were able to tolerate the low temperatures. However, we would emphasize that our analyses were made on only the one cruise, and on the same cruise only small differences were observed in blood salts of adult cod caught above and below 2°C; the evidence for low temperature tolerance would have been more convincing had it been shown that the older cod were affected by temperatures when the young fish were unaffected. We present these results as being of considerable interest, but would hesitate to draw far-reaching conclusions concerning post-larval survival and distribution until more work has been done.

REFERENCES

BEVELANDER, G. 1935. A comparative study of the branchial epithelium in fishes, with special reference to extrarenal excretion. *J. Morph.*, 57: 335-348.

1936. Branchial glands in fishes. *J. Morph.*, 39: 215-222.

BEVERTON, R.J.H., and A.J. LEE. 1964. The influence of hydrographic and other factors on the distribution of cod on the Spitsbergen shelf. *This symposium, Contribution No. A-14.*

BLACKER, R.W. 1957. Benthic animals as indicators of hydrographic conditions and climatic changes in Svalbard Waters. *Fish. Invest.*, Lond., Ser. 2, 20 (10): 1-49.

BRETT, J.R. 1946. Rate of gain of heat tolerance in goldfish, *Carassius auratus*. *Univ. Toronto Stud.*, Biol. Ser., No. 53 (*Pub. Ont. Fish. Res. Lab.*, No. 64): 9-28.

1952. Temperature tolerance in young Pacific Salmon, genus *Oncorhynchus*. *J. Fish. Res. Bd. Canada*, 9: 265-323.

COLOMBO, G. 1961. Chloride-secreting cells in the gills of European eels. *Nature,* Lond., 190: 101.

COPELAND, D.E. 1948. The cytology of the secretory cells of *Fundulus*. *J. Morph.,* 82: 201.

1950. Adaptive behaviour of the chloride cell in the gill of *Fundulus heteroclitus*. *J. Morph.,* 87: 369-376.

CUSHING, D.H. 1959. *In*: Richardson *et al*. Echo sounding experiments in the Barents Sea. *Fish. Invest.* Lond., Ser. 2, 22 (9): 48-55.

DANNEVIG, A. 1930. The propagation of our common fishes during the cold winter 1924. *Rep. Norweg. Fish. Invest.,* 3 (10): 1-133.

DOUDOROFF, P. 1942. The resistance and acclimatization of marine fishes to temperature changes. I. Experiments with *Girella nigricans* (Ayres). *Biol. Bull.,*Woods Hole, 83: 219-244.

1945. The resistance and acclimatization of marine fishes to temperature changes. II. Experiments with *Fundulus* and *Atherinops*. *Biol. Bull.,* Woods Hole, 88: 194-206.

DOYLE, W.L. and D. GORECKI. 1961. The so-called chloride cell of the fish gill. *Physiol. Zoöl.,* 34: 81-85.

ELIASSEN, E., H. LEIVESTAD, and D. MØLLER. 1960. The effect of low temperatures on the freezing point of plasma and on the potassium/sodium ratio in the muscles of some boreal and subarctic fishes. *Årb. Univ. Bergen, Mat-Naturv. Ser.,* Nr. 14: 1-24.

ELLIS, M.M. 1947. Temperature and fish. Fish. Leafl. Wash. No. 221: 1-3.

GETMAN, H.C. 1950. Adaptive changes in the chloride cells of *Anguilla rostrata*. *Biol. Bull.,* Woods Hole, 99: 439-445.

GRAHAM, M., G.C. TROUT, R.J.H. BEVERTON, J. CORLETT, A.J. LEE, and R.W. BLACKER. 1954. Report on research from the *Ernest Holt* into the fishery near Bear Island, 1949 and 1950. *Fish. Invest.,* Lond., Ser. 2, 18 (3): 1-87.

HACHEY, H.B., F. HERMANN, and N.B. BAILEY. 1954. The waters of the ICNAF convention area. *Annu. Proc . int. Comm. Northw. Atlant. Fish.,* 4: 67-102.

HART, J.S. 1952. Geographic variations of some physiological and morphological characters in certain freshwater fish. *Univ. Toronto Stud.,* Biol. Ser., No. 60. (*Pub. Ont. Fish. Res. Lab.,* No. 72): 1-79.

HERMAN, F., P.M. HANSEN, and S.V. HORSTED. 1964. The effect of temperature and current on the distribution and survival of cod larvae at West Greenland. *This symposium Contribution No. B-14.*

HILL, H.W., and A.J. LEE. 1957. The effect of wind on water transport in the region of the Bear Island fishery. *Proc. Roy. Soc.* (B), 148: 104-116.

HOAR, W.S. 1955. Seasonal variations in the resistance of goldfish to temperature. *Trans. Roy. Soc. Can.* (5) 49: 25-34.

1956. Photoperiodism and thermal resistance of goldfish. *Nature,* Lond. 178: 364-5.

HOAR, W.S. and M.R. COTTLE. 1952. Dietary fat and temperature tolerance of goldfish. *Canad. J. Zool.* 30: 41-48.

HOAR, W.S. and J.E.C. DORCHESTER. 1949. The effect of dietary fat on the heat tolerance of goldfish (*Carassius auratus*). *Canad. J. Res.,* D, 27: 85-91.

HOAR, W.S., and J.G. EALES, 1963. The thyroid gland and low-temperature resistance of goldfish. *Canad. J. Zool.*, 41: 653-669.

HOLLIDAY, F.G.T. and G. PARRY. 1962. Electron-microscopic studies of the acidophil cells in the gills and pseudobranchs of fish. *Nature,* Lond., 193: 192.

HOLMES, W.N. 1959. Studies on the hormonal control of sodium metabolism in the rainbow trout (*Salmo gairdneri*). *Acta endocr. Kbh.* 31: 587-602.

IRVINE, D.G., K. NEWMAN, and W.S. HOAR. 1957. Effects of dietary phospholipid and cholesterol on the temperature resistance of goldfish. *Canad. J. Zool.,* 35: 691-709.

JENSEN, Ad. S. 1939. Concerning a change in climate during recent decades in the Arctic and Sub-arctic regions, etc. *Biol. Medd. Kbh.* 14: 1-75.

JOHANSEN, A.C. 1929. Mortalities amongst porpoises, fish and the larger crustaceans in the waters around Denmark in severe winters. *Rep. Danish biol. Sta.,* 35: 63-97.

KEYS, A.B. 1931. Chloride and water secretion and absorption by the gills of the eel. *Z. vergl. Physiol.,* 15: 364-388.

1933. A mechanism of adaptation to varying salinity in the common eel and the general problem of osmotic regulation in fishes. *Proc. roy. Soc.* (B), 112: 184-199.

KEYS, A.B., and E.N. WILLMER. 1932. Chloride-secreting cells in the gills of fishes with special reference to the common eel. *J. Physiol.,* 76: 368-378.

KOCH, H.J., and M.J. HEUTS. 1942. Influence de l'hormone thyroidienne sur la regulation osmotique chez, *Gasterosteus aculeatus* L., forma *gymnurus* Cuv. *Ann. Soc. Roy. Zool. Belg.,* 73: 165-172.

LEE, A.J. 1952. The influence of hydrography on the Bear Island cod fishery. *Rapp. Cons. Explor. Mer,* 131, 74-102.

1956. British fishery research in the Barents Sea. *Polar Rec.,* 8 (53): 109-117.

1959. The influence of environmental factors on the Arcto-Norwegian cod stocks. *Internat. Oceanogr. Cong.,* Washington. Ed. M. Sears, 243-244.

1963. The hydrography of the European Arctic and Subarctic Seas. *Oceanogr. Mar. Biol. Ann. Rev.,* 1: 47-76.

LEIVESTAD, H. 1964. Supercooling and osmoregulation in teleosts of the subarctic and arctic region. *This symposium, Contribution No. F-9.*

LIU, C.K. 1942. Osmotic regulation and "chloride-secretory cells" in the Paradis fish, *Macropodus opercularis. Sinensia,* 13: 15-20.

LUMBY, J.R., and G.T. ATKINSON. 1929. On the unusual mortality amongst fish during March and April, 1929, in the North Sea. *J. Cons.,* 4: 309-332.

MASLOV, N.A. 1944. The bottom fishes of the Barents Sea and their fisheries. *Trudy PINRO,* 8: 3-186. (In Russian).

1960. Soviet investigations on the biology of cod and other demersal fish in the Barents Sea. *Soviet Fish. Invest. North European Seas,* Moscow. 185-231.

MIDDTUN, L. 1959. The distribution of cod-haddock in the central and south-eastern Barents Sea, September/October, 1958. *Rapp. Cons. Explor. Mer,* 149: 210-211.

MIRONOVA, N.V. 1958. The distribution of cod. *In: "Regular features in the concentrations and migrations of commercial fishes in the Murman coast zone, and their relation to biological, hydrological and hydrochemical processes".* Soviet Acad. Sci. Press., Moscow, 234-253.

MORRIS, R. 1957. Some aspects of the structure and cytology of the gills of *Lampetra fluviatilis*. *Quart. J. micr. Sci.*, 98: 473-485.

1960. General problems of osmoregulation, with special reference to cyclostomes. *Symp. Zool. Soc. Lond.*, No. 1: 1-16. Edited by I.C. Jones.

NESIS, K.N. 1960. Changes in the Barents Sea bottom fauna under the influence of fluctuations in the hydrological regime. *Soviet Fish. Invest. North European Seas*, Moscow, 129-138.

PARRY, G., F.G.T. HOLLIDAY, and J.H.S. BLAXTER. 1959. Chloride-secretory cells in the gills of teleosts. *Nature*, Lond., 183: 1248-1249.

PRECHT, H. 1955. Wechselwarme Tiere und Pflanzen. *In*: Precht, H., Christophersen, J. and Hensel, H. *Temperatur und Leben*, Springer Verlag. Berlin, 1-177.

SAETERSDAL, G. 1956. Fisheries Research in northern waters - study items and results. *Forskning og Fiske*, Nr. 1: 1-23. (In Norwegian).

SCHLIEPER, C. 1935. Osmotic regulation in aquatic animals. *Biol. Rev.*, 10: 334-359.

SIMPSON, A.C. 1953. Some observations on the mortality of fish and the distribution of plankton in the southern North Sea during the cold winter of 1946-47. *J. Cons.*, 19: 150-177.

SMITH, H.W. 1930. The absorption and excretion of water and salts by marine teleosts. *Amer. J. Physiol.*, 93: 480-505.

TÅNING, A.C. 1953. Long term changes in hydrography and fluctuations in fish stocks. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 3: 69-77.

TEMPLEMAN, W. 1964. Mass mortalities of marine fishes in the Newfoundland area presumably due to low temperatures. *This symposium, Contribution No. A-5.*

TEMPLEMAN, W. and A.M. FLEMING, 1964. Cod and low temperatures in St. Mary's Bay, Newfoundland. *This symposium, Contribution No. A-4.*

THOMPSON, H. 1943. A biological and economic study of cod, *Gadus callarias* L., in the Newfoundland area. *Res. Bull. Div. Fish. Res. Newfoundland*, 14: 1-160.

TROUT, G.C. 1957. The Bear Island cod. Migrations and movements. *Fish. Invest.* Lond., Ser. 2, 21 (6): 1-51.

VICKERS, T. 1961. A study of the so-called "chloride-secretory" cells of the gills of Teleosts. *Quart. J. micr. Sci.*, 102: 507-518.

WELLS, N.A. 1935. Variations in the respiratory metabolism of the Pacific killifish, *Fundulus parvipinnis*, due to size, season and continued constant temperature. *Physiol. Zool.*, 8: 318-356.

WIKGREN, B.J. 1953. Osmotic regulation in some aquatic animals with special reference to the influence of temperature. *Acta zool. fenn.*, No. 71: 1-102.

WOODHEAD, A.D. 1959. Variations in the activity of the thyroid gland of the cod, *Gadus callarias* L., in relation to its migrations in the Barents Sea. I. Seasonal changes. *J. Mar. biol. Ass., U.K.*, 38: 407-415.

WOODHEAD, A.D., and P.M.J. WOODHEAD, 1964. Seasonal changes in the physiology of the Barents Sea cod, *Gadus morhua* L., in relation to its environment. I: Endocrine changes particularly affecting migration and maturation. *This symposium, Contribution No. F-6A.*

WOODHEAD, P.M.J. 1964*a*. The death of fish and sublittoral fauna in the North Sea and the English Channel during the winter of 1963. *J. anim. Ecol.*, 33: 169-173.

1964*b*. The death of North Sea fish during the winter of 1963, particularly with reference to the Sole, *Solea vulgaris*. *Wiss. Meeresuntersuch. abt. Helgoland* (in press).

1964*c*. Changes in the behaviour of the Sole, *Solea vulgaris*, during cold winters and the relation between the winter catch and sea temperatures. *Wiss. Meeresuntersuch. abt. Helgoland* (in press).

WOODHEAD, P.M.J., and A.D. WOODHEAD. 1959. The effect of low temperatures on the physiology and distribution of the cod, *Gadus morhua*, L. in the Barents Sea. *Proc. zool. Soc. Lond.*, 133: 181-199.

F-7

FACTORS DETERMINING OR LIMITING THE PHYSIOLOGICAL REACTION OF HERRING TO ENVIRONMENTAL CHANGES

By

T.D. Iles[1]

ABSTRACT

The variation in the seasonal timing of zooplankton production over the range of herring stocks is much smaller than that of the spawning times and there can be no simple relationship between food availability, representing a variable environmental factor and the seasonal cycles of growth maturation and spawning.

Data from North Shields herring indicate that rapid seasonal somatic growth precedes rapid gonad growth and from other stocks and for sprat, that these processes do not go on at the same time of year. The Shields data confirms Holliday's work by demonstrating the acceleration of the gonad growth resulting from pituitary gonadotrophic activity, and the prolongation of stage V in some herring stocks indicates that the timing of the production of luteinising hormone controlling ovulation may differ considerably in its relation to the timing of the gonadotrophic activity of the pituitary. It follows that the reaction to changes in environmental factors, which might affect growth, maturation and spawning, may depend on the way in which they are mediated by the hormonal cycles.

The use of partial condition factors in defining seasonal fat, water and protein cycles, reveals new information and the significance of the fat cycles in these terms is discussed. It is suggested that in Shields herring an earlier physiological stage during which protein provides energy for all purposes, coincides with that of rapid food intake and somatic growth. Later the fat reserves are mobilised to provide energy and the protein is conserved to allow overwintering. This physiological arrangement is part of the adaptation to feeding on zooplankton, which is available in abundance for only a short period each year.

THE ORGANISATION OF GONAD AND SOMATIC GROWTH IN HERRING

The changes in the environments of the herring that occur during the course of a single year are greater than the changes for the same season from year to year, for almost all of the environmental factors. During the first 50 years of this century, for instance, the seasonal temperature range in the North Sea, about 9°C, was more than twice the range of either the winter minimum or the summer maximum (ICES tables 1962), and similar conclusions could be drawn for such changes in food abundance and many other factors both physical and biotic. A particular herring stock reflects its adaptation to the seasonal changes by undergoing parallel or related physiological changes, indicated by variation in feeding and growth rates and in maturation, migration and spawning cycles; hence, the study of the physiological processes underlying these cycles is, essentially, a study in the adaptation of the population to its environment.

In the last decade marked changes have been recorded in important European herring stocks, involving, for example, increases of growth rate of the East Anglian herring, and in the Norwegian winter herring changes in the mean spawning time and the location of spawning grounds, in both cases accompanied by decreases in stock abundance.

It is unlikely that the biological changes associated with these events can be unequivocally correlated with environmental factors until more is known of the organisation and control of the relevant seasonal cycles, and as herring fisheries are typically restricted to short periods during the year the amount of detailed knowledge of the timing of quite basic processes, such as somatic growth or gonad maturation, even in important stocks, is not great.

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One of the most important seasonal variables is that of available food; the zooplankton on which herring feed is available reliably and in quantity for only a relatively short time of the year and its abundance is determined by the primary production cycles. The timing of these cycles varies over the whole range of the Atlantic herring (Colebrook and Robinson, 1960), but although this variation is, between extremes, quite large, it is small compared to the range of spawning times shown by the different spawning communities. Spawning herring can be found at any time of the year and moreover at any time relative to the zooplankton production cycle, either before it (for example the Channel spawners or the Norwegian spring spawners), during it (Icelandic summer spawners, Jakobsson, 1962) and Onega herring,(Mikhailovskaya, 1957) or after it (Dogger autumn spawners of central North Sea). It follows that no simple relationship exists in the herring between feeding and the time of spawning. If we consider somatic growth we find for Norwegian immature herring that seasonal somatic growth begins at a time when the temperature, although beginning to rise, is near the seasonal minimum, and that the rate of growth declines sharply before the highest seasonal temperature is reached (Lea, 1911). This is indicated also for maturing herring of the North Sea in Fig. 1 below, so that we can assume also that somatic growth and environmental temperature are not simply related.

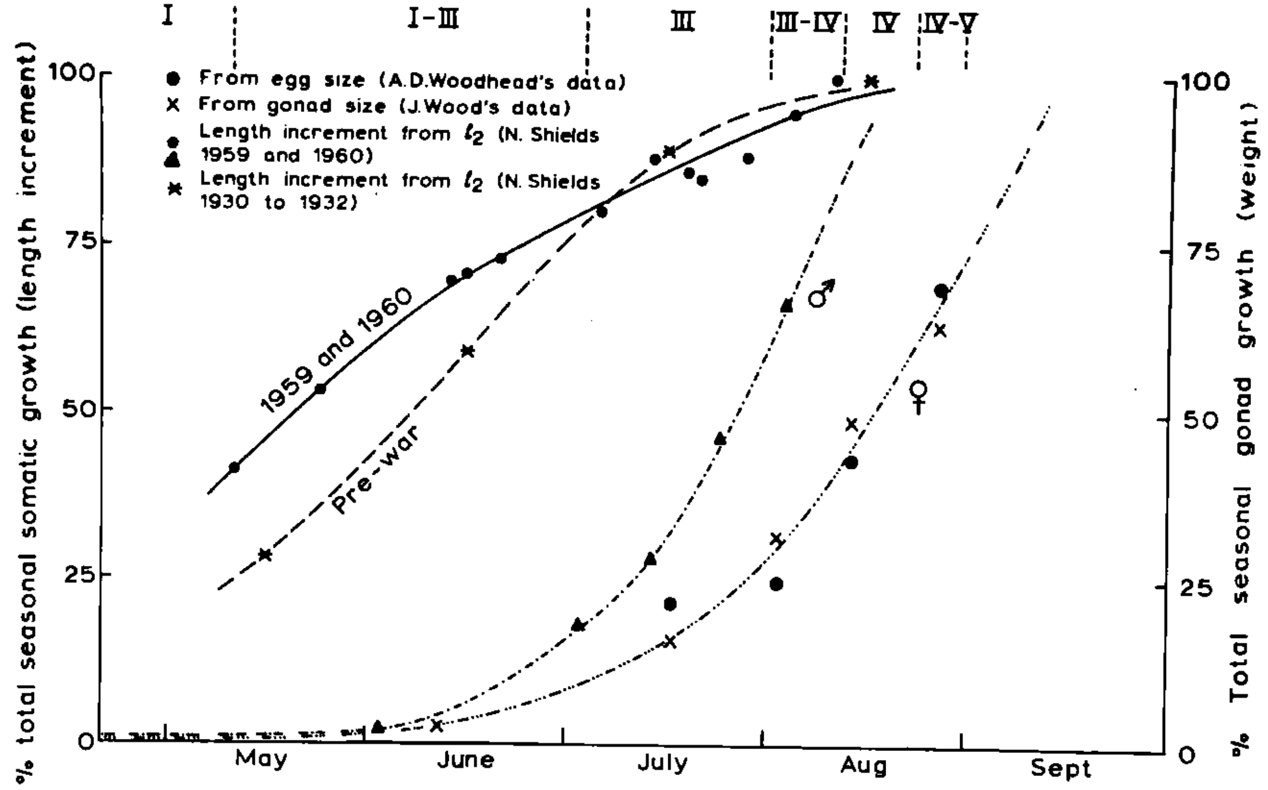

Fig. 1. Seasonal gonad and somatic growth, North Shields herring.

Recent work at the Lowestoft laboratory has concentrated on the time relationships between somatic growth and gonad maturation in relation to feeding and to spawning times, and Fig. 1 illustrates the somatic and gonad growth cycles for herring caught in the North Shields area from May to September in the 1950's.

The somatic growth was determined by back calculation on scale readings (Lea, 1911) and gonad growth from data on the distribution of maturation stages (Iles, 1964) converted to durations for individual stages. The gonad data for males and females have been dealt with separately to illustrate the growth differences between the sexes first suggested by Holliday (1962).

The point to be emphasized is that the period of rapid somatic growth does not coincide with that of rapid gonad growth, and Fig. 2 (compiled from data available for the 1920's and 1930's when the growth of the North Sea herring differed significantly from that found in the 1950's) gives substantially the same picture. (The data in Fig. 2 are based on Hodgson (1924) and on maturation data for the period 1924-28 collected at the Dove Marine Laboratory at Cullercoats and kindly made available by the Director).

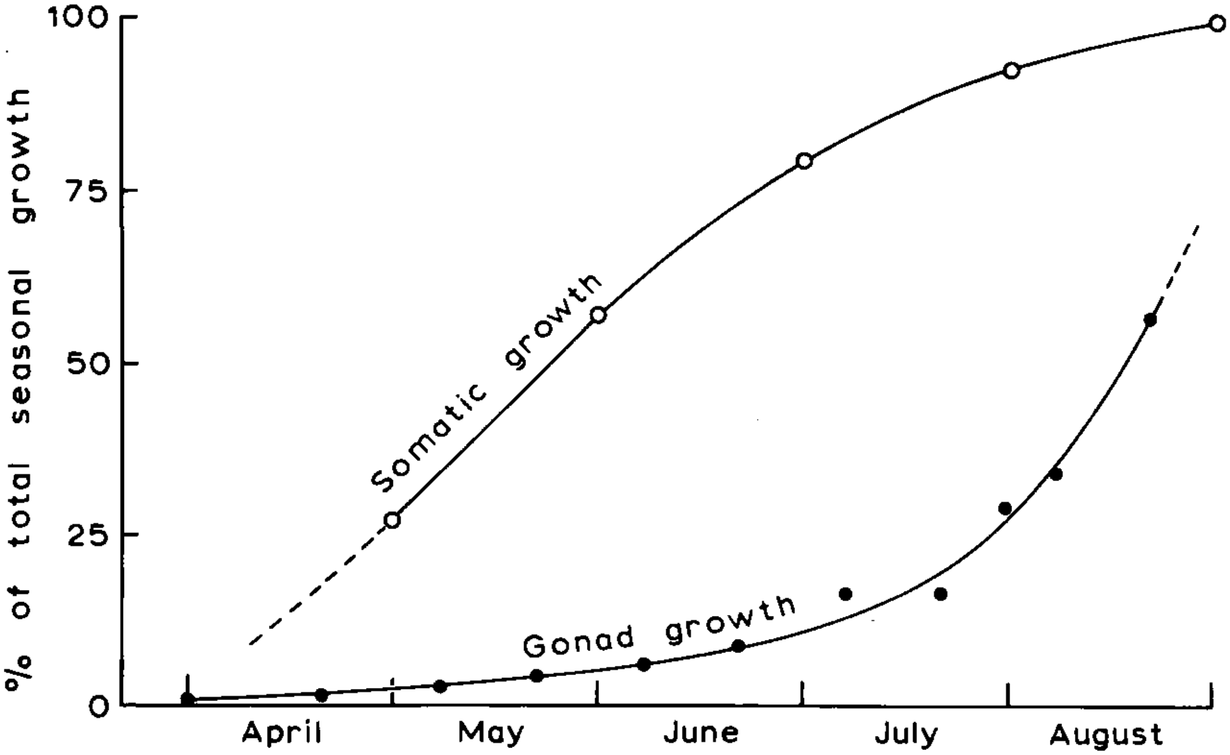

Fig. 2. Seasonal gonad and somatic growth, pre-war period.

Comparative data for other herring stocks are difficult to find, but we do have the observations of Mikhailovskaya (1957) on the herring of the Gulf of Onega, which spawn from late May to July. Mikhailovskaya states that the herring begin to feed at about the end of April, which coincides with a time of "intensive development of the gonads", and do not feed during the spawning period. It is not until July and August, after spawning has taken place, that the zone of growth is observed on the scale, this coinciding with a period of intensive feeding. Elwertowski and Maciejczyk (1960), in their study of the adult sprat of the Gdansk Bay, state that feeding in the spring (May and June) is "rather intensive" but is not "accompanied by an increase in length" due to the fact that "the sprat organism is developing the reproductive organs exclusively". The end of the spawning period in July is marked by the beginning of an intensive feeding period, as a result of which the body length increases and fat is accumulated.

Now, Holliday (1960*a*) distinguished two phases in the maturation of the herring gonad, the first being dependent on adequate feeding conditions and occurring in the absence of pituitary gonadotrophic activity, and a later stage (during which most of the increase in gonad size occurs) coinciding with increased pituitary gonadotrophic activity. These two phases are demonstrated in Fig. 1, which also confirms Holliday's suggestion that the effect of the pituitary gonadot ophin is to accelerate gonad growth. It would appear therefore, from Fig. 1 and 2 and the observations on the Onega herring and Gdansk sprat, that rapid somatic growth and pituitary-stimulated gonad growth do not usually go on simultaneously, and if it be accepted that somatic growth in fishes generally is controlled by a pituitary growth hormone (Holliday, this symposium) then it must be accepted also that differences between herring stocks in the seasonal timing of somatic and gonad growth can be related to and influenced by differences in the cycles of production of two distinct pituitary hormones. Any change in growth rate or in maturation rate resulting from environmental changes must therefore be effected via changes in two pituitary hormonal cycles which, although probably interconnected, do not necessarily react in the same way at any one time.

The position is complicated by the demonstration (Holliday, 1960 *b*) that the process of ovulation in the female herring, and the shedding of gametes for both sexes, is under the control of another pituitary hormone, the luteinising hormone, and it is well established for fishes in general that the release of this hormone may depend on the action of environmental factors other than those ultimately responsible for the production of gonadotrophic hormone. That this applies to herring is indicated by the fact that, in some herring stocks, stage V, at which the gonad has been provided with all the necessary proteinaceous materials and at which maturation in terms of gonad growth can be said to be completed, may be prolonged and therefore not followed immediately by spawning. This applies to the Manx stock of autumn spawners, for instance, and also to the winter spawners sampled in the East Anglian fishery (Iles, 1964). In one respect at least it probably applies to most herring stocks, for Jakobsson (1962) shows that in both Icelandic spring and summer spawners the males mature earlier than the females; this is also shown by the data presented by Bowers (1963) for the West Coast Manx herring. This phenomenon is demonstrated quantitatively in Fig. 1 and it must be accepted therefore that the time relationships between maturation and spawning differ between males and females for many and perhaps all herring, in that maturation takes place at different times but spawning, presumably, is synchronised.

These considerations strongly suggest that changes in growth rates, maturation rates and spawning times in herring, resulting from environmental changes, are mediated through complex hormonal cycles and that in any given stock the different physiological processes may, at any particular time of year, be "sensitised" to a greater or lesser degree and therefore be more or less able to react. It is possible, for instance, to postulate that in a particular year the spring outburst of zooplankton in May would be markedly greater than usual, both for the Onega herring and for the Shields herring. It is unlikely that the physiological reaction would be the same in both stocks as far as the growth and maturation cycles are concerned.

GROWTH AND FAT CYCLES IN HERRING

A particular seasonal cycle in herring which has been investigated in some detail is the fat cycle, and Wood (1958) lists the important work of the last 50 years or so.

The ability to store fat in large quantity to tide the herring over the long period when food is not available is a necessary part of the adaptation to feeding on zooplankton. Wood (1958) describes fat cycles for North Sea herring and shows the marked seasonal variation in percentage fat in whole herring, rising to a peak by the end of June and falling thereafter to low values during the winter; the overall relationship between the fat cycle and the feeding cycle is close (Savage, 1931 and 1937 for the timing of the feeding cycle in North Shields herring).

Many workers have drawn attention to the inter-relationships in herring between fat and water percentages, Brandes and Dietrich (1953), for instance, recording an inverse relationship with a high degree of correlation for herring muscle; and Wood (unpublished data), for whole herring, finds correlation coefficients as high as 0.997. Blaxter and Holliday (1963) suggest that this linear relationship is in fact artificial, resulting from the expression of fat and water content as percentages. Wood's extensive original data are available and they have been re-calculated to yield not percentages, but what may be called *partial condition factors* for fat and water, by expressing the weight of each of the two constituents as a proportion of the cube of the length. These partial condition factors are in fact concentrations and their use as indicators of fat and water content (and by implication, of gross protein content) has revealed interesting information concerning the physiological changes occurring seasonally in herring. Thus although during May and June the *water percentage* of individual herring falls from about 78 to below 60%, the *water condition factor* if anything rises. The "water" content of herring therefore changes seasonally much less than is indicated by percentages. Again, and comparing the cycles for different years, there is relatively little difference between the maximum fat percentages recorded. For herring caught in the North Shields area, for example, 1956 gives a near maximum *fat percentage* in July of 22.3% and 1957 one of 23.58%, a relative increase of rather less than 6%. The difference in *fat condition factor* for these years is much greater, the value for 1956 being 187 units and for 1957, 232 units, an increase of 22%. The importance of these observations lies in the fact that 1956 was, for the herring investigated, a relatively poor year for growth, whereas 1957 was a relatively good one (Burd and Cushing, 1962), a fact not reflected obviously in the fat percentage cycle but shown clearly in the condition factor cycle. Dementjeva (1956) dealing with growth of the salaka (the Baltic herring), which varies widely from year to year, comments on the poor growth of 1952, although her figure 6 indicates that the maximum fat percentage was as high as that of 1953. It is important, therefore, in describing seasonal changes in the composition of herring, to use units which reflect quantitative and not proportional changes.

It was consideration of facts such as these that led to the suggestion (Iles, in preparation[2]) that there is a limit to the percentage of fat that can be accumulated by the herring and that this may, in certain circumstances, limit growth by preventing further food intake; such little information as is available suggests that the fall in feeding intensity for North Shields herring recorded by Savage (1931, 1937) from May to July is not related to total food abundance. Thus figure 20, p. 45 (Savage, 1931) relating both numbers and volume of food in the stomachs of herring, on the one hand, and in the sea in the feeding area, on the other, indicates that during June, when fat is increasing in both percentage and condition factor, the intake of available food falls rapidly. More recently Bowers (personal communication), referring to Manx herring in 1962, stated that herring stomachs were virtually empty in July although zooplankton was still available. None of this evidence can be considered as proof that fat is a limiting factor for somatic growth, but it does indicate the possibility that appetitive factors may regulate food intake at certain times independently of available food, and if it is true that spawning Onega herring and Gdansk sprat stop feeding during the spawning period these would be other similar examples.

There is a final point to be made concerning seasonal growth. The period of rapid somatic growth rate in May and June is one of intensive protein metabolism. Now, Gerking (1954) and Menzel (1959), and others, have shown that in adult fish the conversion rate of food protein to growth protein is low, of the order of 20%, and perhaps for older fish even lower. It follows that the energy value of that portion not incorporated in new tissue is high. A herring recruiting for the first time as a 3 year old to the North Sea stocks will for instance increase its weight by about 20%, representing a protein uptake of something like 100% of its initial weight.

It is contended that the energy available from the 80% not incorporated as permanent growth will be sufficient for all energy requirements. This being so, the fat which is being assimilated at this time, for the rate of increase in fat content is most marked in May and June, is neither needed nor in fact used as an energy source. Now, Lovern's (1951) work on fat assimilation and metabolism indicates that during the time of rapid food intake fat is not an important metabolite, being laid down in the herring almost unchanged, which would fit well with the hypothesis. Another point to be mentioned is that the loss of fat is not marked until after July in North Shields herring (Wood, 1958, figure 3). Other workers on fat cycles in herring have usually associated the fall in fat levels with the time when final maturation of the gonad is going on or spawning is imminent. This is often interpreted as indicating that fat is used for gonad maturation, but the facts do not support this contention, for the amount of fat measured in ripe gonads is usually small, of the order of 3%, and this in terms of the total body weight is less than 1%, which is too little to account for the fall in fat content recorded over the maturation and spawning period. What is more likely is that the end of the somatic growth period, which coincides with the increased maturation rate, marks the end of a stage when protein is available for energy requirements and throws the herring back on to its fat reserves. While the herring is actively feeding and growing the fat reserves are shielded by a reliance on protein for energy, and while the gonads are maturing, during the spawning period, and during the long winter starvation period, the protein is shielded by the fat reserves; it is suggested that here is a key factor in the adaptation of the herring to feeding on zooplankton, subject to marked seasonal fluctuations in abundance.

A link-up with the basic hormonal cycles referred to above is achieved if it is assumed that the pituitary growth hormone phase is associated with the reliance on protein for energy, while subsequent stages are characterised by the use of energy derived from the oxidation of fat.

The herring is remarkable for the fact that although it produces a relatively large amount of high protein content gonad each year (about 20% of the weight of the fish) which in many stocks is

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[2] Report of Challenger Society Meeting held at Lowestoft, October 1963.

deposited towards the end of the relatively short feeding season, and although it undergoes annual migrations which may be very extensive, it has a relatively low natural mortality; neither migration nor spawning appears normally to be accompanied by the heavy mortalities such as occur, say, in salmon. The reproductive drain in herring is large and yet it does not, apparently, run down the essential protein of the body to a non-viable level. This indicates a high degree of adaptation, which in turn implies a level of seasonal control and organisation of the physiological processes which may well restrict the extent to which the herring, or a particular stock of herrings, is able to react to environmental changes.

REFERENCES

BLAXTER, J.H.S., and F.G.T. HOLLIDAY. 1963. The behaviour and physiology of herring and other Clupeids. *In* F.S. Russell (Ed.). *Advances in marine biology,* 1. New York and London, Academic Press. 261-393.

BOWERS, A.B. 1963. Manx herrings in 1962: age, stocks, gonad condition, vertebral count and size. *Rap. Mar. biol. Sta. Pt Erin,* No. 75: 21-27.

BRANDES, C.H., and R. DIETRICH. 1953. Über die Fettverteilung im Körper des Herings. (Fat distribution in the body of the herring.) *Veröff Inst. Meeresforsch,* 2: 109-121.

BURD, A.C., and D.H. CUSHING. 1962. I. Growth and recruitment in the herring of the southern North Sea. II. Recruitment to the North Sea herring stocks. *Fish. Invest., Lond.*, (2), 23 (5).

COLEBROOK, J.M., and G.A. ROBINSON. 1961. The seasonal cycle of the plankton in the North Sea and the north-eastern Atlantic. *J. Cons.,* 26, 156-165.

DEMENTJEVA, T.F. 1957. Researches in the USSR on Baltic herring and cod. *J. Cons.,* 22: 309-321.

ELWERTOWSKI, J., and J. MACIEJCZYK. 1960. Growth and fat accumulation in the adult sprat in the Gdansk Bay. *ICES Sardine Committee paper* No. 67.

GERKING, S.D. 1954. The food turnover of a bluegill population. *Ecology,* 35: 490-498.

HODGSON, W.C. 1924. Investigations into the age, length and maturity of the herring of the southern North Sea. Part 1. - Some observations on the scales and growth of the English herring. *Fish. Invest., Lond.* (2), 7 (8).

HOLLIDAY, F.G.T. 1960(*a*). The control of spawning in the herring. *ICES Herring Committee paper* no. 38.

1960 (*b*). The control of maturation in the herring. *ICES Herring Committee* paper No. 39.

1962. Hermaphroditism in the herring (*Clupea harengus* L.). *Proc. roy. Soc. Edinb.*(B) 68: 208-214.

ILES, T.D. 1964. The duration of maturation stages in herring. *J. Cons.,* (in press).

JACOBSSON, J. 1962. The annual cycle of the maturity stages of the Icelandic herring. *ICES Herring Committee paper* No. 97.

LEA, E. 1911. A study on the growth of herrings. *Publ. Circ. Cons. Explor. Mer,* No. 61: 35-57.

LOVERN, J.A. 1951. The chemistry and metabolism of fats in fish. *Biochem. Soc.* Symp. No. 6: 49-62.

MENZEL, D.W. 1959. Utilization of food by a Bermuda reef fish, *Epinephelus guttatus*. *J. Cons.*, 25: 216-222.

MIKHAILOVSKAYA, A.A. 1957. The biology and fishing of the Gulf of Onega herring. *In Materials for a complex study of the White Sea*, 1. Academy of Sciences of the USSR. 74-89. (MAFF Translation).

SAVAGE, R.E. 1931. The relation between the feeding of the herring off the east coast of England and the plankton of the surrounding waters. *Fish. Invest., Lond.*, (2), 12 (3).

1937. The food of the North Sea herring 1930-1934. *Fish. Invest., Lond.*, (2), 15 (5).

WOOD, R.J. 1957. Fat cycles of North Sea herring. *J. Cons.*, 23: 390-398.

F-8

ENERGY METABOLISM AND MIGRATION OF FISH

By

Gunnar Sundnes[1]

ABSTRACT

The present paper deals with the energy required by Clupeiformes for swimming. Hydrodynamic measurements from experiments made by towing or dragging a fish body are presented. Increased growth by preventing migration is discussed.

In fisheries research some of the approaches and problems are similar to those in agricultural research. The production chain is one topic of great interest as the end products in both fields are of vital importance to man. In fisheries research we are also thinking, in a sense, of how to make "bigger and better fish" when we attempt to increase the total catch or to increase the catch in relation to effort.

Speculations on how to act upon the production chain to increase the yield have been made. While these approaches may be useful in freshwater fish farming, they are not yet possible in the sea. If we look at the production chain from phytoplankton to fish and marine mammals, we find that there are many links where the rate of energy utilization is unknown.

Another approach is to begin with the fish and try to obtain information on the minimum quantities of energy which they require. In order to do so we need data on the size of the stock; the basal metabolism; the growth metabolism and the swimming of the fish. The first three points will not be discussed here, but it may be mentioned that there are methods for making these calculations.

The fourth point is of considerable interest to fisheries dependent upon migrating species. The Norwegian fisheries are extensively based upon migrating fish stocks. From a physiological point of view it is very interesting to look into the problem of swimming and the energy budget on these long journeys. Experiments of Gero (1952) using a piscatometer give information on the dragging effect. Most experiments have utilized live fish, but indirect methods (Sundnes, 1957, 1963) have also given information about the energy required for swimming.

The Clupeiformes have been chosen for these studies. The hydrodynamic resistance data for salmon and herring are those reported previously, together with a description of the dragging or towing experiments (Sundnes, 1963). Figure 1 is a schematic drawing of a salmon prepared for a dragging experiment.

The salmon and herring show relatively low hydrodynamic resistance compared, for example, with the cod (Fig. 2). The body size also plays an important role in the total swimming distance but this factor is not investigated at the present stage. The energy required for overcoming the resistance is shown in Fig. 3. The curves are based on an assumption of 80% efficiency of the propelling effect of the tail fin. From calculations based on the dragging experiments and energy metabolism (Sundnes, 1963) we find that a reasonable cruising speed of salmon and herring is 2 knots. This figure is in accordance with the data found in tagging experiments on salmon (Dahl and Sømme, 1935) and the echo-survey on herring (Devold, 1963) and may not be too high when extrapolating the results of Boyar (1961).

Calculations based on this swimming speed and the resistance data presented above offer the possibility of obtaining an idea of what the stocks have to "pay" for the long journeys. The energy used for these migrations could possibly be used for increased growth if the fish could stay "at home".

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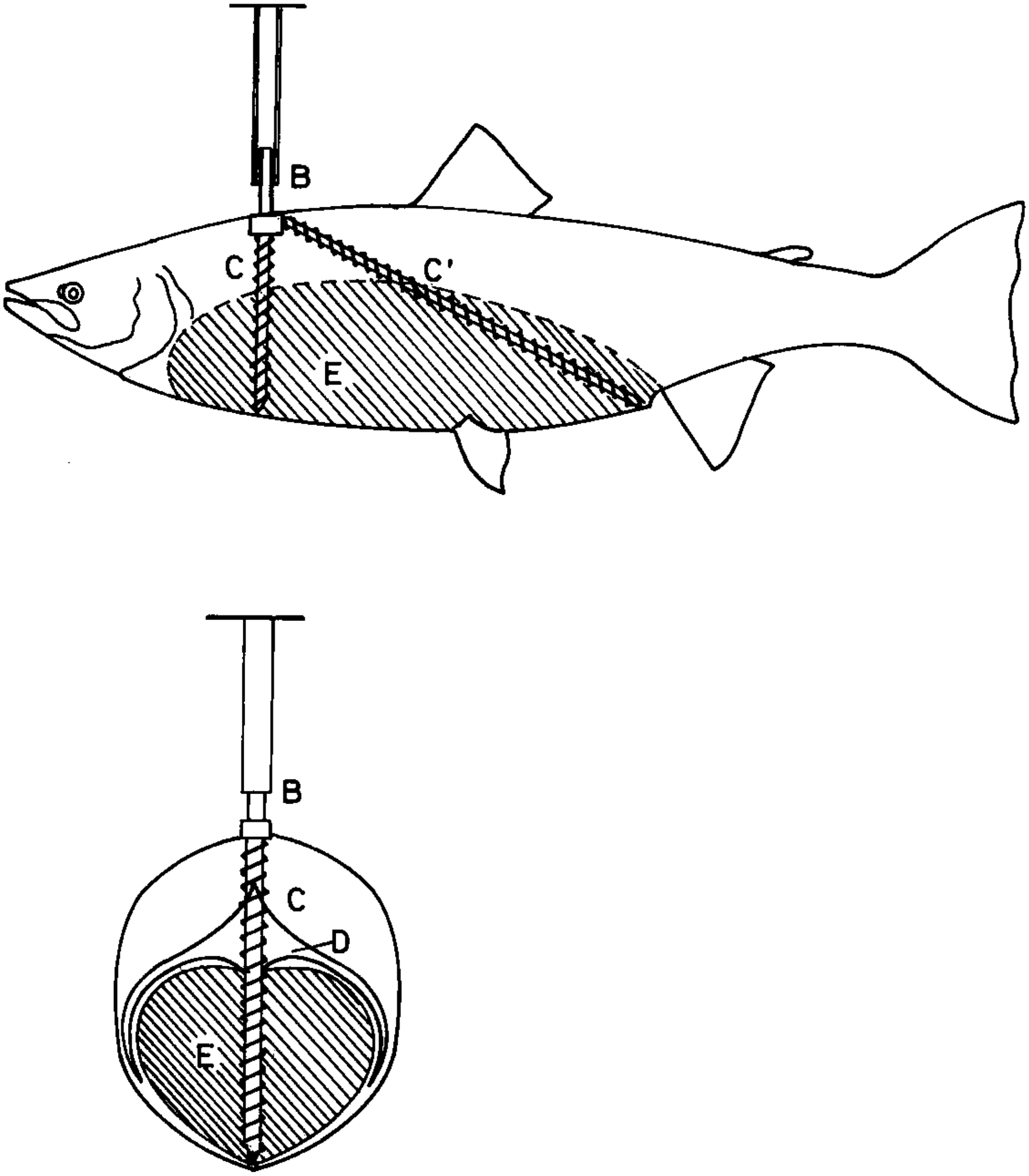

Fig. 1. B = attachment of vertical rod to towing machinery, C = vertical rod, C' = diagonal rod, D = backbones, E = cement filled body cavity.

This would give increased quantities of fish for human consumption if they took care of the fish stock and if the available food for the fish was unchanged. Similar results are seen with domestic animals which use the energy to increase body weight instead of expending it on locomotion as wild animals do. In freshwater fish farming the increased growth of the fish is possibly caused by the reduced locomotion.

In order to get a better idea of the quantities involved we can consider a salmon weighing 11.7 kg which travels 1,000 km at about 2 knots. To overcome the hydrodynamic resistance 840 kcal are required and this is equivalent to 93 gm of fat. However, the energy required for overcoming this resistance is only a part of the total increased energy metabolism during swimming.

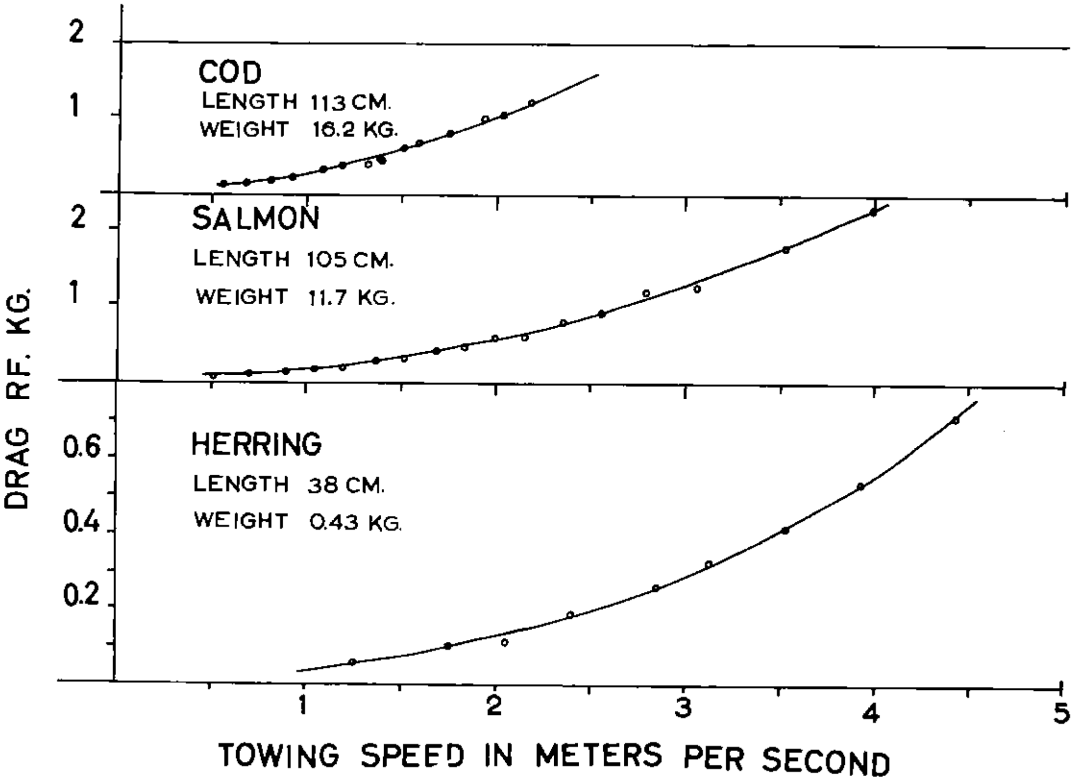

Fig. 2. The relation between drag and towing speed.

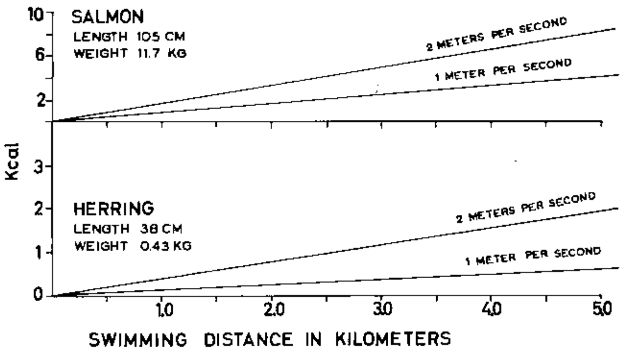

Fig. 3. The energy required for different speeds and swimming distances.

It is also interesting to make some calculations on a whole stock. Here we have to use a stock of fish of relatively uniform body size, such as the Norwegian spring spawning herring. Judanov (1963) estimates this stock in 1961 to consist of 6,515 million mature herring with an average weight of 366 gm. If we assume that half the individuals are bigger than 366 gm we can use the resistance data of herring, shown in Fig. 3, to calculate the energy required for that part of the stock. According to the data of Devold (1963) we will assume here that herring can swim with an optimal speed of 40 nautical miles per day for at least 110 nautical miles. This gives a total energy requirement for 3,257 million individuals of 74,911 million kcal or 8,323 tons of fat to overcome the hydrodynamic resistance. This estimate shows that tons of herring tissue could possibly be added to the body weight even if this migration of 110 miles could be prevented, which is only a small part of the annual migratory cycle. A reasonable figure is 10% increase of the total weight of the stock.

While these are interesting thoughts, is it possible that we can ever observe such a situation in nature? In the case of the Atlanto-Scandian herring this possibility would exist if the hypothesis of Devold (1959) is correct. Devold believes that for one year the herring will remain in Norwegian waters. If food could be available to the herring in the same amounts as it is in the Norwegian Sea we should have the possibility of measuring a growth difference in that part of the stock which is not migrating as usual.

When it comes to the question of what man can do in order to prevent the migration, we have a wide field with many difficult problems to face. While these approaches will not be discussed here, mention can be made of large-scale fish raising with controlled environment to condition the fish to a certain behaviour, or perhaps altering other factors within the fish to control migration. In a dense schooling population we may be able to affect the fish in nature to desired ends. These ways of thinking should be kept in mind when considering future fisheries research.

REFERENCES

BOYAR, H.C. 1961. Swimming speed of immature Atlantic herring with reference to the Passamaquoddy Tidal Project. *Trans. Amer. Fish. Soc.* 90: 21-26.

DAHL, K., and S. SØMME. 1935. Experiments in salmon marking in Norway 1935. *Skr. Norske Vidensk.-Akad.* (12): 1-27.

DEVOLD, F. 1959. Otto Petersons teori om de skandinaviske sildeperioder sett i sammenheng med de senere års undersøkelser over den atlanto-skandinaviske sild. *Naturen* (2): 83-92.

1963. The life history of the Atlanto-Scandian herring. *Rapp. Cons. Explor. Mer.* 154: 98-108.

GERO, D.R. 1952. The hydrodynamic aspects of fish propulsion. *Amer. Mus. Novit.* (1601): 1-32.

JUDANOV, I.G. 1963. Obscie rezul'taty issledovanij po ocenke sostojanija zapasa atlanticesko-skandinavskikh sel'dej. *Materiali Rybokhozjajstvennykh issledovanij severnovo basseina.* 1: 3-6.

SUNDNES, G. 1957. Energiforbruket hos fisk under svømming. *Fauna* (4): 130-134.

1963. Swimming speed as a factor in gear research. *Fiskeridir. Skr. Havundersøk.* 13 (6): 126-132.

F-9

SUPERCOOLING AND OSMOREGULATION IN TELEOSTS OF THE BOREAL AND SUB-ARCTIC

By

H. Leivestad[1]

ABSTRACT

Several species of teleosts found at subzero temperatures in the Barents Sea have their body fluids supercooled. Boreal cod tolerate supercooling if seeding with ice crystals is prevented. Low temperatures induce a rise in plasma osmolarity which is considered to be adaptive. The muscle cells lose potassium and gain sodium when exposed to low temperatures. The physiological consequences of these adaptations are discussed.

INTRODUCTION

Since the freezing point of sea water is 1°C lower than that of the teleost blood (-1.8°C against -0.5 to -0.8°C) the theoretical possibility exists that marine teleosts may meet temperature conditions in nature where an increased osmolarity of the body fluids, or a permanent supercooling, are the only alternatives for survival. It has been shown that both alternatives function in nature.

THE PLASMA

Scholander *et al.* (1957) showed that in Hebron Fjord, Labrador, the shallow water species increase the osmolarity of their blood during the winter, whereas the bottom species, living at a temperature of -1.7°C are permanently supercooled. In 1960, Eliassen *et al.* (1960) reported that cod (Fig. 1) and some other species (Fig. 2) are found in a supercooled state in the cold waters of the Barents Sea. We were able to acclimate the sculpin, *Cotteus scorpius*, to -1.5°C in the laboratory. As seen from the freezing point of their plasma, these animals were supercooled at this temperature (Fig. 3). Gordon *et al.* (1962) verified their earlier findings in Labrador and tried to supercool the sculpin and the tomcod in the laboratory in New Brunswick, but with a negative result.

At the aquarium of The Institute of Marine Research in Bergen I have made a series of experiments on cod, *Gadus morhua* (*callarias*), where the body temperature of the animals has been kept 0.2° to 0.9°C below the freezing point of the body fluids. In Figure 4 the animals at "60 days acclimation were kept supercooled by 0.65°C for 2 months.

We might question how stable is this supercooled state. Except for some of the shore fishes in Labrador (Scholander *et al.*,1957) and the acclimated sculpin (Eliassen *et al.*,1960) the supercooled animal will not tolerate the touch of ice crystals. It is fascinating to watch a supercooled cod after you have been touching it with a piece of ice. In a few seconds the body will start to shiver violently and after some minutes the fish will lie motionless at the bottom. Attempts at revival by immediate transfer to warmer water were without success. Few marine teleosts live in the absolute proximity of ice, however, and it seems as if the others will tolerate supercooled conditions for prolonged periods.

All the authors quoted have found that the osmolarity of the body fluids increases upon lowering the temperature. This increase is large in some of the shore fishes of Labrador (Scholander *et al.*, 1957) where the plasma was nearly isotonic with sea water. These animals were therefore able to tolerate ice crystals. The effect seems to vary with the species and with the thermal pre-history of the specimens (Fig. 1-4). That this "compensatory adaption" is not a question of a mere breakdown

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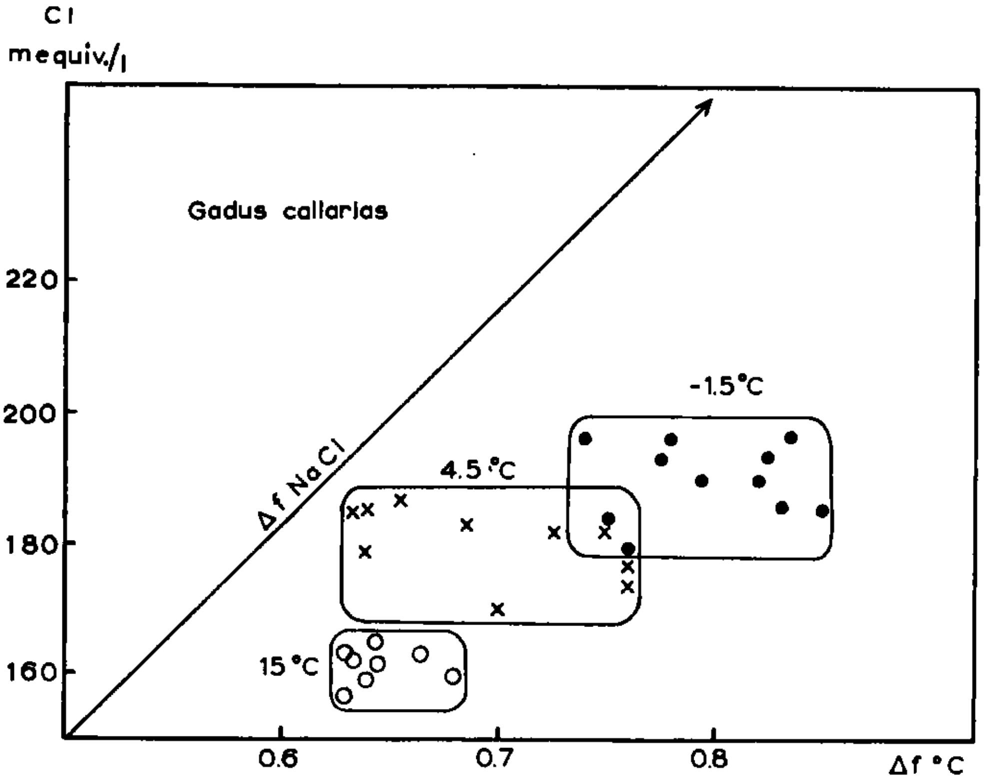

Fig. 1. Plasma freezing point depression versus corresponding chlorides in the cod. Data from the Barents Sea (+4.5°C and -1.5°C) and waters near Arendal (+15°C).

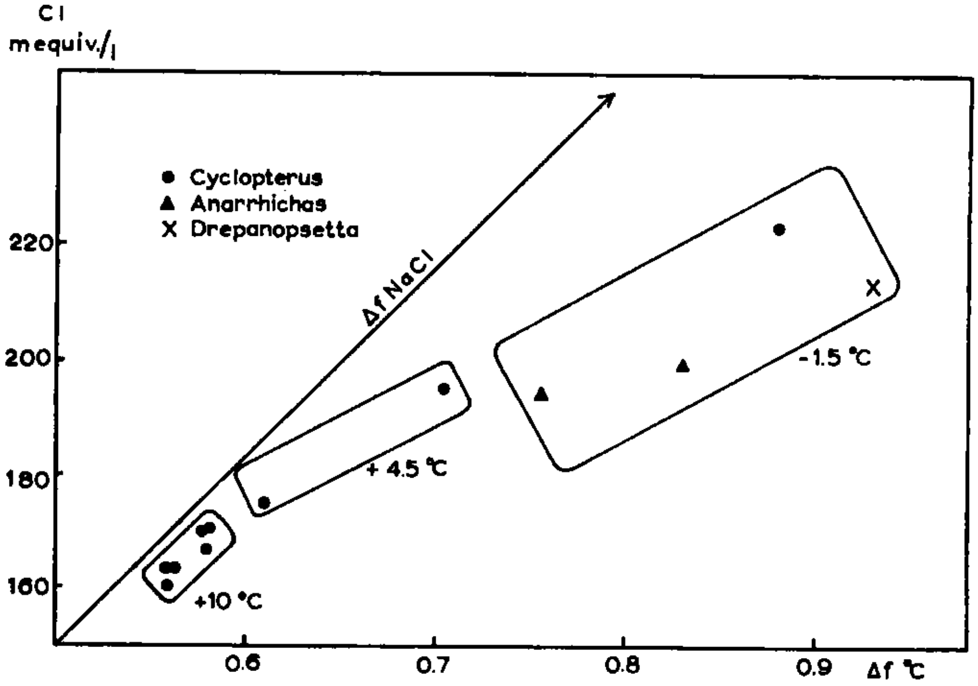

Fig. 2. Plasma freezing point depression versus corresponding chlorides in some teleosts from the Barents Sea (+4.5°C and -1.5°C) and from waters near Bergen (+10°C).

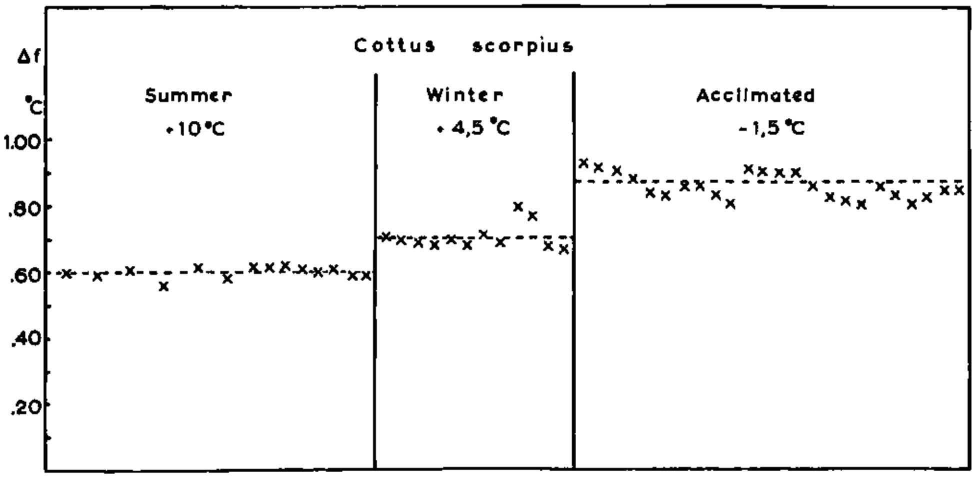

Fig. 3. Plasma freezing point depression in *Cottus scorpius* L. taken in June and September (Summer + 10°C), in February (Winter +4.5°C) and for animals acclimated to -1.5°C.

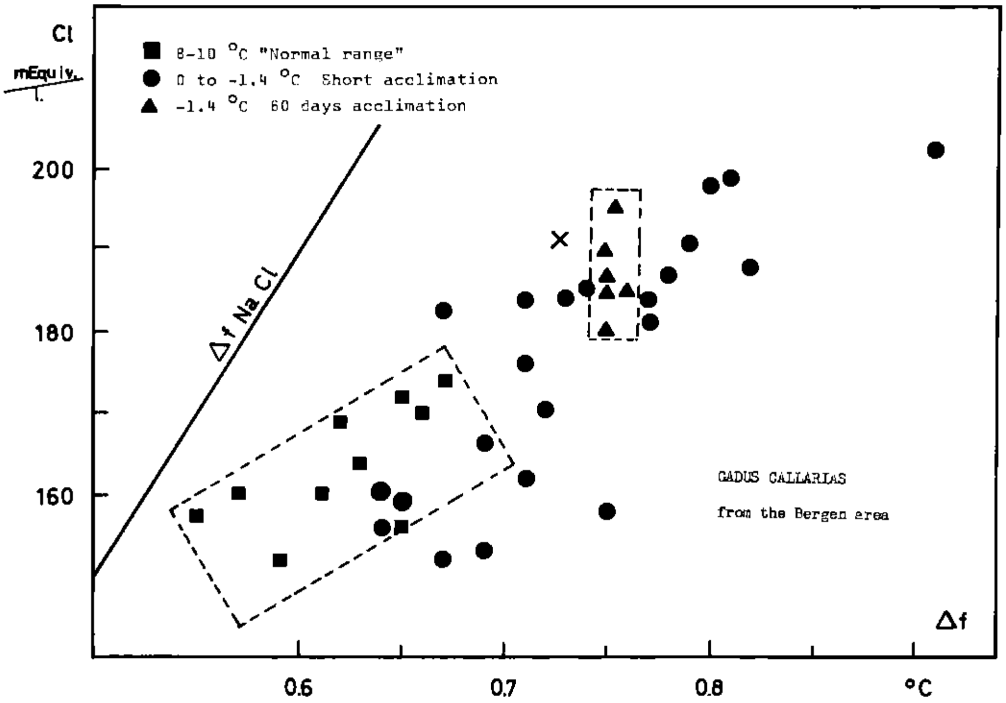

Fig. 4. Plasma freezing point depression versus corresponding chlorides in the cod. Data from animals kept at the research aquarium in Bergen. "Short acclimation" consists of experiments performed in the months from Dec. to Aug. mostly at subzero temp. and lasting from 2 to 14 days. The 60 days-acclimation was performed in Dec. and Jan.

of the osmoregulatory ability is seen from the fact that the chlorides are responsible for a smaller fraction of the osmotically active substances than in "normal" plasma (Fig. 1, 2 and 4; Scholander *et al.*, 1957; Gordon *et al.*, 1962). Gordon *et al.* (1962) have tried to identify this "non-salt" fraction or "anti-freeze substance". There are some indications that the non-protein-nitrogen fraction is responsible for at least some of the increased osmolarity in the fjord-cod (*Gadus ogac*) and in the tomcod (*Microgadus tomcod*). The present author has searched in vain to find an increase in the NPN-fraction in cold-acclimated cod.

Woodhead and Woodhead (1959) use the term "osmotic imbalance" to describe some measurements of increased osmolarity in the cod at low temperatures in the Barents Sea. Their values of both freezing point and chloride do not accord with the data in the literature for cod plasma. It is therefore difficult to assess whether their data verify the tendency for the salts to reduce their relative importance in the total osmolarity. Further they claim to have found a sharp "borderline" at +2°C, below which temperature the "imbalance" starts to function. Besides being physiologically improbable, I can hardly find this verified in their data. We have found that a decrease of 10° to 15°C in temperature represents a sufficient stimulus to induce an increase in osmolarity (Fig. 1, 2, 3) in three species.

It is always tempting to guess what a good reason an animal might have for changes in a physiological parameter. Gordon *et al.*(1962) put the label "antifreeze" and the Woodheads "osmotic imbalance" on the phenomenon described. We know that the osmoregulatory work needed is proportional to the osmotic gradient between the body and the exterior. This in-out gradient will be reduced in these fishes and the metabolic cost of osmoregulation will be reduced. I therefore tentatively propose that the "compensatory increase" is undertaken to reduce the metabolic load on the gills.

THE MUSCLE

Samples of muscle tissues were taken from all the species represented in trawl catches from cold waters in the Barents Sea. For comparison some samples were taken from the Bergen area (Eliassen *et al.*, 1960). The contents of sodium and potassium in the muscle tissue were determined.

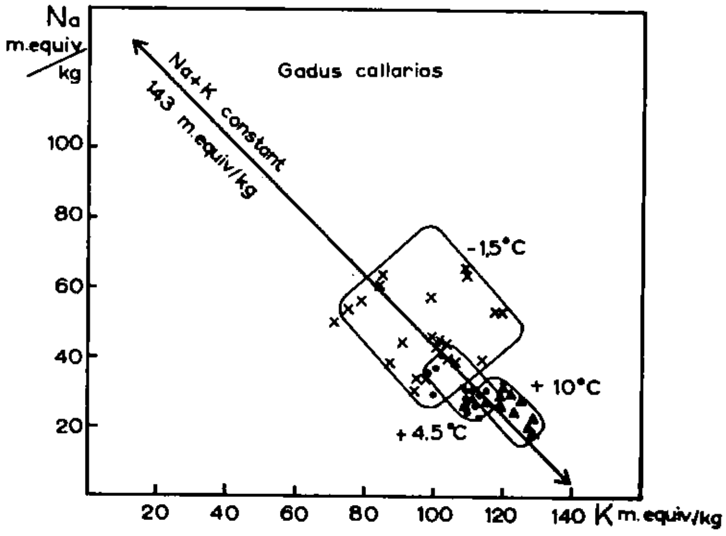

Fig. 5. The content of sodium and potassium in the muscles of the cod from Barents Sea (+4.5°C and -1.5°C) and near Bergen (+10°C).

For the cod (Fig. 5), it will be seen that there is a marked difference in the ratio between sodium and potassium in the samples from the three localities. The K/Na ratio decreases as the temperature is lowered. When presented on a molar basis as in the figure, it seems that sodium is added in similar amounts to the loss of potassium, thus keeping the sum of the two cations fairly constant. A line has been drawn representing the constancy of the K + Na concentrations

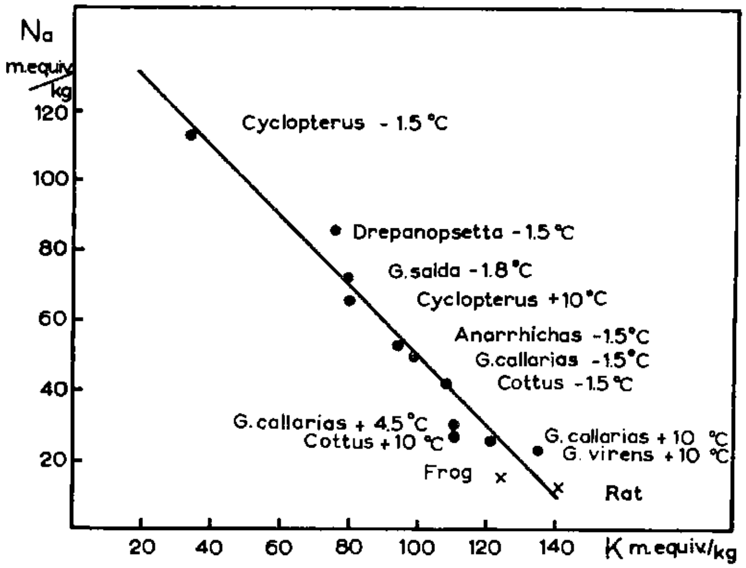

Fig. 6. The content of sodium and potassium in the muscles of teleosts taken in Barents Sea (at -1.5°C, -1.8°C and +4.5°C) and near Bergen (+10°C). *Cottus* at -1.5°C is after some weeks exposure at -1.5°C in the laboratory. The points represent arithmetic means. The data for frog and rat sarcoplasm are from Hodgin (1951).

(K + Na = 150 mEquiv.). In Fig. 6 the data on all the species are represented by the mean value for each species from the different localities. First it may be noticed that the sum of the two cations is reasonably constant, distributed around 145 mEquiv./kg. This is about the same as quoted for rat and frog sarcoplasm (Hodgin, 1951). For the cold locality it is surprising to find that the sodium concentration is increased at the expense of potassium and to such an extent that in some species the two are equal, or even sodium being present in higher concentration than potassium (*Drepanopsetta* and *Cyclopterus*). We conclude on the basis of these data that the intracellular content of potassium is greatly reduced in the subarctic species of the Barents Sea area, and that more boreal species like the cod will show the same tendency, but in a more moderate degree.

Potassium is known to be the typical intracellular cation. There is hardly a living cell that does not step up its potassium level in relation to its environment. For a multicellular organism this environment is the body fluid; for a protozoan it is the environment. This elevated potassium is responsible for the establishment of a membrane potential and thereby underlies such fundamental phenomena as excitability and nervous impulses. It is fascinating, therefore, to speculate how the nerves and muscles in *Cyclopterus* or in *Gadus saida* are able to function with a membrane potential a fraction of that in more southern species.

If I might suggest a possible ecological consequence along this line of thought, it would be the following: the ability to penetrate successfully into cold arctic waters is dependent on the ability of the body cells to function at low intracellular potassium levels. It is reasonable to place the basic reason for this special effect of cold exposure in the energy-demanding "sodium pump" mechanism of the cell. Future work along these lines should try to determine directly the decrease in membrane potential we suspect to be present on the basis of ionic equilibria.

REFERENCES

ELIASSEN, E., H. LEIVESTAD, and D. MØLLER. 1960. The effect of low temperatures on the freezing point of plasma and on the potassium/sodium ratio in the muscles of some boreal and subarctic fishes. *Arb. Univ. Bergen,* Mat-Naturv. Ser., No. 14.

GORDON, M.S., H. AMDUR, and P.F. SCHOLANDER. 1962. Freezing resistance in some northern fishes. *Biol. Bull., Woods Hole,* 122: 52-61.

SCHOLANDER, P.F., L. vanDAM, J.W. KANWISHER, H.T. HAMMEL and M.S. GORDON. 1957. Supercooling and osmoregulation in arctic fish. *J. cell. comp. Physiol.,* 49: 5-16.

WOODHEAD, P.M.J., and A.D. WOODHEAD. 1959. The effect of low temperatures on the physiology and distribution of the cod, *Gadus morhua,* L., in the Barents Sea. *Proc. zool. Soc. Lond.,* 133: 181-199.

F-10

THE OPTOMOTOR RESPONSE AND THE SCHOOLING OF FISH

By
Evelyn Shaw[1]

ABSTRACT

Certain features of the response of fish in an optomotor apparatus resemble certain features of fish in a school. These similarities are discussed. It is proposed that the optomotor response may be the mechanism by which fish can change position and velocity within the school without disrupting the forward movement of the school.

INTRODUCTION

A school of fish is composed of like individuals which maintain parallel orientation and some set range of distances from one another when they are moving. It appears, at first glance, as if the members of a school are in the same positions during forward movement of the school, but closer study reveals that there are changes in the position and in the velocity of individual fish. These changes are necessarily within the limitations "imposed" by parallel orientation; nevertheless, fish move anteriorly, posteriorly, medially, laterally and horizontally, without disrupting the apparent cohesion of the school and without affecting the total forward movement of the school. Breder (1959) pointed out that "the movement of the school as a whole is a composition of the velocities of each individual in it, or is the geometric sum of their individual trajectories and speeds in which each fish represents a vector." Breder observed that there is little change of position in a tight school, but that there is constant shifting in a looser one. Thus, in schooling we have a situation where the intrinsic movement of the fish does not disrupt the forward movement of the entire school. In order to keep the forward movement continuous, during positional and velocity changes, the stimuli that maintain forward movement must be of such nature that they can function at a great range of speeds and also when the fish are in a variety of positions. In a previous study (Shaw and Tucker, 1964) we noted, in work with carangids, one experimental laboratory situation in which the behaviour of fish resembles the behaviour of fish in a school in the field. In the laboratory situation the fish are placed into an optomotor apparatus; within the apparatus the fish can change velocity, position and continue to move "forward". It duplicates some of the features of fish in a school.

This paper describes some studies on *Mugil* sp. in an optomotor apparatus.

THE OPTOMOTOR APPARATUS

It consisted of a stationary cylindrical lucite aquarium, 7 cm high, 6 cm diameter and a motor driven rotating horizontal turntable which was fitted with a vertical drum, 11.5 cm high, 10.5 cm diameter. The entire apparatus, except the motor, was submerged in sea water. The aquarium did not rotate, and an opening in the bottom allowed a continual inflow of fresh sea water. The drum rotated, clockwise and counterclockwise, at speeds of 1 to 22 rpm, and the interior of the drum was lined with one of the following various backgrounds:1) entirely white; 2) alternating black and white vertical stripes, each 3 mm wide, entirely lining the interior, 3) four panels, each 18 mm wide consisting of the above stripes, superimposed vertically on a white background at 90° intervals; 4) three panels, as above, at 120° intervals; 5) two panels, as above, at 180° intervals; 6) one panel, as above. In each test a *Mugil* sp., 25-35 mm in length, was allowed to adapt to the aquarium, and then observed for 1 min while the drum was stationary. Subsequently the fish was observed for 1 min at each one of five speeds, 3,6,10,14 and 20 rpm, clockwise and counterclockwise. Records of qualitative behaviour were made by motion picture and the number of times the fish rotated in response to drum rotation was counted (Table 1). Five fish were observed in each of the various backgrounds.

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[1] The American Museum of Natural History, New York, N.Y., USA.

TABLE 1.

Rotational speed of drum	Mean Rotational Speed of Fish		
	Field of vertical stripes	Field of 4 striped panels	Field of 3 striped panels
3	2.6	2.2	2.0
6	5.5	5.0	6.0
10	9.3	9.3	8.5
14	13.3	12.0	14.0
20	19.3	18.8	19.3

BEHAVIOUR OF THE FISH

In the white drum the fish were mainly motionless and they frequently rested in the same position, near the bottom, throughout the tests.

In the background containing uniform black and white stripes, the fish displayed a number of different behavioural activities. The first three were more frequently seen than the latter three. These activities were:

1) A continuous and regular movement in the same direction as the movement of the background stimulus lining the drum with increase in angular speed as drum speed increased. The fish were oriented parallel to the aquarium wall and close to the bottom.
2) During some revolutions the angular speed of the fish was faster than the speed of the drum, during others, it was slower, although at the end of a minute, each may have moved the same number of rpm. In some trials, fish consistently swam at greater angular speeds than that of the apparatus, and in others, consistently slower.
3) At 3 and 6 rpm a number of fish showed pronounced body vibrations.
4) Fish swam to the top of the aquarium, down to the bottom, up again, continuing to follow the direction of movement of the drum. The fish described a sine curve.
5) In two instances, suddenly interrupting a smooth course, the fish oriented perpendicular to the stripes and nipped at the wall of the aquarium, as if feeding for a few seconds.
6) At slower speeds fish sometimes remained stationary for a few seconds during which time they showed eye nystagmus.

Behaviour was similar in the backgrounds consisting of four or three panels. The following activities, some of which were unvaried during the entire series, were seen.

1) The fish oriented to one of the panels and remained next to that panel throughout. The eye was opposite the leading edge of the panel. Fish and drum showed the same number of rpm..
2) The fish oriented at a point midway between two panels, parallel to the aquarium wall, with the eye opposite a white section. The fish frequently maintained the same orientation throughout the entire series of increasing numbers of revolutions.
3) They swam in short bursts, sometimes more quickly than the angular speed of the drum, other times, more slowly. After the change in angular velocity they again oriented to a panel.

In the field of two panels, the fish kep altering their orientation, clockwise or counterclockwise, regardless of the direction of the drum. Their behaviour was consistently erratic.

In the field containing one panel only two fish responded by moving in the direction of movement of the background with consistent increase in angular speed as drum speed increased. The other fish followed for 1/4 or 1/2 of a revolution, stopped and then followed briefly again as the panel approached them, tail to head.

DISCUSSION

Many features of *Mugil* orientation to the moving stimuli of an optomotor apparatus were similar to *Mugil* orientation in a school. Fish altered positions and changed velocities relative to some of the moving backgrounds, but the fish continued to move in the same direction as the background movement. If we consider the entire school as a moving background, individuals within the school can be stimulated by the movements of surrounding fish. Since one fish is essentially equivalent to another each would be influenced by the neighbouring sphere of moving fish and the group would intrinsically impel itself forward. Fish in a school probably take an optical fix on other fish and fish in a drum probably take an optical fix on some stripes. But since there is constant movement in both conditions of the individual and the background, there is, in all likelihood, a temporal change of optical fixation points. Atz (1953) has suggested that one reason fishes of the same species and size generally school together is that they alone provide points of optical fixation which travel at comfortable speeds.

In order to keep the fish moving forward the movement of the background evidently must approach the visual field of the fish from tail to head (Horstmann, 1959; Harden Jones, 1963). Protasov and Altaknov (1961) reported that, in order to guide the movement of fish, the moving visual field of the fish must be horizontally greater than the visual field of the fish and the vertical stripes must be no less than one half the vertical visual field of the fish. If we combine these two features we may understand what occurred in the moving background consisting of two panels. There, when one panel passed the fish, tail to head, the other panel passed it, head to tail. Although fish do not follow the direction of movement of the far panel, without the additional stimulation of approaching panels on its near side, the fish was confounded by simultaneous movements in opposite directions. In the background containing only one panel, the panel was not a sufficiently strong stimulus to maintain a following response in three of five fish; movement was obtained in two. In this situation a fish had to contend with a stimulus moving in one direction, but the stimulus may have been of marginal intensity.

An objection that might be raised regarding the suggestion that the optomotor response is the mechanism by which fish change position, velocity and continue to move forward is that optomotor responses are found in non-schooling fish. However, as discussed here, this response operates in a school after it has formed. A combination of many other factors, such as, for example, the development of visual attraction (Shaw, 1960) and the general maturation of the nervous system, serve to give rise to schooling behaviour. It is only after the school has formed that the optomotor response may facilitate forward movement while fish reorient, accelerate and decelerate.

ACKNOWLEDGEMENTS

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I would like to thank the Stazione Zoologica, Napoli, for their kind hospitality during the time I worked on this research problem.

REFERENCES

ATZ, J.W. 1953. Orientation in schooling fishes. *Proc. Conf. Orientation in Animals.* ONR. p. 103-130.

BREDER, C.M. 1959. Studies of social groupings in fishes. *Bull. Amer. Mus. nat. Hist.*, 117: 397-481.

HARDEN JONES, F.R. 1963. The reaction of fish to moving backgrounds. *J. exp. Biol.* 40: 437-446.

HORSTMANN, E. 1959. Schwarmstudienvunter Ausnutzung einer optomotorischen Reaktion bei *Mugil cephalus* (Cuv.). *Pubbl. Sta. zool. Napoli.* 31: 25-35.

PROTASOV, V.R., and U.P. ALTAKNOV. 1961. The possibility of using the optomotor reaction for controlling the movements of fishes. *Plan. Khoz.* 2: 29-32 (Referat. Zhur. Biol., 1961, 200412).

SHAW, E. 1960. The development of schooling behavior in fishes. *Physiol. Zoöl.* 33: 79-86.

SHAW, E., and A. TUCKER. 1964. The optomotor reaction of schooling carangid fishes. *Anim. Behav.* (In press)

SECTION

G

G-1

A FIRST LOOK AT SOME WAVE AND WIND DATA FROM TRAWLERS

By

J.A. Ewing[1] and N. Hogben[1]

ABSTRACT

The paper presents some of the early results obtained from the analysis of wave and wind observations made by selected trawler skippers. It would be premature to draw any firm conclusions from the sample of data so far analysed but it is encouraging to find already a meaningful picture emerging from the data.

INTRODUCTION

Seakindliness is particularly important for trawlers. Model tests in waves can greatly help the designer to achieve good seagoing qualities but they must be coupled with knowledge of the sea conditions both average and extreme to be encountered in service. At present, knowledge of conditions in the northern fishing grounds where distant water trawlers operate is very inadequate. A scheme has therefore been organised (in collaboration with the White Fish Authority and the Ministry of Agriculture, Fisheries and Food) for collecting systematic sea data observations from selected trawler skippers. Accounts of this scheme and the preliminary studies made to explore the reliability and the practical problems and techniques of observation have been given in the references (Hogben and Chaplin, 1961; Hogben, 1962; Hogben, 1963). The present paper takes a first look at some of the observations which have meanwhile been collected from the selected trawler skippers. The analysis carried out of the data so far available was intended mainly to test analysis procedure and to examine various forms of presentation and interpretation. It has been thought worth recording however because already the outline of a useful picture of sea conditions is appearing.

THE ANALYSIS

The Observations

The trawler skippers who have kindly agreed to cooperate in this research have been supplied with guidance notes and accessories such as stop watches to help them in making the observations. The guidance notes and procedure recommended have been based on a study of the Marine Observer's Handbook and on the experience gained from the special visual observation trials (Hogben, 1962). The observations are recorded on data sheets using a "ticking" principle for ease of subsequent coding onto punched cards. A sample is shown (Fig. 1) and it will be seen that there is space for 15 sets of observations on each sheet.

Data processing

The punching of the cards is being carried out by the Combined Tabuluting Installation of the Stationery Office and each set of observations is punched on one card; the cards are being sorted using a machine in Mathematics Division, National Physical Laboratory. At the time of writing (June, 1963) there are about 1,100 punched cards recording observations mainly from four trawlers.

Choice of season and area

Each card bears the date, time and geographical position of observation and for convenience the cards are sorted (following the practice of the Meteorological Office) into months and classified according to the Marsden system of numbered 10 degree squares of sea area. For this preliminary analysis it was decided to choose those cards for the months of December, January and February and for the area shown in Fig. 2, which covers Marsden Squares 217, 218, 219, 251, 252,

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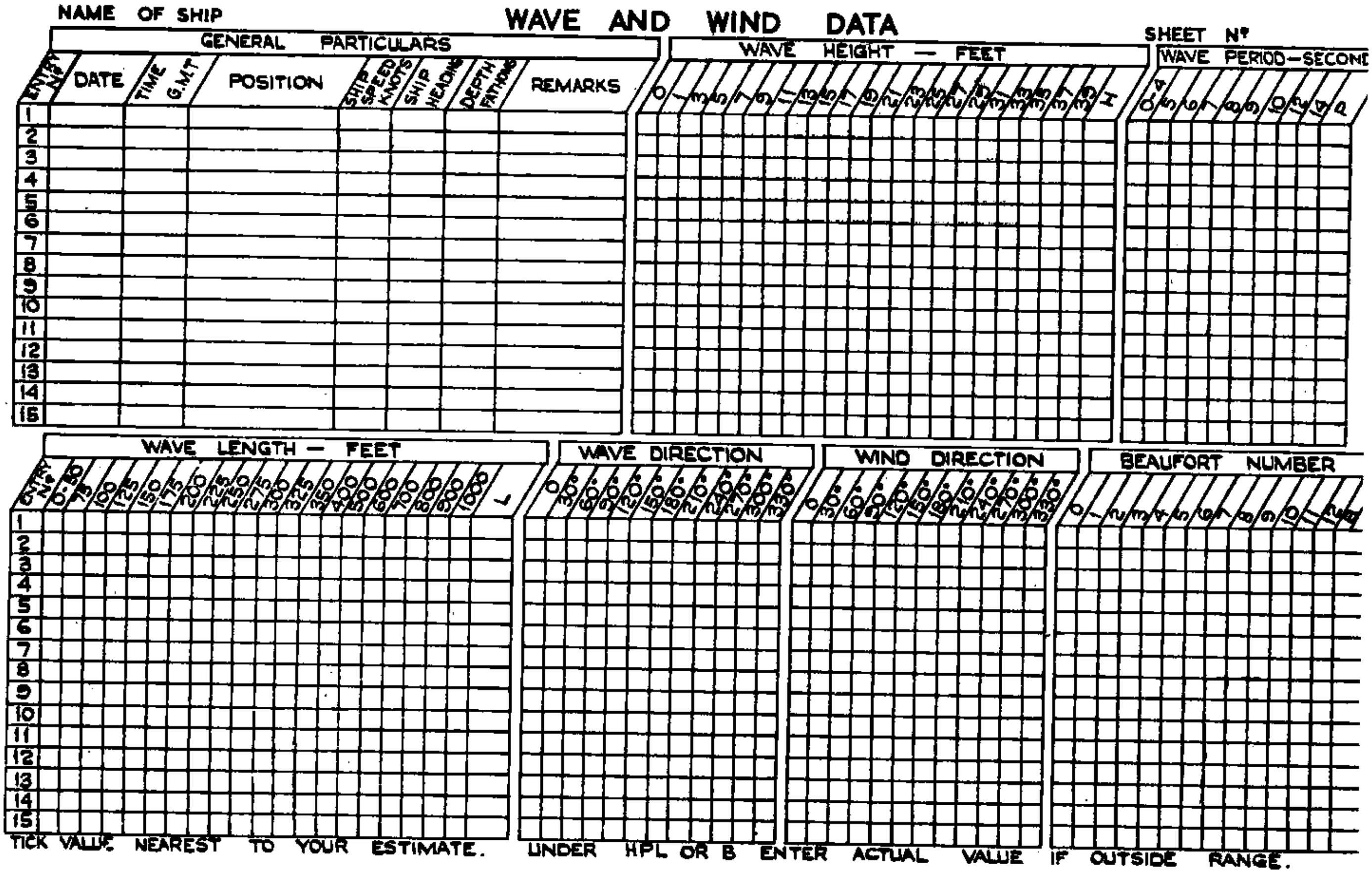

FIG. 1.

285, 286 and 287. The number of cards satisfying these conditions was found to be 334; the subsequent sorting operations were carried out using this group of cards.

Tabular presentation of results

Tables 1, 2, 3 and 4 show the distributions of wave height/wave period, wave height/wave direction, wave/direction/wave period and wind direction/Beaufort Number respectively.

These four tables represent the basis for Fig. 2 and contain more information than is shown in this figure. In Tables 2, 3 and 4 the total number of observations is less than 334; this is because some entries on the data sheets did not have an observation of one of the two variables concerned.

Graphical presentation of results

In addition to tables of the results it is desirable to have a picture of wave and wind conditions occurring in various sea areas; Fig. 2 has been constructed with this in view.

The small graphs shown in Fig. 2 have been drawn using information given in Tables 1-4.

Graph (a) shows the 2-way cumulative frequency curves for wave height and wave period together with three wave period/wave direction roses.

Graph (b) gives information on the steepness of waves - the curves show the probability of exceeding a given wave height when the wave length is specified.

Graph (c) shows the Beaufort Number/wind direction rose. Below the rose is a small table giving the frequency of occurrence of various Beaufort Numbers for all wave directions.

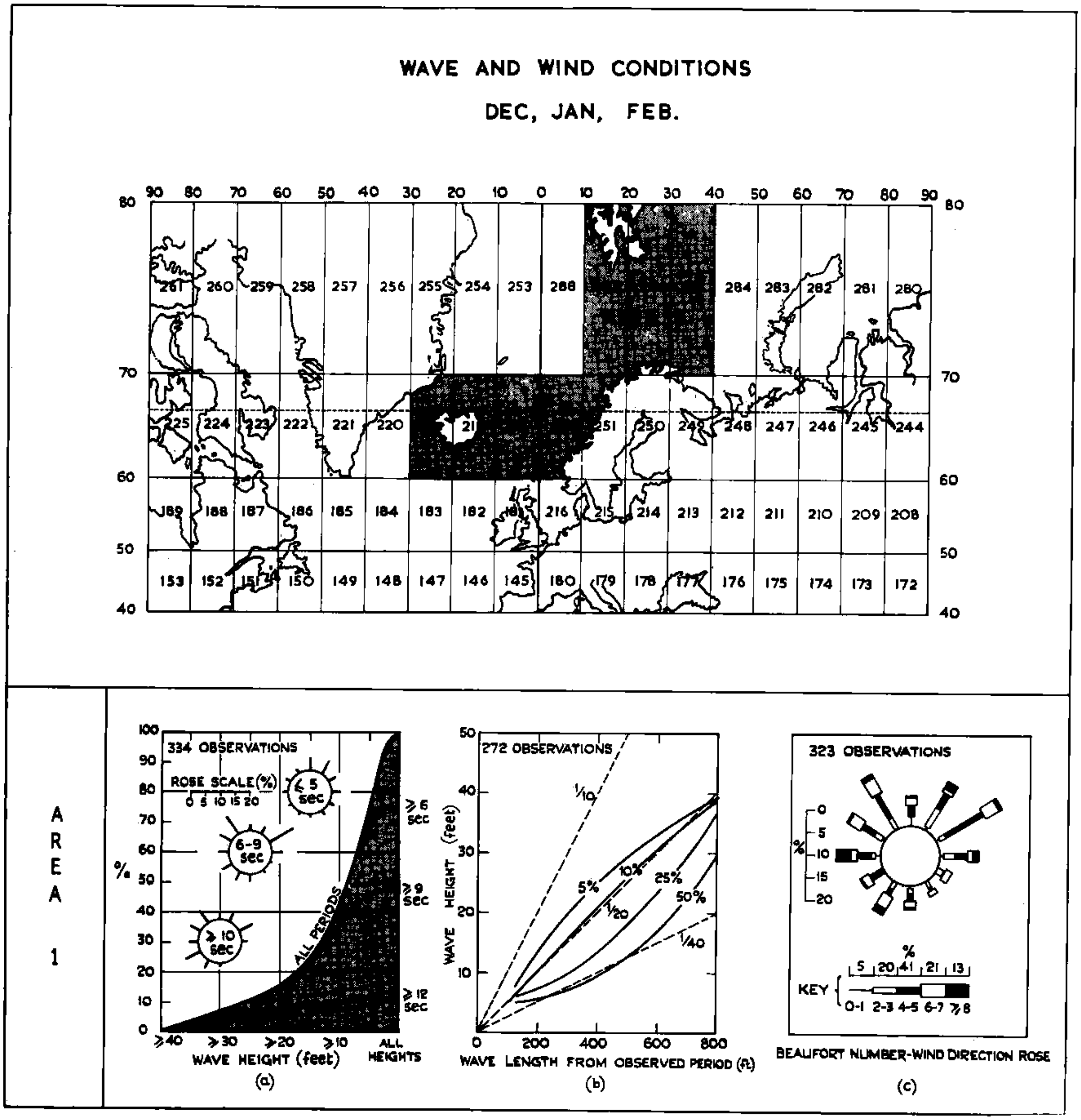
WAVE AND WIND CONDITIONS
DEC, JAN, FEB.
90 80 70 60 50 40 30 20 10 0 10 20 30 40 50 60 70 80 90
80
70
60
50
40
261 260 259 258 257 256 255 254 253 288 284 283 282 281 280
225 224 223 222 221 220 21 251 250 249 248 247 246 245 244
189 188 187 186 185 184 183 182 181 216 215 214 213 212 211 210 209 208
153 152 151 150 149 148 147 146 145 180 179 178 177 176 175 174 173 172
AREA 1
334 OBSERVATIONS
ROSE SCALE (%)
0 5 10 15 20
≤5 sec
6-9 sec
≥10 sec
≥6 sec
≥9 sec
≥12 sec
ALL PERIODS
%
0 10 20 30 40 50 60 70 80 90 100
≥40 ≥30 ≥20 ≥10 ALL HEIGHTS
WAVE HEIGHT (feet)
(a)
272 OBSERVATIONS
1/10
5%
10%
25%
50%
1/20
1/40
WAVE HEIGHT (feet)
0 10 20 30 40 50
0 200 400 600 800
WAVE LENGTH FROM OBSERVED PERIOD (ft.)
(b)
323 OBSERVATIONS
%
0 5 10 15 20
KEY
%
5 20 41 21 13
0-1 2-3 4-5 6-7 ≥8
BEAUFORT NUMBER-WIND DIRECTION ROSE
(c)

FIG. 2

TABLE 1. WAVE PERIOD (SEC)

WAVE HEIGHT (FEET)	0-4	5	6	7	8	9	10	12	14	Totals
0(0.00m)	11									11
1(0.31m)	13	5		2		2				22
3(0.91m)	23	12	9	7	2					53
5(1.52m)	7	10	6	4	18	8	7			60
7(2.13m)		2	4	4	5	9	2	2		28
9(2.74m)			4	3	6	4	16	2		35
11(3.35m)				1	6	3	9	3		22
13(3.96m)					2	7	7	3		19
15(4.57m)			1		2	5	11	3	1	23
17(5.18m)					1	1	3			5
19(5.79m)				1	2	5		1		9
21(6.40m)					2	2	1			5
23(7.01m)					1		3	1		5
25(7.62m)						1	2	3		6
27(8.23m)			1				4	1		6
29(8.84m)						2				2
31(9.45m)							1			1
33(10.06m)								2		2
35(10.67m)							2	7		9
37(11.28m)							1	2		3
39(11.89m)									4	4
40(12.19m)								1	2	3
45(13.72m)									1	1
TOTALS	54	29	25	22	47	49	69	31	8	334

TABLE 2. WAVE DIRECTION (DEG)

WAVE HEIGHT (FEET)	000	030	060	090	120	150	180	210	240	270	300	330	Totals
0(0.00m)	8	1											9
1(0.31m)	1	2	2	5	2	2	1	1	2		3		21
3(0.91m)	3	9	7	8	3	2	3	2	1	2	5	6	51
5(1.52m)	1	10	15	3	2	3	2	1	3	4	4	10	58
7(2.13m)	3	3	6	2			1	5	3	2	1	2	28
9(2.74m)	2	2	7	2			1	1	6	4	7	3	35
11(3.35m)	3	1	7						6	1	1	3	22
13(3.96m)	2	1	4	2		1			1	1	2	5	19
15(4.57m)			2	4	1		1	1	5	2	1	6	23
17(5.18m)							1			1		3	5
19(5.79m)	1	1	1	1				1		2	2		9
21(6.40m)	1		1			1				1		1	5
23(7.01m)				1			1			2	1		5
25(7.62m)							1	1	1		3		6
27(8.23m)		1	1			1		1			1		5
29(8.84m)							1	1					2
31(9.45m)								1					1
33(10.06m)			1							1			2
35(10.67m)		1	1	1		1	1	2		1		1	9
37(11.28m)							1					2	3
39(11.89m)								2		2			4
40(12.19m)		2										1	3
45(13.72m)		1											1
TOTALS	25	35	55	29	8	11	15	20	28	26	31	43	326

TABLE 3. WAVE PERIOD (SEC)

WAVE DIRECTION (DEG)	0-4	5	6	7	8	9	10	12	14	Totals
000	12	1		1	1	2	6	2		25
030	10	8	2	2		4	4	3	2	35
060	6	3	2	5	16	8	12	3		55
090	8	2	2	2	5	3	6	1		29
120	5	1	2							8
150	1	3	2		1	2	1	1		11
180		2	1	1	5	2	4			15
210	1		2	2	2	5	2	4	2	20
240	1		1	3		6	12	5		28
270	3	2	1	1	6	3	4	3	3	26
300	3	2	1	3	8	3	6	5		31
330	2	3	5	2	3	11	12	4	1	43
TOTALS	52	27	21	22	47	49	69	31	8	326

TABLE 4. BEAUFORT NUMBER

WIND DIRECTION (DEG)	0	1	2	3	4	5	6	7	8	9	10	Totals
000	7		1		4	3	2	3	1			21
030	1	1	7	9	6	6	2	1	3	2	1	39
060		1	1	5	20	11	5	7	3			53
090		2	2	7	5	4	1	2	4	1		28
120			3	3	3			2				11
150			2	2	1	2	2	1	1			11
180		1	1	2	3	2	2	3	2			16
210			4	1	2	3	3	3	3	2	1	22
240					4	7	3	1	2			17
270		3	1	2	2	8	3	2	7	4		32
300		1	2	2	6	8	2	7	2			30
330				8	8	12	8	3	3	1		43
TOTALS	8	9	24	41	64	66	33	35	31	10	2	323

In almost all cases the wave and wind directions given in each entry of the data sheets were found to be the same. It was therefore not considered necessary to give roses of wave height/wave direction corresponding to Table 2 since the Beaufort Number/wind direction rose was available in graph (c), and also there was found to be good correlation between wave height and Beaufort Number (Fig. 3).

Study of the relations between wave height/Beaufort Number and wave/length/wave
wave length calculated from wave period

A separate study was carried out to investigate the relationship between wave height/Beaufort Number and wave length/wave length calculated from wave period. All the cards available at the time were used and sorting operations were carried out. Tables 5 and 6 show the results.

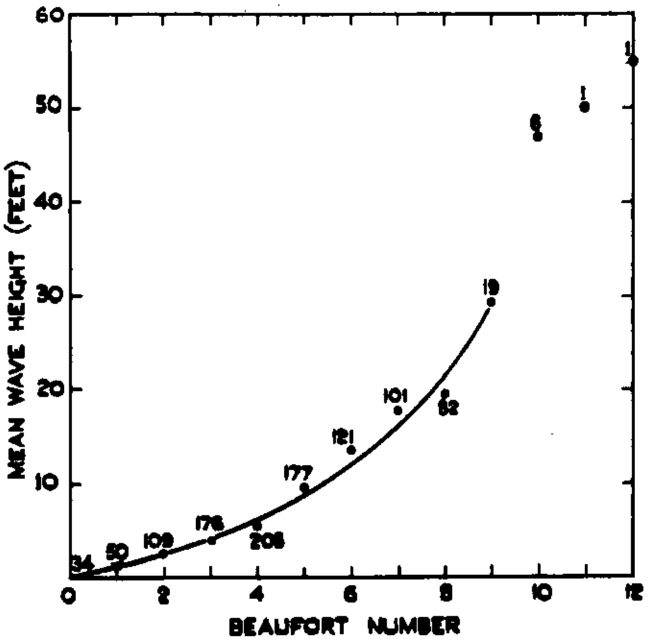

FIG. 3

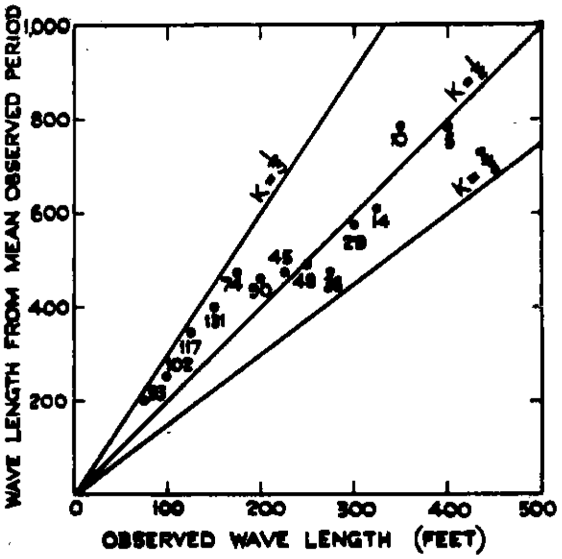

FIG. 4

Wave height/Beaufort Number

From Table 5 the mean wave height for each Beaufort Number was calculated and the results plotted in Fig. 3. The number adjacent to each point in Fig. 3 gives the number of observations at that Beaufort Number. A curve has been drawn through the points up to Beaufort 9.

This figure could be used to predict the wave height in a given area if the wind force is known.

Wave length/wave length calculated from wave period

Table 6 was used to determine the mean wave period corresponding to each observed wave length. The wave length corresponding to the mean wave period was then calculated using the classical formula

TABLE 5. BEAUFORT NUMBER

WAVE HEIGHT (FEET)	0	1	2	3	4	5	6	7	8	9	10	11	12	Totals
0(0.00m)	33	27	16	2	2	2		2						84
1(0.31m)		18	35	26	16		1	1	1					98
3(0.91m)		2	40	89	38	9	1	1						180
5(1.52m)	1	2	14	41	75	18	6	2	2					161
7(2.13m)			2	8	40	26	9	6	3					94
9(2.74m)			1	4	29	42	14	3	6					99
11(3.35m)				3	8	35	13	10	5					74
13(3.96m)						26	14	8	6					54
15(4.57m)			1	3		18	24	21	18	2				87
17(5.18m)		1				1	18	1	6					27
19(5.79m)							10	3	6	3				22
21(6.40m)							7	3	7	3				20
23(7.01m)							2	6		1				9
25(7.62m)							2	15	2					19
27(8.23m)								12	1					13
29(8.84m)								4	2					6
31(9.45m)								1	1					2
33(10.06m)								2	2					4
35(10.67m)									9	2				11
37(11.28m)									5					5
39(11.89m)										5	1			6
40(12.19m)										3				3
42(12.80m)											1			1
45(13.72m)											1			1
50(15.24m)											2	1		3
55(16.76m)											1		1	2
TOTALS	34	50	109	176	208	177	121	101	82	19	6	1	1	1085
Mean wave height (ft)	0	1.0	2.4	3.8	5.5	9.5	13.6	17.8	19.3	29.4	46.8	50	55	
Mean wave height (m)	0.00	0.31	0.73	1.16	1.68	2.90	4.15	5.43	5.88	8.96	14.26	15.24	16.76	

TABLE 6. WAVE PERIOD (SEC)

	0-4	5	6	7	8	9	10	12	14	Totals	Mean Period
50(15.2m)	200	47	16	7	4	1	5			280	-
75(22.9m)	2	42	21	6	9	6	6		1	93	6.3
100(30.5m)	3	8	32	22	23	7	5	2		102	7.0
125(38.1m)		3	20	17	26	25	22	4		117	8.2
150(45.7m)	1	2	5	24	28	13	46	10	2	131	8.8
175(53.3m)		1	3	13	16	5	14	14	8	74	9.6
200(61.0m)				5	27	14	29	11	4	90	9.5
225(68.6m)				1	15	8	11	8	2	45	9.6
250(76.2m)				1	7	18	10	11	1	48	9.8
275(83.8m)					2	17	13	3		35	9.6
300(91.4m)						5	13	11		29	10.6
325(99.1m)						2	5	7		14	10.9
350(106.7m)							2	4	4	10	12.4
400(121.9m)							1	2	2	5	12.4
500(152.4m)									1	1	14.0
TOTALS	206	103	97	96	157	121	182	87	25	1074	

$$\lambda = \frac{gT^2}{2\pi} \quad \text{where} \quad \lambda - \text{wave length}$$

$$T - \text{wave period}$$

Figure 4 shows the graph of wave length calculated from mean wave period against (observed) wave length. Also drawn are straight lines corresponding to the ratios of

$$K \equiv \frac{\text{observed wave length}}{\text{wave length from mean wave period}} = \frac{1}{3}, \frac{1}{2} \text{ and } \frac{2}{3}$$

It is seen that all the points lie between the two lines $K = 1/3$ and $K = 2/3$ and that at short wave lengths the points lie close to the line $K = 1/3$. This finding is in agreement with results shown in (Hogben, 1962).

The value of K depends on the nature of the wave spectrum. When the spectrum contains only a narrow band of frequencies and is also long-crested then K is close to unity. The theoretical value of K for a Neumann spectrum (modified by a factor $\cos^2\theta$ to give the angular dispersion of the waves) has been given (Pierson, 1954) as $K = 2/3$.

NOTE ON APPLICATIONS

An indication of the practical applications of data of this type has been given (Hogben, 1961) but it may be useful to include here some further comments. Data about sea conditions in the fishing grounds are of interest from many different points of view and no doubt will be of value to trawler operators as well as to designers. Here in Ship Division, NPL, they are to be used partly for planning the waves to be generated in the tank for seakeeping tests and partly as information to be applied to miscellaneous design problems and to be available for consulting purposes. The most immediate and clearcut application is to the planning of wave generation.

In the tank in Ship Division, tests studying such features as speed loss, motions and wetness can be conducted in regular or irregular waves as occasion demands and the irregular waves can be given any required spectral and statistical characteristics (Ewing, 1962). Thus for example it is possible to generate spectra which represent the sea likely to be generated by a given wind force (according to a Darbyshire, 1961; or Neumann, 1953; formulation). Spectra can also be set such that the estimates of mean height and period likely to be made by an observer will have any chosen values. Hence it is possible to generate wave spectra representing average or extreme conditions in a given area in terms of observed wave and wind data such as have been described.

CONCLUDING REMARKS

It would be premature to draw any elaborate or firm conclusions from the sample of data so far analysed. It is encouraging however to find already a meaningful picture emerging in a form which has direct application to the planning and interpretation of trawler tests in waves. It is also of interest to note results such as the relation of Beaufort Number and wave height in Fig. 3 and the relation of wave length and wave length calculated from wave period in Fig. 4 which have a wider and more fundamental significance.

ACKNOWLEDGEMENTS

This paper is presented by permission of the Director of the National Physical Laboratory and the Chairman of the White Fish Authority. Grateful acknowledgement is made for the cooperation of the Ministry of Agriculture, Fisheries and Food, the Combined Tabulating Installation of the Stationery Office and Mathematics Division, NPL.

The authors wish to express particular appreciation to all members of the above organisations who contributed to this work and also to the trawler skippers, Captain W. March (*Portia*), Captain Wood (*Arctic Vandal*), Captain W.G. Hardie (*Arsenal*), Captain J. Gower (*Cape Adair*), and Captain E.A. Binnington (*Ernest Holt*) for their patient efforts in collecting the data.

REFERENCES

DARBYSHIRE, J. 1961. The one dimensional wave spectrum in the Atlantic Ocean and in coastal waters. Conference on Ocean Wave Spectra, Easton, Maryland, USA.

EWING, J.A. 1962. The generation of discrete wave spectra in a ship tank. Ship Division Report 35.

HOGBEN, N., and P.D. CHAPLIN. 1961. A note on sea state and seakeeping studies on the research trawler *Ernest Holt*. FAO Research Vessel *Forum*, Tokyo.

HOGBEN, N. 1961. Sea state information and ship design. *Mar. Obs.*, January, 1961.

1962. Sea state observation studies on the S/S *Cairndhu* and R/V *Ernest Holt*. Ship Division Report 32.

1963. Sea state studies at the Ship Hydrodynamics Laboratory, Feltham. *Mar. Obs.*, June, 1963.

NEUMANN, G. 1953. On ocean wave spectra and a new method of forecasting wind-generated sea. *Tech. Mem., 43, Beach Erosion Board.*

PIERSON, W.J. 1954. An interpretation of the observable properties of 'sea' waves in terms of the energy spectrum of the Gaussian record. *Trans. Amer. Geophys. Un.*,vol.35, no.5.

G-2

RELATIONSHIP BETWEEN DRIFT-ICE, ATMOSPHERIC CIRCULATION AND FISHING POSSIBILITIES OFF SOUTHEAST GREENLAND DURING THE FIRST HALVES OF THE YEARS 1959-1963

By

Arno Meyer[1]

ABSTRACT

In spite of the big ice-drift along the coast of Southeast Greenland during the first half of the year, German trawlers have developed a surprisingly steady fishery since 1959. The study of all ice reports revealed that the ice is moved extensively by the wind. Westerly winds drive the ice seaward, often beyond the edge of the shelf, winds from north to east squeeze the ice against the coast leaving the banks ice-free. Twenty-four hours after the wind shifts to a westerly direction, the ice appears on the fishing banks.

The surprisingly low frequency of 14.7% ice-days (average for 1959-63) is the result of the specific atmospheric circulation over the Greenland area causing frequent N, NE and E winds (62% frequency). Westerly winds are mostly caused by lows moving towards Denmark Strait. Years with much ice show an Atlantic low shifted northward, years with little ice show a stronger developed Greenland "high" and a "low" shifted southward. Compared with the period from 1900 to 1939 the atmospheric circulation and the NE wind component were intensified in 1959-63.

Large quantities of ice are transported southward by the East Greenland Current during the first half of the year. Judging from the "Atlas of Ice-Conditions" and the reports on the first research and scouting trips (since 1955) it was doubtful if ice conditions would allow a more or less continuous trawl fishery during the first half of the year within the region from 60°N to 63.30°N (Fig. 1). However, Icelandic scouting trips found Fylkir Bank and Bille Bank already free from ice at the end of May and June 1957. Also early in May, and at the end of June 1958, five German trawlers succeeded in fishing on the Tordenskjold Bank, unhampered by ice. Early in May, 1959, a new attempt was made and in spite of some obstructions by ice, many trawlers fished there without interruption until 10 June. Then all ships were driven away from Tordenskjold Bank by ice and did not return until December, despite their good fishing.

After this first start of a successful fishery off Southeast Greenland a scouting trip in early winter 1959 found, from 10 to 18 December, the waters off South Greenland covered with ice at an extremely early date (Fig. 1), while the banks off Southeast Greenland were entirely ice-free. This scouting trip again revealed very good fishing possibilities off Southeast Greenland and by the end of December 1959 the first winter landings were made. Repeated attempts in January 1960 failed owing to unfavourable ice conditions. But since 14 February 1960, German trawler captains have succeeded in developing a more continuous and paying fishery for redfish and cod, though temporarily hampered or interrupted by ice.

A second scouting trip in April-May 1960 offered the opportunity for studying very different ice conditions and the relation between the specific ice situation and atmospheric circulation. On 16 April all German trawlers were driven from Tordenskjold Bank by eastward moving ice. From 19 to 21 April the biologist of this scouting trip sketched the extreme, eastern ice-edge (Fig. 2) showing ice at a distance up to 56 nautical miles from land. Eleven days later, when the ship returned from West Greenland, the ice was only 4 1/2 to 6 1/2 miles from the coast. All banks were free from ice and the trawlers had already resumed fishing by 23 April.

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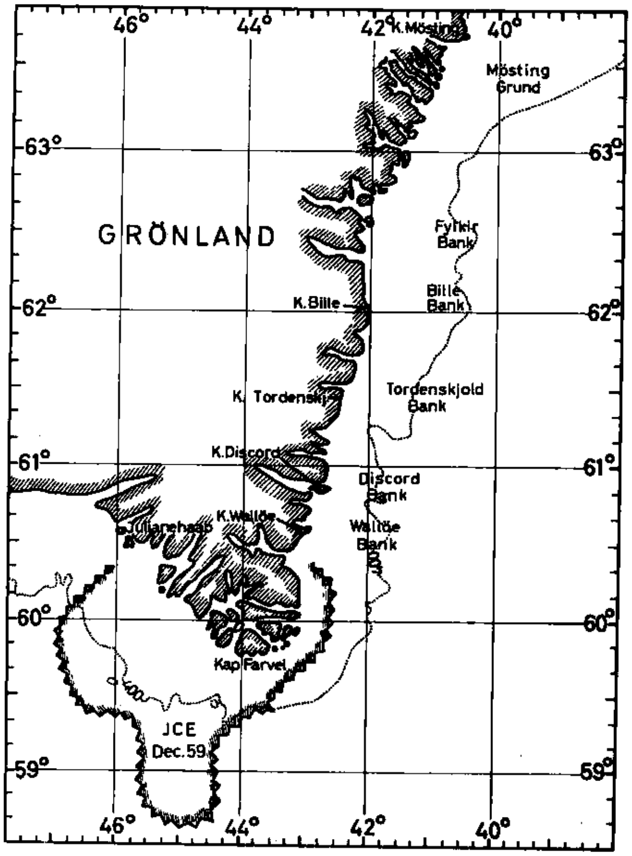

Fig. 1. The fishing banks off SE Greenland.

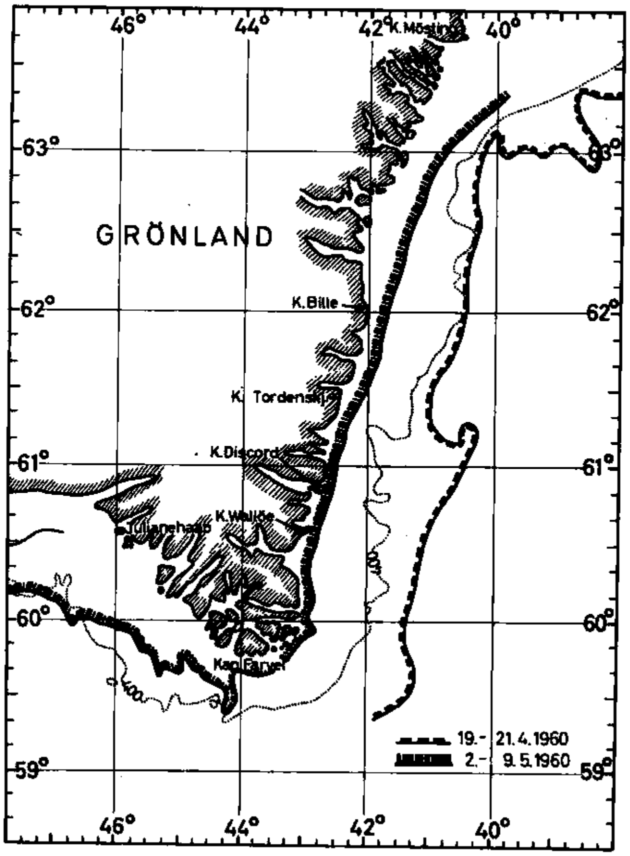

Fig. 2. The boundaries of ice off SE Greenland, 19-21 April and 2-9 May,1960.

The study of atmospheric circulation during this period and the examination of 78 reports of "ice on the fishing ground" given by German trawlers from the Southeast Greenland area in 1959-63 showed clearly that the movement of the ice is greatly affected by the wind. N, NE and E winds drive the ice clear of the banks and towards the coast while westerly winds drive the ice seaward again but seldom beyond the border of the shelf. The study of the ice reports showed further that usually within 24 hr after the winds had changed to a westerly direction the ice appears on the fishing ground hampering or stopping fishing activity. In some cases, when NE winds prevailed for longer periods a dead calm or light variable winds were sufficient to disperse the ice which was pressed against the coast in a seaward direction towards the fishing grounds.

Despite the immense ice masses transported southward during the first half of the year, ice is surprisingly rare on the Southeast Greenland banks which are from 28 to 45 miles from the coast. The reason is that NE winds, blowing at frequent intervals, accelerate the transport of ice and press it towards the coast. Table 1 (compiled from the daily weather reports of the trawlers, in the "catch reports" and "ship's observations", as well as the "weather charts" of the meteorological office) shows that on 62.6% of the days when German trawlers fished off Southeast Greenland, winds were blowing from the N, NE, or E. Winds from this northeastern quadrant were thus twice as frequent as winds from the other three quadrants together.

In the beginning, before the captains knew about the high frequency of NE winds off Southeast Greenland, they left the area when the ice approached and often they did not return for a long time. Today, after some years of experience, the trawlers rarely leave the Southeast Greenland area. When ice makes fishing impossible they move northward to evade the ice. This is because the southern banks (Walloe, Discord, Tordenskjold) are covered with ice earlier and usually in a heavier form than the northern grounds (Bille, Fylkir, Mösting). Two or three days later, when the wind has again changed to NE, they return to fish on the more productive, southern banks.

TABLE 1. FREQUENCY OF WIND DIRECTIONS AND OF ICE (IN DAYS AND PERCENT) ON THE SOUTHEAST GREENLAND FISHING GROUNDS IN THE FIRST HALVES OF THE YEARS 1959-1963.

	1959 7 May- 11 June	1960 10 Feb.- 18 June	1961 21 Jan.- 18 June	1962 8 Jan.- 27 June	1963 1 Jan.- 17 June	1959-63
N, NE and E winds	16(47%)	77(77%)	67(66%)	84(58%)	92(59%)	336(62.6%)
Other directions	14(41%)	19(19%)	28(27%)	51(35%)	56(36%)	168(31.3%)
Light variable winds or dead calm	4(12%)	4(4%)	7(7%)	10(7%)	8(5%)	33(6.1%)
Total days	34	100	102	145	156	537(100%)
Ice-days	5(15%)	9(9%)	17(17%)	30(21%)	18(12%)	79(14.7%)

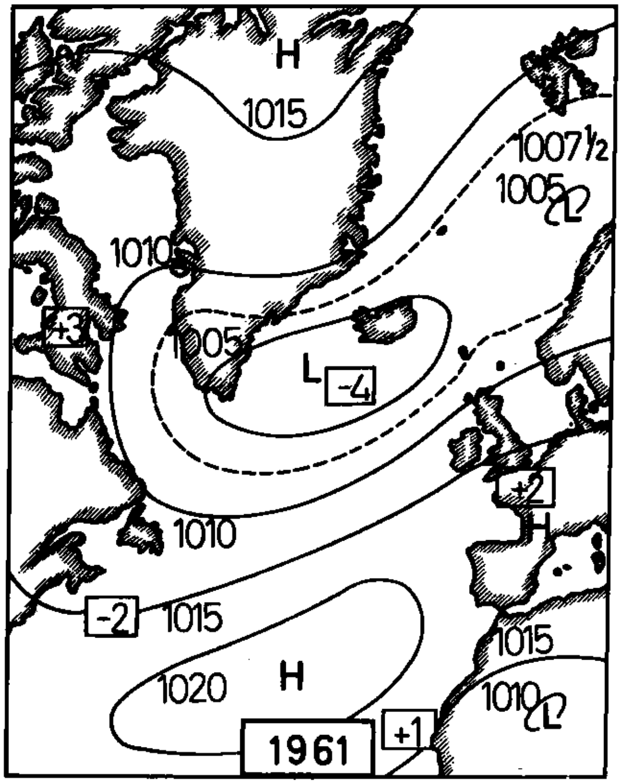

Fig. 3. Mean atmospheric pressure (in mb) and position of centres of anomalies, 1961.

The study of atmospheric circulation in the Greenland area gives a further insight into the ice and wind conditions. Charts of yearly and monthly mean atmospheric pressure distribution show that Greenland lies mostly within the range of a more or less well-developed high. A zone of low pressure extends from the south of Greenland east-north-east far beyond Iceland, usually with the centre over the Irminger Sea. The position of Southeast Greenland fishing grounds at the southeastern flank of the Greenland high or at the northwestern side of the Atlantic low explains the frequency of the NE wind situation (Fig. 3). Generally speaking, the lows coming from Newfoundland and Labrador pass Greenland to the south on their way to Europe. A few lows turn in a north-east track off South Greenland and move towards Denmark Strait, particularly when a strong high is blocking the eastward track. Studying the "days with ice" reported in 1959-63 shows that two-thirds of the SW to NW wind conditions, which carry the ice to the fishing grounds, were caused by cyclones moving toward Denmark Strait. Moreover an ice situation may result from a stationary high south or southeast of Greenland. Such an anticyclone develops S and SW winds off Southeast Greenland, and often small lows are guided along the Northwest and North side of such a high into the Icelandic area. In very rare cases, a low can move westward in the Irminger Sea, and then, when it is a low pressure system consisting of several secondaries, it becomes stationary in the southern Irminger Sea and the secondaries move in a counterclockwise circle.

Table 1 shows that the rapid development of the German fishery off Southeast Greenland in 1960 was especially favoured by a pronounced NE situation (77% of all days) with only 9% ice-days (average 1959-63 = 14.7%). A comparison of Fig. 3 with Fig. 4 demonstrates further, that, in 1960 when the Greenland high was stronger, the Atlantic low was less developed and shifted slightly to the south. The positive centre of anomalies over Greenland in 1960 showed, with 6 millibars(mb) the highest value of yearly anomalies from 1959-62 in the northern hemisphere. This pronounced NE situation in 1960 is even more evident from the monthly charts of mean pressure distribution. Already in October and November, 1959 (Fig. 5), a considerable, additional NE wind was blowing (+8 mb anomaly over South Greenland). In February, 1960 (Fig. 6), the NE situation was still more pronounced (+20 mb against -13 mb anomaly). These high pressure deviations not only account for the exceptionally early accumulation of ice around South Greenland in December 1959 (Fig. 1) but also for the rapid development of the German fishery on the Southeast Greenland banks.

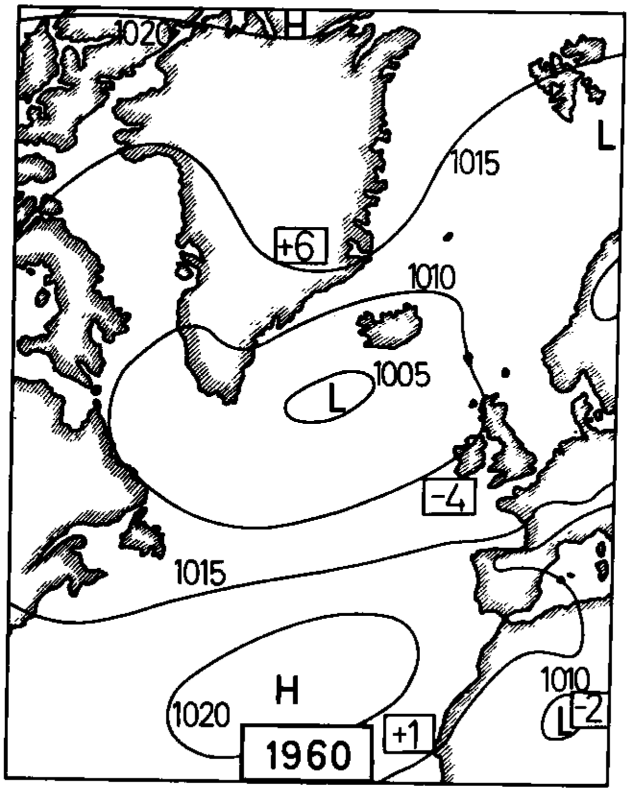

Fig. 4. Mean atmospheric pressure (in mb) and position of centres of anomalies,1960.

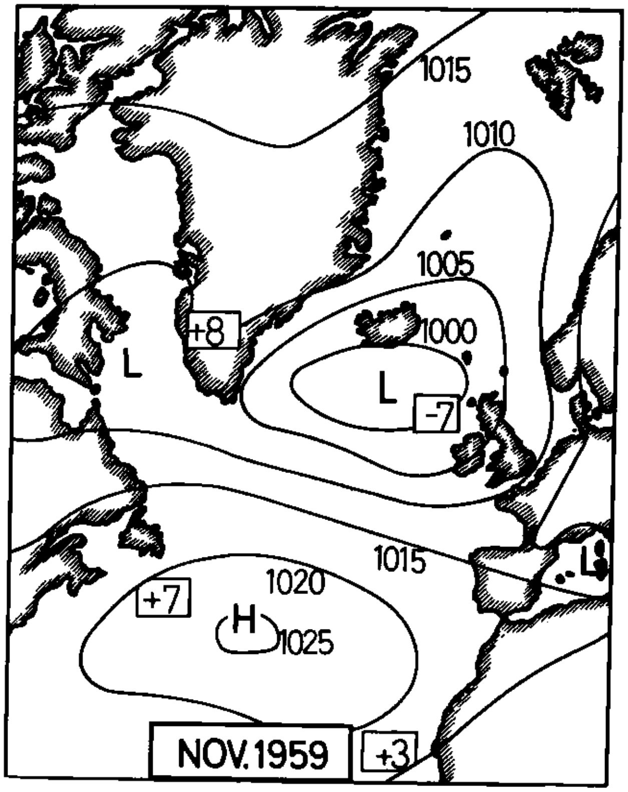

Fig.5. Mean atmospheric pressure (in mb) and position of centres of anomalies, November, 1959.

In contrast to 1960 which had little ice, 1962 was, to the present, the year with the most ice (21%). Ice was reported particularly frequently in January and February, mainly from 30 January to 16 February (11 ice-days). Lows moving steadily toward Denmark Strait caused westerly winds which brought the ice. Several times trawlers reported "steaming because of ice". The mean pressure distribution in January and February 1962 indicated a distinct northern position of the zone of low pressure (Fig. 7 and 8). In March, however, no ice hampered the trawlers owing to a big high which began developing over Greenland on 28 February. In this month, all Greenland lay within the 1,020 mb and North and East Greenland lay above 1035 mb (Fig. 9). On several days the extremely high pressure of 1,060 mb was found in the centre of the high! The centre of the Atlantic low was

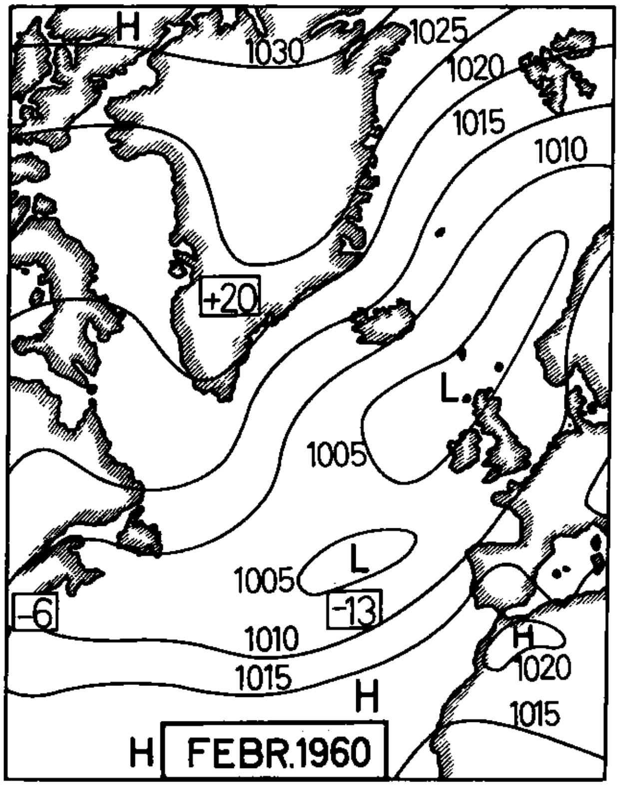

Fig. 6. Mean atmospheric pressure (in mb) and position of centres of anomalies, February 1960.

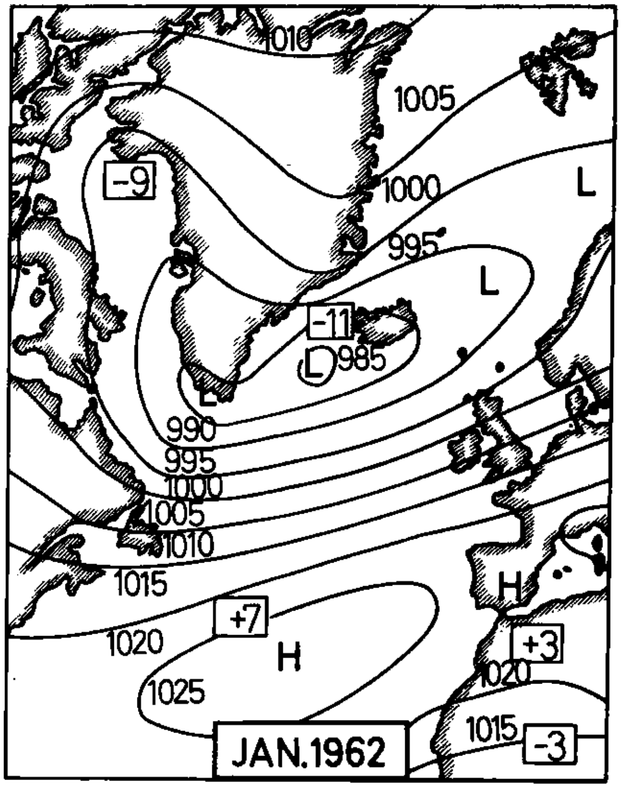

Fig. 7. Mean atmospheric pressure (in mb) and position of centres of anomalies, January 1962.

shifted more than 1,200 miles to the south as compared with the two preceding months. A positive centre of anomalies of +22 mb. over Greenland was opposed by a negative centre of -16 mb. near Weather Ship D. Such pronounced contrasts of atmospheric pressure led, of course, to a considerable crowding of isobars off South Greenland giving persistent, strong NE gales. The Southeast Greenland fishing grounds in March 1962 were entirely free from ice, but from 1 to 19 March the trawlers were only able to fish on two days! In May and June, however, the pressure situation was similar to that of January and February. May and June again had a high ice frequency of 26%.

These examples of varying atmospheric circulation show that fishing in the Southeast Greenland area is favoured by a somewhat extended high. However, the extreme atmospheric pressure differences between the Greenlandic high and the Atlantic low which keep the fishing banks free from ice, hamper fishing more by high winds than by pronounced ice conditions, for the normal distribution of pressure over Greenland leads already to considerable wind velocity and high waves off Southeast Greenland.

This study of the ice conditions off Southeast Greenland revealed a mean ice frequency of only 14.7% during the first halves of the years 1959-63, thus allowing a more or less steady fishery on the Southeast Greenland banks. The question is: Was the atmospheric circulation during these five years normal or were the years favoured by an increased NE wind component? Comparison of the mean pressure distribution during the first halves of the years 1900-39 (Fig. 10) and 1959-63 (Fig. 11) shows a marked dislocation of the centre of the low from South Greenland to the southern Irminger Sea and a considerable increase in the Greenland high and thus an intensification of the pressure diffences in the years 1959-63. The approximate doubling of the pressure differences (from 5.7 mb. to 9.9 mb.) and the dislocation of the low caused a considerable strengthening of the NE wind component. It is suggested that during the recent five years this additional wind has caused a diminished ice frequency on the banks, an accelerated ice transport to the south and consequently a smaller ice belt off Southeast Greenland. The stronger NE winds in 1959-63 must have produced

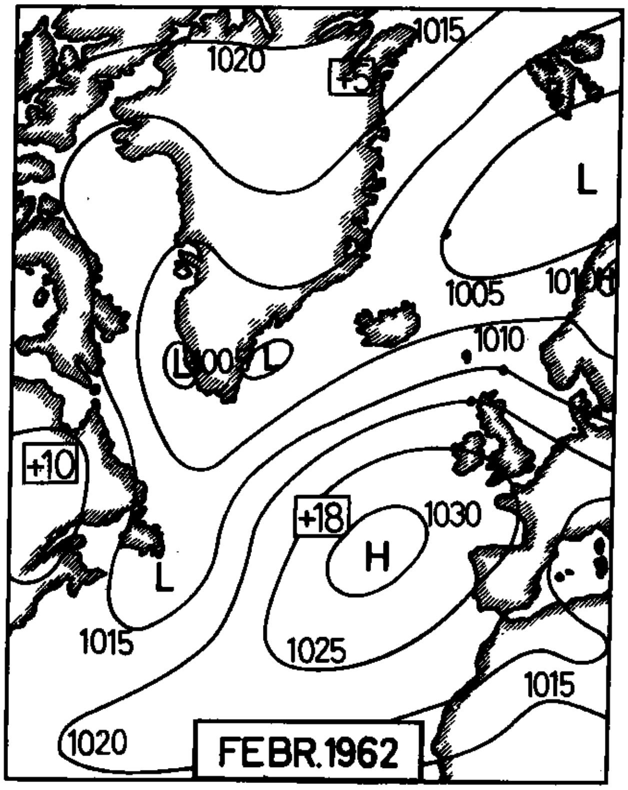

Fig. 8. Mean atmospheric pressure (in mb) and position of centres of anomalies, February 1962.

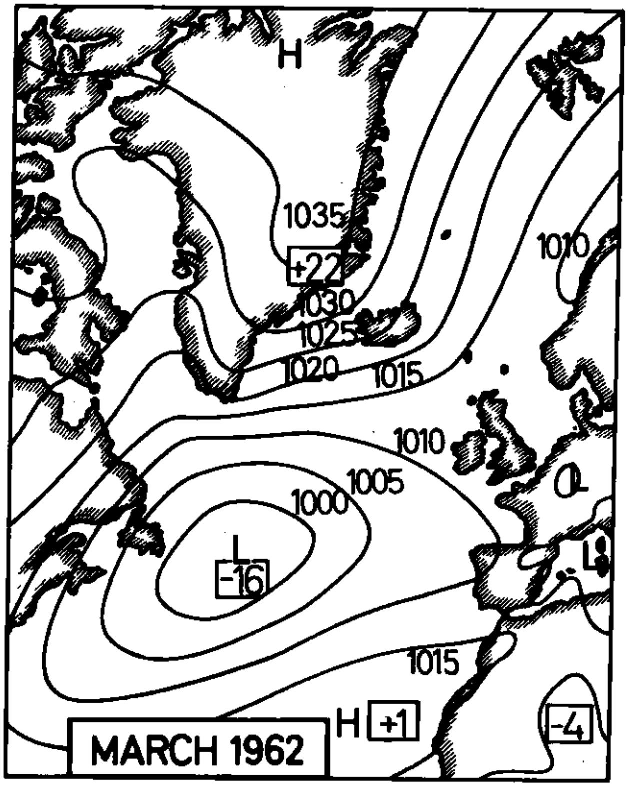

Fig. 9. Mean atmospheric pressure (in mb) and position of centres for anomalies, March 1962.

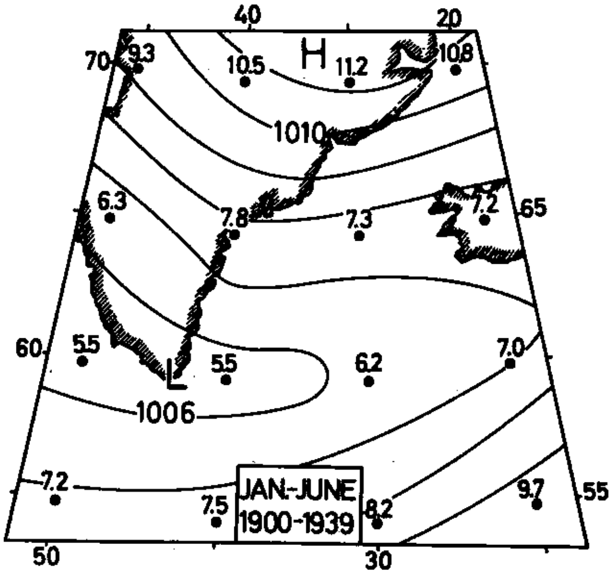

Fig. 10. Mean atmospheric pressure (in mb) in January-June 1900-1939.

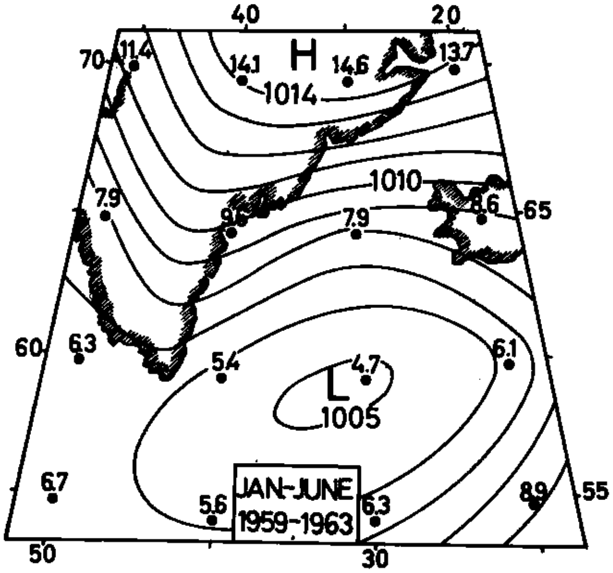

Fig. 11. Mean atmospheric pressure (in mb) in January-June 1959-1963.

(compared with 1900-39) an additional drift-current towards the coast across the direction of the two main currents. For example, a NE wind of wind-force 6 produces a drift-current on the surface of 0.4 knots, not in a southwestern direction, but in a more western direction, for in the northern hemisphere a drift-current turns to the right, as was first observed by Nansen and proved by Ekman (in theory, a 45° deviation). Off Southeast Greenland, NE winds are often blowing constantly for several days and, mostly with high velocity, this drift-current also influences the deeper water layers. But owing to the high latitude of Greenland the drift-current can only effect at the very utmost the first 100 m. Thus this additional current has no direct influence on the catches of the trawlers operating off Southeast Greenland in depths of 200 - 500 m. But the drift-current must have an influence on the fish stocks, for this current changes more or less the environment for eggs, larvae and plankton in the upper water layers. Further research will show whether there exists a correlation between a strengthened atmospheric circulation and the development of the new East Greenland stock of cod. Other open questions are: Were the years 1959-63 favoured by a relatively small ice-outflow from the Arctic Ocean? Which factor is more significant for fishing possibilities off Southeast Greenland, the total quantity of southward drifting ice or the wind-direction factor? Is it possible to forecast the quantity of ice in the coming year or years?

According to Nusser the ice-outflow of the Arctic Ocean is correlated with the atmospheric circulation over the Pacific sector of the Arctic Ocean and a forecast could be made three years in advance. In my opinion the study of atmospheric circulation should be increased with close collaboration between fishery scientists and meteorologists.

Finally, attention must be drawn to a very dangerous fishing practice connected with the fact that the movement of ice depends greatly on the wind. During a pronounced W wind situation an open water channel is formed, often more than 10 miles wide behind the ice belt moving towards the sea. Some young and ambitious captains then risk steaming in the southernmost part of Southeast Greenland behind the ice in order to fish behind the ice belt. This fishery is mostly very successful. But, even when weather forecasts are carefully observed, this fishery is very dangerous owing to the rapidly changing ice. This daring practice may lead some day to an ice tragedy, for even the most modern, big trawlers are not fitted with sufficient ice protection to allow then to break through a Greenland ice belt.

REFERENCES

Deutsches Hydrographisches Institut. Atlas der Eisverhältnisse des Nordatlantischen Ozeans und Ubersichtskarten der Eisverhältnisse des Nord -und Sudpolargebietes. Hamburg,1950.

Tägliche Fangmeldungen der Reedereinen der deutschen Hochseefischerei, Bremerhaven 1959-1963.

Wetterkarten des Seewetteramtes, Hamburg, 1959-1963.

Die Witterung in Übersee, Seewetteramt. Hamburg, 1958-1963.

Die Grosswetterlage Mitteleuropas. Amtsblatt des deutschen Wetterdienstes, Offenbach, 1959-1963.

Normalwerte des Luftdrucks auf der Nordhemisphäre für die Periode 1900-1939. Meteorologische Abhandlungen, Vol. II, No. 1, 1953-1955.

DIETRICH, G., and K. KALLE. 1957. Allgemeine Meereskunde, Berlin.

MEYER, A. 1960. Die 3. Suchreise 1959, eine Winterreise nach Grönland, Erfahrungen und Auswirkungen. Hansa, No. 23/24, Hamburg, 1960 and Informationen für die Fischwirtschaft, No. 3, Hamburg, 1960.

MEYER, A. 1960. Die Suchreise 1960 nach Grönland.-Hansa, No. 41/42, Hamburg, 1960, and Allgemeine Fischwirtschaftszeitung, No. 42, Bremerhaven 1960.

NUSSER, F. 1960. Neue Forschungsergebnisse über das Nordpolarmeer. Naturwissenschaftliche Rundschau, 13 (7), 1960.

Further reports by A. Meyer on Icelandic and German fishery research in: Wissenschaftliche nformationen für die Fischereipraxis, No. 5, 1955; No. 5, 1956; No. 6, 1958; Hamburg. Hansa, No. 39, 956; No. 44/45, 1956; No. 50/51, 1957; No. 7 and 10/11, 1958; No. 2/4, 1959, Hamburg.

G-3

CHANGES IN THE BEHAVIOUR OF FISH DUE TO ENVIRONMENT AND MOTIVATION AND THEIR INFLUENCE ON FISHING

By

H. Mohr[1]

ABSTRACT

The behaviour of fish with respect to availability and vulnerability to fishing is influenced by their surroundings and motivations which are both subject to fluctuations. Regular and predictable changes are caused by the planetary (seasonal, lunar, diurnal) cycles, while irregular changes are usually due to abnormal weather and hydrographical conditions. An increased activity is generally favourable and a reduced activity unfavourable for a passive gear, and vice versa for an active gear. Social behaviour patterns like shoaling are of great relevance for many fishing methods. The presence of other species too may influence the reactions especially in the case of prey or predators.

INTRODUCTION

Most large fisheries of the arctic and temperate zones are seasonal ones or at least show considerable fluctuations. The main reason for this is that the species concerned only form concentrations of sufficient density under special conditions. This is usually the case on the spawning, feeding or wintering grounds. The corresponding physiological conditions of the animals are caused by an endocrine rhythm which, in the extra-tropical areas, is regulated by the different temperature and light conditions. Therefore, the adult animals of a special population are, in the same season, subject to the same physiological condition and motivation. For marine organisms another planetary cycle, that of the moon, is important, especially because of its influence on the tidal phenomena, but also by its changing light. Besides, a "direct" influence of the moon is sometimes assumed. Furthermore, the change of day and night is of great relevance for the activity of animals. In the polar zones this cycle is interrupted temporarily.

These regular changes are influenced by several factors which are difficult or impossible to predict. These are especially the weather and hydrographical conditions which differ widely from year to year. Lastly biological factors in the environment, such as the presence of shoaling partners, prey organisms or predators, may influence the behaviour of animals.

All these factors are superimposed upon the normal cycles and vary them in their temporal course and intensity. The interplay may result in an increase or a decrease of the activity of the animals which is often decisive for success in fishing. But one can not classify these factors simply in two sections which affect the capture either positively or negatively. This depends on the gear and method used. Generally speaking, an increased activity is favourable and a lowered activity unfavourable for a passive gear, and vice versa for an active gear.

In this paper some examples of the points mentioned above are presented, mainly from the literature but also from personal observation. It is not attempted, and often even impossible, to discuss and analyse the behaviour patterns which may be involved, because in most cases we have insufficient information. More detailed descriptions and theoretical explanations may be found in the literature cited.

INFLUENCE OF THE PLANETARY CYCLES

The course of the seasons, by its change of temperature and light conditions causes a change in the surroundings and inner conditions of a fish which are usually so complex, that it is difficult

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to identify the proper reason for altered behaviour in field experiments. Changed reactions to nets of different colours can often be explained by the seasonal water colour caused by plankton organisms (Mohr, 1963) or the lowered light intensity in winter (Aslanova, 1959). By comparing the trawler's echo charts and the records of the "netzsonde", non-spawning shoals of herring were observed to react strongly to the gear, whereas spawners remained completely passive. The most striking seasonal change in availability of fish is associated with the sexual drive, which causes mass movements and concentrations (Woodhead, 1963,*a* and *b*) in so many and well-known cases, that specific examples are unnecessary here. These are most important pre-conditions for commercial fisheries, but the behaviour changes at the time of spawning influence the method of capture. For example, many species do not actively feed at this time and, therefore, bait is quite ineffective. Also, the reactions of the fish to stimuli unrelated to spawning are less strong at this time and, therefore, the conditions are usually most suitable for an active fishing gear. With a special type of one-boat midwater trawl, herring could never be caught successfully except in the spawning season, but then catches up to 20 tons were made in a few minutes (Mohr, 1963).

The lowered temperature in the winter often causes a lowered activity in fish. This is obvious in the attacks of sharks on men, which in the extratropical zones occur only in the hot season, when the water temperature is higher than 21°C. Further, spent herring are also easier to catch with a pelagic trawl than pre-spawners, probably because of their physiological condition (Balls, 1961). Besides spent herring stay in higher layers in day-time and their reactions to light change completely (Mohr, 1963; Richardson, 1960). Therefore, their availability to the bottom trawl and pelagic trawl depends a good deal on the season. A similar change from a demersal to a pelagic stage seems to take place in the cod after spawning. In the area of the Lofoten Islands practically no spent cod are caught by the bottom trawl (Trout, 1957).

The moon, by its strong influence on the tides, is a factor of great relevance for the behaviour of fish (as well as for the operation of the gear). In the Southern North Sea the herring shoals are cigar-shaped with the long axis in the line of the tidal stream (Bolster, 1958, 1962). Driftnets, therefore, should be set across this line in order to meet as many shoals as possible. Midwater shoals of herring in this area usually drift along the stream but demersal shoals, which are in visual or immediate contact with the bottom (or other stationary objects), stem the tide (Jones, 1959, 1962, 1963). Therefore, a bottom trawl is more effective when towed with the stream. On the other hand, a midwater trawl should be as, or even more effective when towed against the current. However, the catches are, in fact, usually better when the trawl is towed with the stream. The reason may be that the frightened herring swim against the water current (as many other species do) or they are in visual contact with the bottom (perhaps indirectly through stationary shoals below).

Landing statistics show that a maximum in the drifter catches of herring coincides with the full moon (Jens, 1952; Savage and Hodgson, 1934). Obviously the "swim" is stronger at this time. Whether this phenomenon is due to the light intensity or to a "direct" influence of the moon is unknown. It is said to happen too when the sky is completely clouded. Also, a strong influence of the moon is known on the spawning cycles of a Californian smelt, the common eel and a number of lower marine animals. The catches of migrating silver-eels in the German rivers and parts of the Baltic Sea in the few days of the waning half moon are up to ten times better than during full moon, and it seems to be proved that neither the light change nor the tides are the main factors for the increased migrating activity (Jens, 1952).

The changing light intensity between day and night is responsible for the diurnal vertical migrations which occur in many fishes. This phenomenon is observed not only in the "pelagic species", such as herring and hake (Balls, 1951; Lucas, 1936; Mucinic, 1933; Richardson, 1960), but also in the so-called "demersal" or "semi-demersal" species, such as redfish, cod, saithe, haddock and many flatfish (Seydlitz, 1962; Schmidt, 1955; Woodhead, 1960). In the same species there are often large differences in the direction and magnitude of this vertical movement depending on the maturity stages (Richardson, 1960; Woodhead, 1960). In most cases, the adult fish stay in deeper layers during the day. This is the reason that herring are traditionally caught in day-time with the bottom trawl and at night-time with pelagic gears. With a midwater trawl one can theoretically reach them in all layers. The over-wintering herring in the Norwegian Deep area can be caught in day-time very successfully by a two-boat midwater trawl but, during their vertical movement in dusk and dawn, they are so active that only poor catches are possible. Even during the stationary phase, below the surface, at night the herring avoid the gear by going deeper immediately before the net reaches them, as can be seen clearly in echo-charts (Mohr, 1963). In the case of some flatfish, big differences, which are probably due to different reactions to the gear, occur between the night and day catches.

For example, bottom-trawl catches of soles on the same ground at night are twice as large as daytime ones. Aquarium experiments show that it is likely that, in day-time, the soles react to a disturbance by burying deeper into the seabed, whereas, in the night, they roam freely over the ground. Plaice are caught in considerably higher numbers just after sunrise. Since the plaice is a visual feeder, it may be entirely occupied in feeding at this time (Woodhead, 1960).

IRREGULAR FACTORS

The regular, periodic behaviour is influenced by many scarcely predictable factors which contribute to the short term fluctuations in the commercial fisheries. Most of these factors are associated with the weather and hydrographical conditions which are subject to numerous, irregular changes. The extreme conditions, which hinder or even prevent fishing altogether, are not mentioned further. As stated above, the catch by driftnets is much better when the fleet is set across the direction of the tidal stream; but to do this depends on the direction of the wind (Bolster, 1962; Craig, 1960). During a spell of very clear weather at the end of the winter season off the South Norwegian Coast the herring were so close to the seabed in day-time that the midwater trawls usually became damaged and therefore failed, whereas the bottom trawls, which had very poor catches earlier, now had big ones (Mohr 1963). The direction of the wind also influences the abundance of fish in this area. When the wind shifts to a southern direction, the fish shoals always disappear completely within a few hours. Probably they have dispersed in all layers (v.Brandt and Steinberg, 1962). A similar relation to the wind is observed in the case of the Lofoten saithe. Yet here the catches are two to three times larger when the wind comes from south. The coinciding "internal waves", rather than the direction of the local wind, are supposed to be the main reason for the dispersion of the fish. These "internal waves" are fluctuations of the isothermal lines in the water and are caused by cyclones hundreds of miles away, in the open Atlantic (Schmidt, 1955).

As mentioned above, the temperature conditions influence the abundance of fish as well as their behaviour with respect to the gear. This is very evident in the coincidence of extremely big landings of soles with severe winters. At these times the fish are concentrated in the warmer areas and their avoiding reactions to the trawl, in day-time, decrease or cease at low temperatures (Woodhead, 1960). The effect of temperature on the distribution of herring and roundfish in both the horizontal and vertical directions is well-known (Craig, 1960; Dietrich *et al.*, 1959; Schubert, 1950; Tokarew, 1958). The uncertain conditions in the tuna fishery in the North Sea and the decrease in the cod fishery in the Barents Sea caused by low temperatures are also mentioned (Rodewald, 1960). In 1963, exceptionally good catches were made by drifters in the Western North Sea at times when the trawlers made only poor catches. This was due to the cold water masses at the bottom, which were avoided by the herring (Schubert, 1963). Eels do not feed until the water has reached a temperature of 9°C. After the past, severe winter the eel fishery, with bait, in the estuaries and rivers of Germany began nearly two months later and was very poor.

INTERSPECIFIC AND INTRASPECIFIC INFLUENCES

In addition to abiotic and intrinsic biotic factors (physiological condition and motivation), a number of extrinsic biotic factors also influence the behaviour and vulnerability of fish stocks, especially their shoaling. Here we must distinguish between aggregations and shoals in a narrower sense. In contrast to an aggregation, a shoal is a polarized group of fishes which moves and reacts as a whole (Breder, 1959). In the feeding period, herring form big concentrations in suitable places but the driftnet catches are often poor because the "shoaling pressure", which drives them blindly into the nets, is lacking. Small migrating shoals often bring better results (Tokarew, 1958). The pre-spawners and spawners usually form aggregations too, which shoal temporarily during their vertical migration. In the night they disperse in all directions near the surface. As long as no "swim" takes place, they are caught in small numbers on both sides of the fleet. Yet at a certain time, only once in 24 hours, if at all, the "swim" occurs. Time and intensity seem to depend on tide and moon-phase. Often the "swim" lasts only a very short time but 5,000 - 250,000 herring are caught by a single fleet (Graham, 1931). In the "swim", shoaling takes place, because the fish push from the same direction into the net. The "swim" is supposed to be a sudden panic in the fish. Different intrinsic or extrinsic factors are assumed to govern this panic. In a recently published article, the theory is discussed that the lack of oxygen in the dense concentrations of fish during the time of slack water may be the reason (Kalle, 1963).

In fishing with rod and hook for tuna, fish in small shoals are usually most voracious and their activity stimulates even tuna with full stomachs to take the bait (Inoue, 1959; Hotta *et al.*, 1959). The presence of other species may also influence the availability of fish. Examples, in which feeding organisms cause concentrations and behaviour changes have been reported (Hardy *et al.*, 1936; Tokarew, 1958). Tuna seem to trust in the watchfulness of porpoises and in the case of purse-seining one must be careful not to excite the latter. In some areas sardines are only available for purse seining when they are driven to the surface by dolphins (Cushing, 1959). Even in the cod-end of trawls, predatory species may cause panic and hence a higher rate of escapement or meshing of fish (Clark, 1963).

REFERENCES

ASLANOVA, N.E. 1959. Investigations on the Behaviour of Fish in Respect to the Fishing Gear. *Trudy* VNIRO, Moskow 36, p. 33-51 (in Russian).

BALLS, R. 1951. Environmental Changes in Herring Behaviour. *J. Cons.*, 27, p. 274-298.

1961. Fish Capture. (London).

v.BRANDT, A., and R. STEINBERG. 1962. Schwimmschleppnetzversuche im Gebiet von Egersund. *Prot. FischTech.* 7, p. 256-328.

BREDER, C.M. 1959. Studies on Social Groupings in Fishes. *Bull. Amer. Mus. nat. Hist.*, 117, p. 395-481.

BOLSTER, G.C. 1958. On the Shape of Herring Shoals. *J. Cons.*, 23, p. 228-234.

1962. The Influence of Wind and Tide on the Catch by Drift Nets in the East Anglian Herring Fishery 1952-1956. *J. Cons.*, 27, p. 150-161.

CLARK, JOHN R. 1963. Size Selection of Fish by Otter Trawls Results of Recent Experiments in the Northwest Atlantic. *Spec. Publ. int. Comm. Northw. Atlant. Fish.*, No. 5, p.24-96.

CUSHING, D.H. 1959. Fishing Gear and Behaviour. World Sci. Meet. Biol. Sardines, Rome. Methol. paper No. 3 (mimeogr.)

CRAIG, R.F. 1960. A Note on the Dependence of Catches on Temperature and Wind in the Buchan Pre-Spawning Herring Fishery. *J. Cons.*, 25, p. 185-190.

DIETRICH, G., D. SAHRHAGE and K. SCHUBERT. 1959. Locating Fish Concentrations by Thermometric Methods. Modern Fishing Gear of the World I (London).

GRAHAM, M. 1931. Some Problems in Herring Behaviour. *J. Cons.*, 6, p. 252-265.

HARDY, A.C., C.E. LUCAS, G. HENDERSON and J.H. FRASER. 1936. Ecological Relations between Herring and Plankton. *J. Mar. biol. Ass., U.K.*, Nov. 1936.

HOTTA, H., T. KARIYA, and T. OGAWA. 1959. A Study on the "Biting" of Skipjack in Live Bait Fishery. *Bull. Tohoku Fish. Res. Lab.* 13, p. 60-78.

INOUE, M. 1959. On the Relation of Behaviour of Skipjack and Tuna Schools to their Catch Inferred from Data for Seine Fishery. *Bull. Soc. Sci. Fish.* 25, p. 12-16.

JENS, G. 1952-53. Über den lunaren Rhythmus der Blankaalwanderung. *Arch. FischWiss.* 4, p. 54-110.

1954. Untersuchungen über rhythmische Erscheinungen beim Heringsfang in der Nordsee. *Arch. FischWiss.* 5, p. 113-119.

JONES, F.R.H. 1959. Movements of Herring Shoals in Relation to the Tidal Current. *J. Cons.*, 22, p. 322-479.

1962. Further Observations on the Movements of Herring (*Clupea harengus* L.) Shoals in Relation to the Tidal Current. *J. Cons.*, 27, p. 52-76.

1963. Fish and Water Currents. *World Fishing* 12, No. 7 and 8.

KALLE, K. 1963. Zur Frage des Schwarmverhaltens von Heringen. *Arch. FischWiss.* 13, p. 89-92.

LUCAS, C.E. 1936. On the Diurnal Variation of Size Groups of Trawl Caught Herring. *J. Cons.*, 11, p. 53-59.

MOHR, H. 1963. Reaction of Herring to Fishing Gear Studied by Means of Echo Sounding. 2. *World Fish. Gear Cong.* (London), paper No. 21 (mimeogr.).

1964. Netzfarbe und Fängigkeit bei Kiemennetzen. *Arch. FischWiss.* 14, p. 153-161.

MUCINIC, S. 1933. Der Rhythmus der Nahrungsaufnahme beim Hering. *Ber. dtsch. Komm. Meeresforsch.* 6, p. 62-64.

RICHARDSON, J.P. 1960. Observations on the Size and Numbers of Herring Taken by the Herring Trawl. *J. Cons.*, 25, p. 204-217.

RODEWALD, M. 1960. Die jüngsten Wassertemperatur- und Fischpendel-bewegungen in der Barentssee als Folge von Schwankungen der Luftzirkulation. *Hansa,* Hamburg, 97, No. 8/9, p. 481-482.

SAVAGE, R.E., and W.C. HODGSON. 1934. Lunar Influence on the East Anglian Herring Fishery. *J. Cons.*, 9, p. 223-237.

v.SEYDLITZ, H. 1962. Untersuchungen über die Tagesperiodizität des Rotbarsches, *Sebastes marinus*, auf Grund von Fanganalysen. *Kurz. Mitt. Inst. FischBiol. Univ. Hamb.* No. 12, p. 27-36.

SCHMIDT, U. 1955. Beiträge zur Biologie des Köhlers (*Gadus virens* L.) in den isländischen Gewässern. *Ber. dtsch. Komm. Meeresforsch.* 14, p. 46-82.

SCHUBERT, K. 1950. Der Heringsfang im Juli in der Nordsee. *Fischereiwelt* 2, p. 149-151.

1964. Bessere Heringsfänge im vergangenen Jahr. *Allg. FischwirtschaftsZtg.* 1/2, p. 56-60.

TOKAREW, A.K. 1958. Special behaviour Patterns of the Atlantic Herring in the Feeding Period. *Trudy* VNIRO, Moskow, 36, p. 6-118. (In Russian).

TROUT, G.C. 1957. The Bear Island Cod. Migration and Movements. *Fish. Invest., Lond.* (2), No. 21.

WOODHEAD, A.D. 1963*a*. The Migration of Fish. *World Fishing* 12, No. 3 and 4.

WOODHEAD, P.M.J. 1963*b*. Concentrating Factors in Fisheries. *World Fishing* No. 5 and 6.

1960. Diurnal Changes in the Trawl Catches of Fishes. ICES CM 1960, Near North. Seas Comm. paper No. 18 (mimeogr.).

1960. A Change in the Normal Diurnal Pattern of Capture of Soles during the Severe Winter of 1963. ICES CM 1960, Near North. Seas Comm. paper No. 19 (mimeogr.).

G-4

BOTTOM CONTOURS AND NATURE OF GROUNDS AND THEIR SIGNIFICANCE FOR TRAWL FISHING

By

I.K. Avilov[1]

ABSTRACT

This paper describes the correlation between trawl fishing and the bottom topography and the nature of grounds in the ICNAF area. The author shows that the main factors governing the formation of relief deal with processes of subaerial erosion and glacial abrasion and the main sources of material for the formation of grounds are the underlying morainic deposits. Different rates of change under the influence of the hydrodynamic processes result in different concentration of stone material in deposits and in some areas glacial clay and solid rock are also exposed. The author gives an appraisal, for various parts of the ICNAF area, of the suitability of the grounds for trawl fishing. In this respect the area off West Greenland is considered to be the most difficult, while toward the South the conditions are better. In comparison with other regions of the North Atlantic, which were formed under the same conditions, the ICNAF area is the most complicated one.

Past experience has shown that trawl fishing depends to a considerable extent on bottom topography and the nature of bottom deposits (grounds).

Although the surveyed areas of the Northwest Atlantic, including the regions of West Greenland, and the coasts of Labrador, Newfoundland and Nova Scotia (Fig. 1) are substantially uniform, the individual sectors differ notably among themselves.

The formation of the present bottom contours and deposits and of their characteristic features took place under the influence of numerous factors, some of them referring to the remote past. Our present knowledge about the development of oceanic sectors of this area of the Atlantic is entirely based on geology and the history of formation of its shores. This knowledge, apparently can only be applied confidently to the shelf and partly to the upper sectors of the continental slope *i.e.*, to the areas of the bottom involved in trawl fishing. Some additional information on the history of development of this area is being provided by detailed studies of underwater topography.

The northwestern part of the Atlantic was essentially formed during the Pre-Cambrian age, under the influence of ancient folding. It includes the Canadian Crystalline Shield, the marginal zone of which forms the Labrador Coast, and the central part of Greenland. The sectors of the ocean bottom between Labrador and Greenland,— Davis Strait and the Labrador Sea,— should be considered as a part of the same area. During the Paleozoic age, mountain structures of Caledonic and Hercynian orogeneses appeared along the periphery of the zone of Pre-Cambrian folding. Appalachian structures and their extensions on the bottom of the Atlantic Ocean represented by Nova Scotian and Newfoundland banks, including the Newfoundland Grand Bank and Flemish Cap Bank, were probably formed in the main in the Caledonian age. Many sectors of the surveyed area of the Atlantic were subsequently subject to numerous fractures and were broken by granite intrusions.

The West Greenland Coast is composed mainly of ancient gneisses, crystalline schists and intrusive granites. In the area of Disko Island, basalts and Tertiary sedimentary strata are developed. The Labrador Coast is built up of granites, granodiorites and gneissose granites. In the area of Newfoundland the prevailing rock types are of sedimentary complex.

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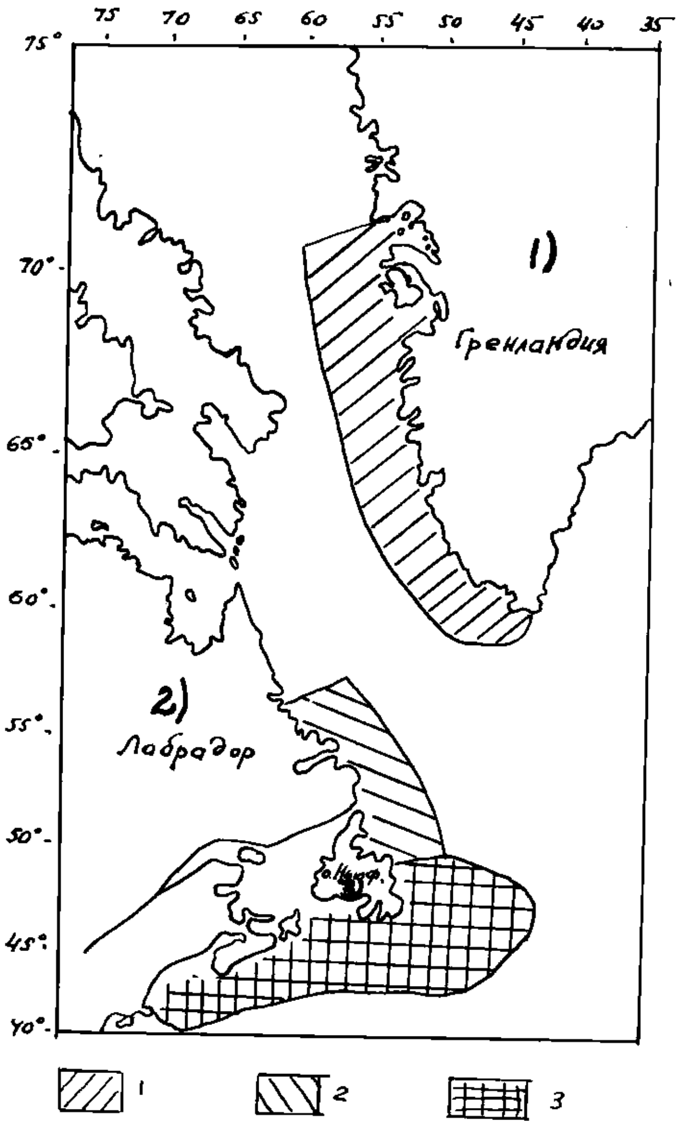

Fig. 1. Fishing areas in the Northwest Atlantic 1) The West Greenland Area 2) The Labrador Area 3) The Newfoundland and Nova Scotia Area.

(English translation of place names
1 — Greenland,
2 — Labrador,
3 — Newfoundland Island).

At the time of Alpine folding the northwest Atlantic was subject to multiple depressions of surface level and fractures which basically shaped the present contour. The appearance of the Davis Strait and Labrador Sea should also be referred to that period (Neogen). The subsequent effect of powerful processes of subaerial river erosion and glacial abrasion on the underlying surface resulted in its notable transformation and in the appearance of topographic forms peculiar to these processes.

We believe that the processes of subaerial erosion and glacial abrasion played a more important role in the formation of the present topography of land than all the other factors mentioned above. The duration of these processes must also have been a factor of some importance for the formation of the relief. The marked differences in the topography of the northern and southern sectors of this area should evidently be explained by the duration of the effect of the above factors and by their varying intensity, determined primarily by variations in isostatic movements in individual sectors of the area. A brief description of their topography is given below.

The topography of the West Greenland Coastal zone is characterised by an Alpine landscape. The ice-free area of the shore, from 1.5 to 180 km wide, represents a system of massifs crushed by faults, with peaks up to 1,600 m high. The coast is dissected by numerous fjords up to 100-180 km long, with depths reaching 500 m in estuaries. The shores are bordered with numerous islands making up a wide belt of skerries.

The Labrador Coast is much less dissected. The surface of Labrador represents a plateau from 400 to 800 m high, with individual peaks standing out. The shore line of the Labrador Peninsula is uneven, indented with fjords and bays, but dissected to a much lesser degree than that in Greenland. The Newfoundland Island's relief is still more smoothed out. The plateau, occupying its surface is from 400 to 500 m high. The height of the remaining extended elevations, known as mountain ranges, does not exceed 805 m. On Nova Scotia, low-lying hilly plains prevail. Its shores are dissected with bays which often look like fjords but are still smaller than those on Newfoundland.

Bottom contours

Although the shelf and the continental slope have much in common, there are also marked differences between them. The width of the shelf and continental slope is variable. The general tendency of the shelf to widen from north to south in some sectors of the Northwest Atlantic is reversed. The nature of dissection of the shelf into individual banks isolated from each other and from the shore, typical for the entire Area, varies markedly by regions. The gradients and the nature of dissection of the continental slope also vary.

Off the west coast of Greenland, for example, the width of the shelf decreases abruptly from north to south. Whereas off Disko Island depths of less than 500 m extend 70 to 90 miles from the coast in the south then extends about half that distance. In contrast, the width of the shelf off Labrador more than doubles from north to south, *i.e.*, from 60 miles near northern Hamilton Bank to 150 miles in the area off Belle Isle Bank. Still farther south, in the latitude of the northern Newfoundland Bank, the width of the shelf reaches 200 miles, and it even exceeds that range on the Grand Newfoundland Bank. To the west of the Grand Bank the width of the shelf decreases and levels off, to 110-120 miles, but farther west in the Gulf of Maine, the shelf considerably widens again.

The depths at the edge of the shelf and of the surfaces of the banks also vary. In Davis Strait, north of its sill (64°N), the edge of the shelf is found at an average depth of 160-180 m, whereas in the southern part of the shelf it increases to depth of 230-240 m. The depths of location of the banks vary accordingly, but within a somewhat wider range. Off the north Labrador Coast the edge of the shelf is located at a depth of about 300 m and in the area off Belle Isle Bank, almost 100 m deeper. At the latitude of the northern Newfoundland Bank, the boundary between the continental shelf and continental slope is found at a still greater depth. The depths of location of the surfaces of the banks vary in a similar way. The minimum depths of northern Hamilton Bank are a little less than 100 m; of Hamilton Bank, about 150 metres; of Belle Isle Bank, around 200 m, and of northern Newfoundland Bank, more than 200 m.

The Grand Bank, with depths mostly less than 90 m, is an exception. The depth of its boundaries varies. In the northeast corner its edge is located at a depth of 200-300 m; in the southeast, it is at 70-80 m; in the south, at 110-120 m, and in the west, at 100 m. Off Nova Scotia it is also at about 110 m.

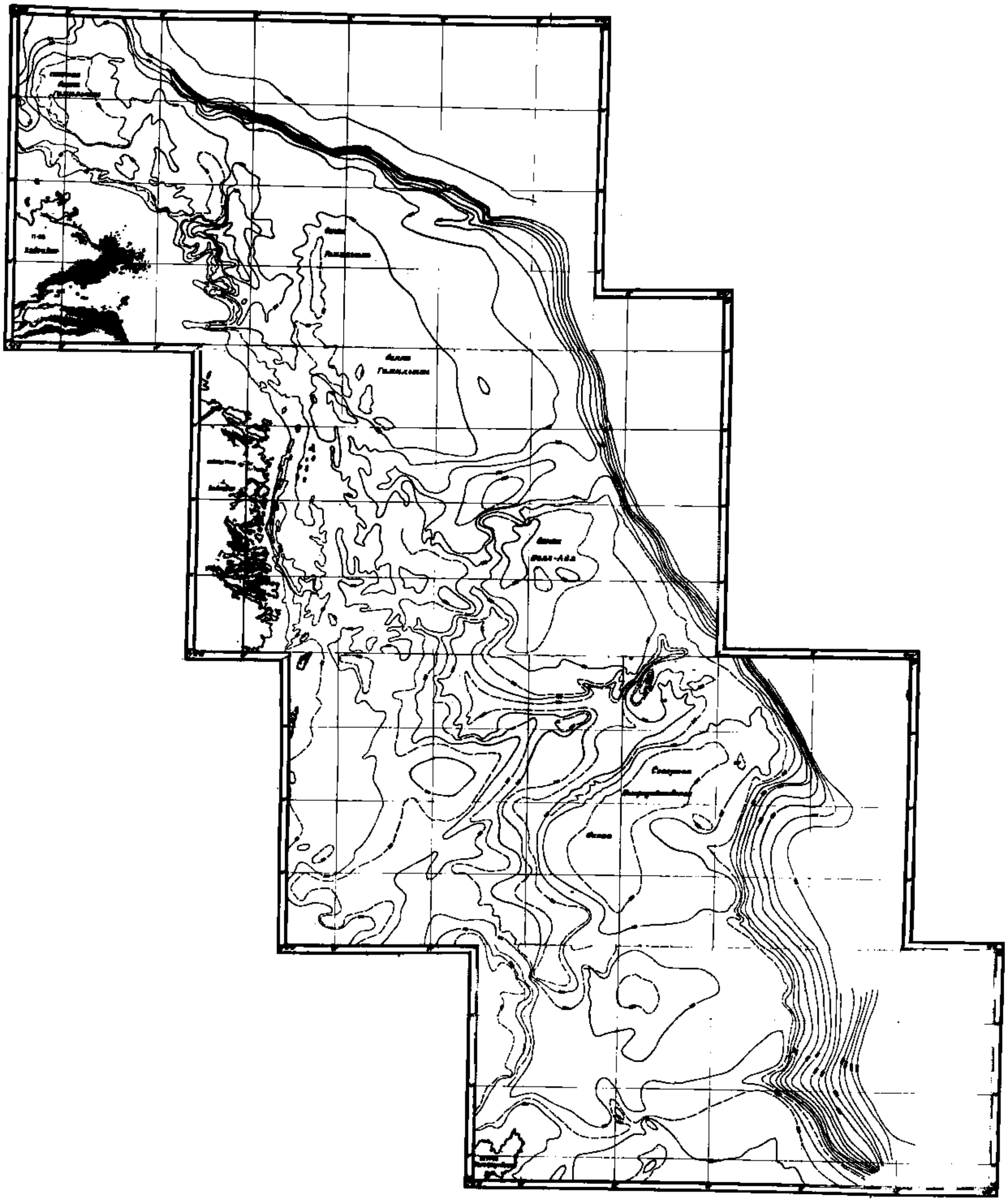

Fig. 2. Bottom contour in the Labrador area.

(English translation of place names — 1) Northern Hamilton Bank, 2) Labrador Peninsula, 3) Hamilton Bank, 4) Labrador Peninsula, 5) Belle Isle Bank, 6) Northern Newfoundland Bank, 7) Newfoundland Island).

The northern part of the West Greenland Shelf, north of Danas Bank, is divided by longitudinal depressions (extending along the shores) into larger, outer and a smaller, inner (coastal) part. The longitudinal depressions do not communicate and are usually quite deep; their depths greatly exceed the depths of the shelf, reaching at some places 500-600 m; their slopes are steep (up to 20-22°) and much dissected.

The outer part of the shelf, north of Danas Bank, and its southern sectors are divided by transverse depressions (running normally to the shore), which represent ancient river valleys, transformed to a considerable extent by Quaternary glacial ice, into individual banks. These transverse depressions, usually have straight and steep slopes (up to 14-15°) and sometimes are more than 200 m deep. In the southern sectors of the West Greenland Shelf, where it is narrow, and partly in its northern zone, the underwater valleys are found on a line with the fjords of Greenland, actually representing their extensions on the bottom of the sea. In the sectors where logitudinal depressions are developed such a relation is difficult to track, since the transverse valleys connect the longitudinal depressions (to which estuaries of a group of fjords are bound) with the open part of the Davis Strait. Most of the transverse valleys have underwater sills located near the edge of the shelf.

Commercial banks are located in the wide outer zone of the shelf. The sizes of the banks decrease greatly from north to south,(*e.g.* the area of Store Hellefiske Bank, within the 100 m isobath, is 15.5/thousand sq. km, and that of Frederikshaab Bank in the south is 0.2 thousand sq. km). In the northern part of the West Greenland Shelf, banks are located somewhat off its outer edge, whereas south of latitude 64°N they are located right on the edge. With the decrease in the area of the banks, the degree of dissection of their surfaces and slopes increases considerably.

The entire area of the shelf south of Frederikshaab Bank represents an undulated valley, intricately dissected with diversely oriented hills and ridges whose relative heights range from 50-100 m.

Practically nothing is known of the continental slope in the coastal area of West Greenland; but judging by the nature of the continental slope in East Greenland and by the structure of the continental slope in the southern part of the West Greenland Coast, where it is much indented, as well as by some other indications, it is safe to assume that its structure is complicated, except maybe for the sectors on the slopes adjacent to the banks.

The structure of the shelf off the Labrador Coast is similar to that off Greenland, except for the much larger sizes of the banks, depressions and other forms of bottom contour (Fig. 3). Longitudinal depressions, extending to a distance of 20-50 miles from the shore can be traced all along the investigated part of the Labrador Coast (south of 56°N); they have gentle gradients and their genesis is somewhat different from that of the depressions off Greenland. Maximum depths of the individual troughs in the longitudinal depressions also reach 500-600 m.

Transverse depressions, (the valleys dividing the shelf into individual banks), are wider and deeper than those on the Greenland Shelf; they have assymetrical slopes, and are often narrowed in their estuarine portions near the continental slope from which they are usually separated by a wide elevation (sill) having relative height of 150-200 m.

All of the topographic features of the Labrador Shelf are more subdued in relief and, accordingly, have gentler gradients than those of the Greenland Shelf. The continental slope is also gentler, especially in its upper zones. Its steepest sector is observed in the north of Hamilton Bank. Farther southwards, east of Hamilton and Belle Isle Banks, the continental slope smoothes out, its maximum gradient not exceeding 4° 20'. Near northern Newfoundland Bank the slope becomes still smoother (up to 1°), and remains so all the way to the northern zones of the Grand Bank.

It is unnecessary to dwell at length on the topography of the Newfoundland and Nova Scotian banks as they have already been described in previous publications; it should only be mentioned that these areas are characterised by the same topographic features as those described above, apart from being still more subdued in relief. This can be explained by a shorter period of exposure to the effect of Quartary glacial ice, and a longer period of influence of marine abrasion after the end of glaciation. The effect of these processes on the continental slope was quite different. It was, evidently, subject to highly intensive dissection, both during and after the period of glaciation. As a result, and because of somewhat different geology as compared with the northern areas, the

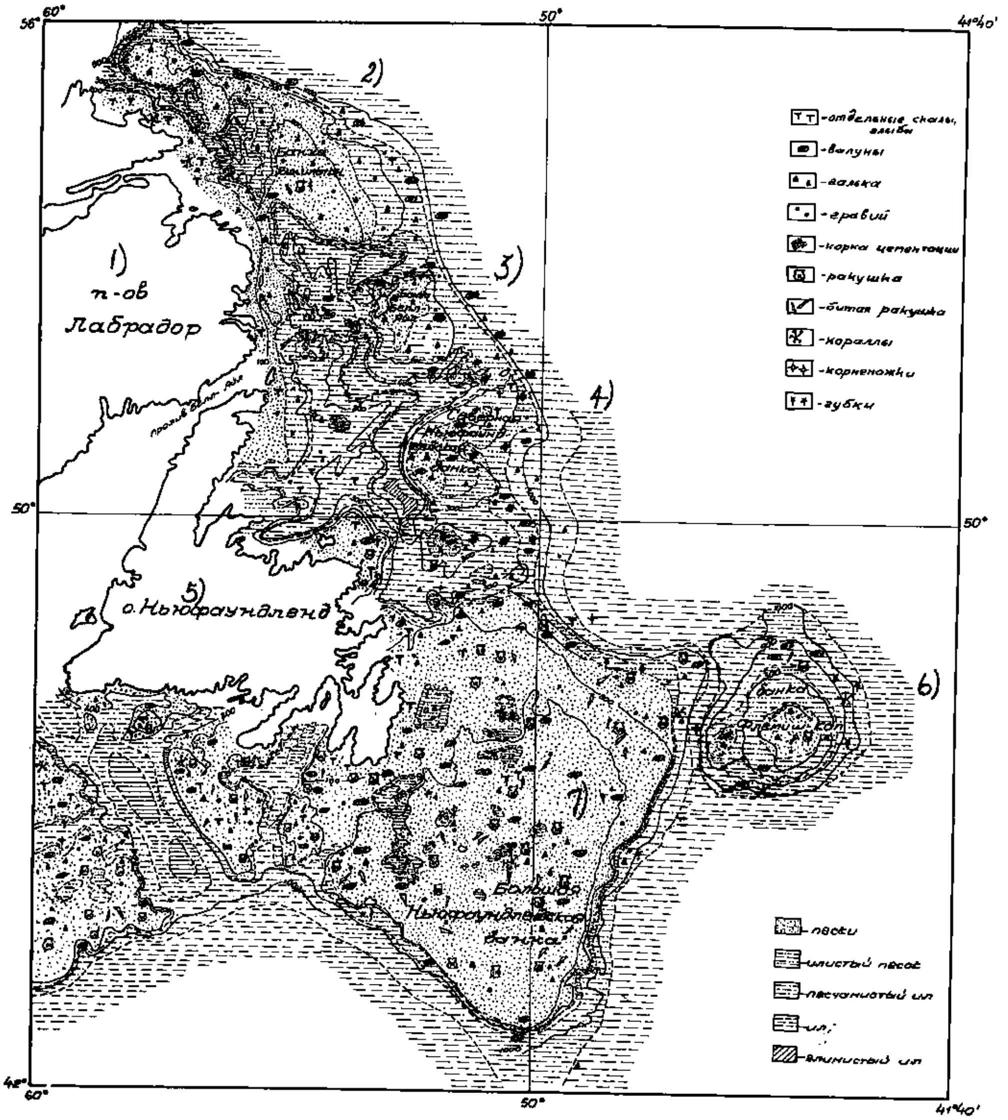

Fig. 3. Sketch map on bottom contour and distribution of bottom deposits in the Labrador and Newfoundland areas.

(English translation of key to the items in the order presented on the map —

1) individual rocks, blocks,	9) rhizopods
2) boulders,	10) sponges,
3) pebble,	11) sand,
4) gravel,	12) clay sand,
5) cement crust,	13) sandy silt,
6) shell,	14) silt,
7) crushed shell,	15) clay silt)
8) corals,	

(English translation of place names —1) Labrador Peninsula, 2) Hamilton Bank, 3) Belle Isle Bank, 4) Northern Newfoundland Bank, 5) Newfoundland Island, 6) Flemish Cap Bank, 7) Grand Newfoundland Bank).

continental slope along the Newfoundland and Nova Scotian banks is very steep and dissected by a continuous network of underwater canyons with peculiar longitudinal and transverse sections. The gradients of the side walls of the valleys are from 10° to 16°; in some places they develop into cliffs. The angle of gradient of the continental slope varies within a narrow range. The southern slope of the Grand Bank is somewhat gentler than the eastern one, around 5.5° at depths from 100 - 1500 m. In the Nova Scotian area, gradients of the slope range from 2° 20' to 5° 50'. The valleys observed on the slope do not usually extend onto the shelf; individual canyons, however, penetrate far into its depths. The greatest of them is the well known Gully Canyon which crosses the entire area of the shelf and reaches the shores of Nova Scotia.

Bottom deposits

In the areas discussed above, the great variety of the morphology of the bottom, varying climatic, hydrochemical and other conditions and uneven solid discharge, resulted in the accumulation and formation of diverse bottom deposits. Since the underlying strata, represented mainly by morainic deposits which cover almost the entire surface of the shelf and part of the continental slope, were the primary source of sedimentary material, the bottom deposits have many characteristics in common.

The whole of the North West Atlantic is characterised by a predominance of coarse sediments with the inclusion, almost everywhere, of coarse stone material, the amount of which generally decreases from north to south. The concentration of stone material in sediments is caused primarily by erosion of the underlying strata, the intensity of which is higher in the narrow and indented sectors of the shelf. In the coastal zones of the shelf, increase in its content should be often attributed to stones brought by ice. Such stones are usually notable for their angularity. High activity of water in the narrow and indented zones of the shelf may even result in complete removal of sand clay and formation of stony ground; in some cases solid rock can also be exposed. As an obvious example of formation of stone ground we can point out the appearance of boulder-pebble accumulations off the West Greenland shores; they line the bottom and slopes of the valley which cuts through the Danish Sill from the south and through the tops of some banks. Zones of boulder-pebble and pebble-gravel grounds can, evidently, be found on the southern, West Greenland banks,too. In the western zone and on the western slope of the Grand Bank the presence of pebble-gravel ground was revealed by underwater photography. Pebble-gravel deposits with admixture of echinus tests are observed in the eastern part of Grand Newfoundland Bank and in the Labrador coastal zone. Fields of stony ground (gravel-pebble-boulder) are found in the Nova Scotia area on a number of banks and crests, amidst the depressions of the shelf. Continuous accumulations of boulders are observed in the coastal zone of this area. Individual rocks are found in the coastal zone of the entire area of the Northwest Atlantic under investigation, as well as on the Grand Bank in the region of Woolfell, Eastern Shoal elevations and Virgin Rocks.

The greater part of the surface of the Shelf is covered with sand of various grades and composition. The marginal zones of the banks are covered with silt sand replaced by sandy silt on the continental slope. Sandy silt covers the greater part of the depressions between the banks and between the inner (coastal) and the outer zones of the shelf. Finer ground, silt and clay silt occupy the depressed zones of the shelf protected against water movements and are found at greater depths on the high seas.

As it has already been mentioned above, all coarse-grained grounds, including sandy silt, contain some stone material with individual boulders and blocks. Some blocks weigh several tons and obstruct the trawl fishery more than anything else. Boulders are usually buried in sand on all the southern West Greenland banks. On the northern Greenland banks boulders are encountered in their peripheral zones only, mostly on their outer slopes.

In the Labrador area and in the areas farther to the south the boulder content in the sedimentary deposits of the shelf and continental slope is much lower. In the Labrador area they are concentrated in the marginal zones of the banks and on the continental slope as well as in the coastal zone of the shelf. Boulders are quite frequent on the northern and southwestern slopes of Flemish Cap. On the Grand Bank they occur almost everywhere, considerable concentrations being observed in its northeastern marginal zone, in the centre (near the above mentioned rocky banks Woolfell etc.), and near the southern end of Newfoundland Grand Bank. On the Nova Scotian banks, boulders are concentrated mostly in the sandy areas.

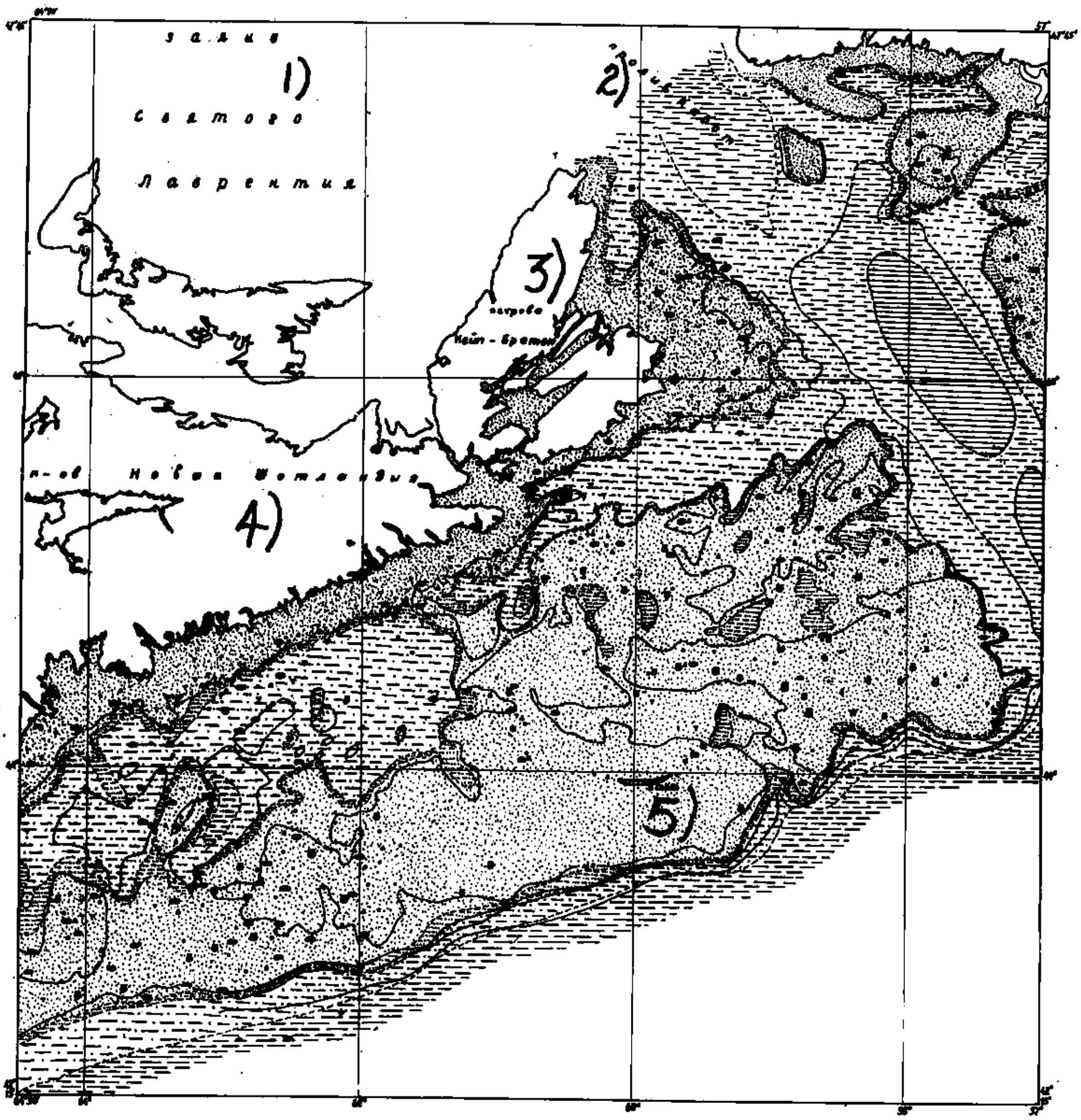

Fig. 4. Sketch map on distribution of bottom deposits in the Nova Scotia area.

(English translation of place names — 1) Gulf of St. Lawrence, 2) Cabot Strait, 3) Cape Breton Island, 4) Nova Scotia Peninsula, 5) Sable Island.)

The underlying morainic glacial deposits, represented by tight, tough bluish clay are exposed on the steep slopes of some banks. In most cases, however, they are covered by a thin layer of sediments. In the West Greenland area clay outcrops are encountered on the slopes of Fiskenaes Bank, at a depth of 100 m and are especially abundant on the slopes of Danas Bank at depths of 200-250 and 230-300 m. On the slopes of Frederikshaab Bank they are exposed at depths of 200-350 m. Glacial clays are also found on the continental slope off Labrador and on Newfoundland Grand Bank. On the Grand Bank clays also occur on the slope of the trough separating it from the coast.

Solid rocks are exposed on the bottom in many places along the continental slope in this part of the Atlantic.

The characteristics of the bottom contour and ground, cited above reveal that part of the surface of the shelf and, to a lesser degree the upper zones of the continental slope can be fished with existing trawling gear. At the same time it becomes evident that some sectors of the bottom offer great difficulties and some others make trawl fishing impossible. The areas with grounds containing individual boulders also make trawl fishing very difficult. According to rough estimations, they occupy about one-fifth of the total fishing area in this part of the Atlantic. Areas covered with solid rocks or with solid rocks exposed in the form of individual cliffs should be classified as bottom surfaces which can not be exploited with present gear. They include rocky zones of the West Greenland banks, Newfoundland Grand Bank and coastal (inner) zones of the shelf throughout the whole of the Northwest Atlantic.

The areas of the bottom covered with sediments containing large numbers of large-size boulders and, evidently, some stony sectors of the bottom containing glacial clays in which trawl boards may stick should be also excluded from the potential trawl fishing area for the time being.

To those areas in which trawl fishing is impossible should also be added the regions characterised by a high degree of dissection and steep gradients, *viz.*, the continental slope of the Grand Bank (beginning from its northeastern corner), the entire continental slope off Nova Scotia, part of the southern slope of Flemish Cap, the slopes of some depressions on the Nova Scotian Shelf, the slopes of a number of longitudinal depressions off Greenland and, apparently, some sectors of the Greenland continental slope, particularly those adjacent to the estuarine portions of transverse valleys.

Trawl fishing can also be obstructed by the accumulations of some immovable living organisms whose development depends not only on hydrological, hydrochemical and other conditions, but also on the contour of the bottom and the nature of grounds. The well known coral thickets surrounding the entire Flemish Cap Bank at depths of 300-700 m and most abundant on its eastern and southern slopes, provide a good example.

The above characteristics of fishing areas in the Northwest Atlantic indicate that the area off West Greenland is the most difficult to exploit because of the contour of its bottom and the nature of its grounds. The Labrador coastal area seems to be definitely better, but the most favourable conditions exist on the Newfoundland and Nova Scotian banks. It is thus obvious that there are considerable areas in the Northwest Atlantic which cannot be exploited by the present trawling fleets, but can be considered as reserve fishing grounds. Individual sectors of the continental slope, up to 1000 m, also constitute reserve grounds. The most promising of these may prove to be the Flemish Cap slopes, the northeastern slope of the Grand Bank, the entire area of the continental slope from Hamilton Bank to northern Newfoundland Bank, and part of the West Greenland slope.

A comparison of the Northwest Atlantic with other North Atlantic areas formed under similar conditions, shows that the area in question has a much more complicated bottom contour and the nature of its grounds is less favourable for trawl fishing. This is further aggrevated by severe climatic and navigational conditions.

In conclusion, it should be pointed out that our knowledge of the bottom contour and grounds in the fishing areas of the Northwest Atlantic are extremely superficial and, except for the southern areas (Newfoundland Grand Bank and Nova Scotia), cannot meet the requirements of the commercial trawling fleet. Therefore, further investigations of this complex and important part of the World Oceans are necessary. It seems that particular attention should be paid to the continental slope.

SECTION

H

H-1

RECENT CHANGES IN THE BENTHOS OF THE WEST SPITSBERGEN FISHING GROUNDS

By

R.W. Blacker[1]

INTRODUCTION

In 1957 the writer published some of the results of the examination of benthos collected by the R/V *Ernest Holt* during research cruises to Svalbard in the period 1949-55. (Svalbard is the Norwegian name for the area including Spitsbergen, Bear Island and Hope Island). These data showed that there were many benthic species which were characteristic of one or the other of the two main water types, Atlantic and Arctic. Several hundred benthic species were identified. Of those most commonly caught in the trawl or most likely to be caught, seven were selected as being indicators of Atlantic conditions and nine were selected as indicators of predominantly Arctic conditions. The seven Atlantic water indicators were: the sponge *Geodia barretti* Bowerbank; the decapod crustacea *Lithodes maia* (Linnaeus) and *Sabinea sarsi* Smith; and the echinoderma *Ceramaster granularis* (Müller), *Pseudarchaster parelii* (Düben and Koren), *Hippasteria phrygiana* (Parelius) and *Gorgonocephalus lamarcki* (Müller and Troschel). The selected indicators of Arctic conditions were: the crustacea *Sabinea septemcarinata* (Sabine) and *Sclerograngon ferox* (Owen) and the echinoderma *Heliometra glacialis* (Leach), *Poliometra prolixa* (Sladen), *Hymenaster pellucidus* Thomson, *Lophaster furcifer* (Düben and Koren), *Gorgonocephalus eucnemis* (Müller and Troschel), *G. arcticus* Leach and *Ophiopleura borealis* Danielssen and Koren.

Plotting the recent distribution of these species up to 1955 clearly showed the areas where the Atlantic water of the West Spitsbergen Current was the predominant hydrographic influence. When this chart was compared with one showing the distribution of the same animals compiled from research cruises made between 1878 and 1931, it was found that Atlantic species had spread northwards along the west coast of Spitsbergen as far as 78°N and that few Arctic species were caught on banks where previously they had been recorded as abundant.

RECENT RESULTS FROM WEST SPITSBERGEN

The results from 1949 to 1955 showed that striking changes had taken place in the benthos off West Spitsbergen, but too few stations had been worked to determine the full extent of the changes. From 1955 to 1959 records of the selected indicator species were obtained from about one hundred additional positions off West Spitsbergen, on the banks northwards from 76°N lat to 80°09'N on the Norske Bank.

These new records show that by 1959 the ranges of *Geodia, Lithodes* and *Hippasteria* extended to at least 79°30'N and that *Sabinea sarsi* had reached 80°09'N. North from 79°N the edge of the bank etween 100 and 200 fathoms has not been fished because it slopes steeply and is rough. Two atempts to survey this area in the summers of 1957 and 1958, using underwater cameras, were unsucessful because of bad weather and ice conditions.

Nesis (1959) gives the results of Russian work off West Spitsbergen during the period 1946-48, adding the material from 155 stations to the present author's published data (Blacker, 1957). Using 23 boreal species and 42 Arctic species, his records show that the Atlantic species *Sabinea sarsi* and *Lithodes maia* (amongst others) occurred as far north as 80°55'N, 17°12'E at a depth of 477 m (261 fathoms). *Gorgonocephalus eucnemis* and other Arctic species occurred at the same tation. Nesis states that "only a few of the more hardy north-boreal species penetrate further to the east". Figure 1B summarises the records of indicator species for the period 1949-59 (Russian tations are not included). Comparison with Fig. 1A, which summarises the period 1878 to 1931, shows

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[1] Fisheries Laboratory, Lowestoft, Suffolk, England.

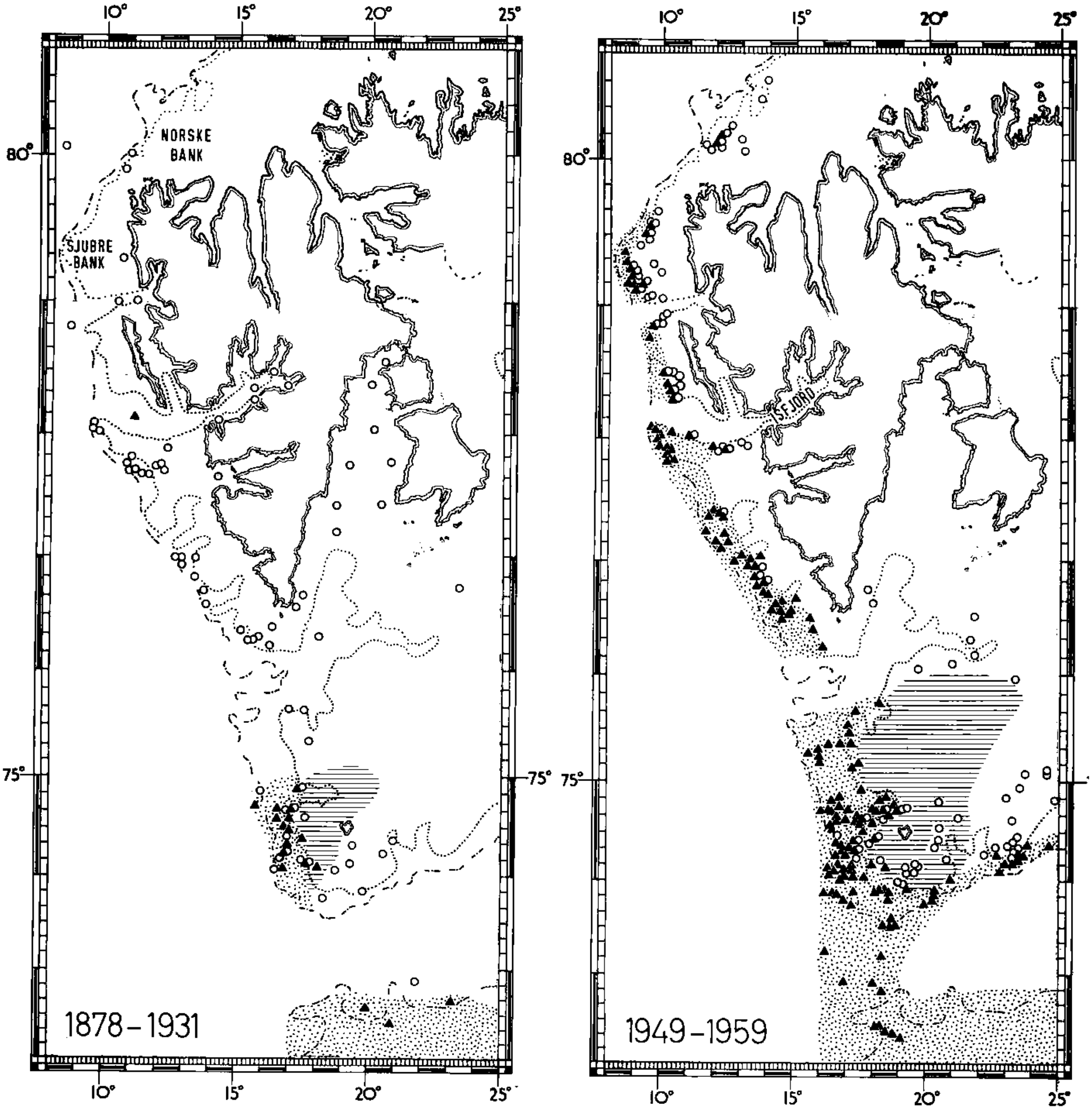

Fig. 1. Summary charts of the distribution of Atlantic species (▲) and Arctic species (O). A. All past records, 1878-1931. B. Present records, 1949-1959 (excluding recent Russian data).

The stippled area indicates the bottom where Atlantic conditions predominate, as deduced from the occurrence of Atlantic species. Comparison of A and B shows how much the Atlantic influence has increased since 1931. The hatched area covers places where conditions may vary from Atlantic to extreme Arctic; similar areas may occur in shallow water off Spitsbergen.

a 300-mile northward spread of Atlantic species along the course of the West Spitsbergen Current during the past 30 years. In addition, from Norwegian researches there are records of the boreal species *Sabinea sarsi* (in 1958) and *Lithodes maia* (in 1960) from the entrance to Isfjord where they had never been found before (Christiansen and Christiansen, 1962).

DISCUSSION

It must not be inferred from the latest data that the spread of Atlantic species northwards has gone on since the period 1949-55. This may have happened, but the data from that period only showed that a change had taken place and they were insufficient to give a basis for inferring a continuation of the warming-up process. As before, the latest records include a number of anomalous ones from the northernmost banks where Arctic species, in particular *Sabinea septemcarinata, Heliometra* and *Gorgonocephalus eucnemis*, were found in water warmer than 2°C. From depths greater than 80 fathoms the anomalous records are of small specimens, few in number, and thus are of little significance. However, in shallower depths, especially on the Norske Bank, these Arctic species are abundant where high temperatures have been recorded. All these records have been obtained during July to October when the water temperatures reach their summer maximum, so it is probable that the shallower parts of these banks are covered with warm water for only a short season each year. There are no hydrographic observations from the winter months, when warm temperatures would perhaps indicate that a change to predominantly Atlantic conditions was taking place. The presence of breeding *Sabinea sarsi* on the Norske Bank shows a considerable Atlantic influence there but insufficient work has been done to determine its full extent. There may be some Atlantic benthos all the way along the edge of the shelf from the Norske Bank to about 81°15'N near Northeast Land, where the West Spitsbergen Current flows away from the continental shelf over the deep cold water of the Arctic Basin. It is here that the benthos should first show signs of a general cooling of the Arctic.

How long it takes for cooling down to affect the benthos is not known. The mechanism by which the recent changes in the distribution of the benthos could have been produced, by variations in the strengths of the warm West Spitsbergen Current and the cold East Spitsbergen Current, was fully discussed in the earlier paper (Blacker, 1957). Nothing new has been found out about the ability of the indicator species to withstand adverse conditions produced by changes in the currents. It may take only a matter of months for some of the species to be killed, while the less sensitive ones may perhaps survive for a year or longer apparently unaffected.

From recent hydrographic observations there are indications that the warming-up of the Arctic has stopped and that cooling may have started. According to Timofeyev (1961) the mean annual temperature of the Atlantic water entering the Arctic Basin was less than average from 1957 to 1960 and in the latter year the discharge of Atlantic water and heat into the Arctic Basin was the lowest on record for the period 1933-60. It is hoped therefore that a more detailed survey of the benthos of the critical area on the northern banks will be carried out before any major change takes place. As ice conditions there make regular hydrographic observations in winter difficult or impossible to obtain, basic data for the detection of changes in the distributions of the indicator species are important.

SUMMARY

1. The results of a benthos survey of the Svalbard region from 1949 to 1955 showing changes in the distribution of selected species during the past thirty years are reviewed.

2. Summary charts for the periods 1878 to 1931 and 1949 to 1959 are given, showing the spread northwards of Atlantic species since 1931.

3. Anomalous results from the northernmost part of the area are discussed.

4. The importance is stressed of surveying the northernmost part of the area soon, before any major climatic change takes place.

REFERENCES

BLACKER, R.W. 1957. Benthic animals as indicators of hydrographic conditions and climatic change in Svalbard waters. *Fish. Invest. Lond.*, (2), 20 (10): 1-49.

CHRISTIANSEN, M.E. and B.O. CHRISTIANSEN. 1958. Tromsø Museum Biological Expedition 1958. The crustacea decapoda of Isfjorden: A comparison with the Swedish Spitsbergen Expedition in 1908. *Acta boreal. Troms. A. Scientia,* No. 19: 1-53.

NESIS, K.N. 1959. The distribution of boreal benthic fauna off the coasts of West Spitsbergen. *Dokl. Acad. Nauk SSSR,* T 127, (3): 677-680.

TIMOFEYEV, V.T. 1961. The movement of Atlantic water and heat into the Arctic Basin. *Okeanologiya,* Moscow 1961 1 (3): 407-411. (Translation in Deep-Sea Res. 9: 358-361).

H-2

ANOMALIES OF SEA TEMPERATURE AT STATION 27 OFF CAPE SPEAR AND OF AIR TEMPERATURE AT TORBAY-ST. JOHN'S

By

Wilfred Templeman[1]

ABSTRACT

Average yearly and part-yearly sea temperatures for 1950-62 at Station 27, 176 m deep, 2 nautical miles off Cape Spear, near St. John's, were expressed as anomalies of mean temperatures during this period. For the yearly means, the general trend in the upper water layers was that of higher than average temperatures in the years at the beginning and end of the period with an intervening period of lower than average temperatures. Over the whole period there was a slight downward trend which was more evident at the deeper than at the shallow levels. For January-May there was a slight but definite downward trend in temperatures from the beginning to the end of the period. In June-December temperatures at the shallower levels were equally high toward the beginning and end of the period with low temperatures in intervening years and no declining trend. In the deeper water there was a declining trend. Mean sea temperatures especially at the surface generally agreed extremely well with air temperatures in the same year at Torbay-St. John's.

At Torbay-St. John's mean yearly air temperatures rose from a low level in the 1880's and showed only a very slight decline from 1890 to the mid-1920's although there were many fluctuations. Mean annual temperatures have been generally above average since the 1930's and were highest in the early 1950's. December-April air temperatures rose until about 1890, remained approximately the same until the early 1900's and then gradually fell until the 1920's. Temperatures have risen again to above average since the late 1920's with the highest temperatures of the period in the early 1950's. May-November air temperatures fell from the 1870's to the early 1900's and then gradually rose to above average in most of the period since the early 1920's. Temperatures in the 1930's were the highest of the period.

The relationships of these air-temperature trends with trends in air and surface temperatures of neighbouring sea areas are discussed.

INTRODUCTION

Intermittently since 1946 and regularly at least once or twice a month from 1950 onward temperatures at standard depths from surface to bottom have been taken at Station 27 which is situated 2 nautical miles off Cape Spear, near St. John's, Newfoundland at 47°31'50"N, 52°35'10"W in 176 m. Occasionally a monthly observation is missed when the area is covered with ice but usually on such occasions the whole water column is at a low temperature both before and after the arrival of the ice and it is possible to interpolate temperatures with considerable accuracy. The research vessels used were the *Investigator II*, the *A.T. Cameron* and the *Marinus*.

The average temperature picture at this Station for the years 1950-62, the basic period taken for the averages used in calculating the temperature anomalies, is shown in Fig. 1. In calculating the anomalies the whole yearly period was taken and also the period January-May, the coldest period in the sea at Station 27 and the time when cod fishing on the east coast of Newfoundland is at its lowest level, and June-December when cod are more generally available near the east coast.

Mean daily, expressed as mean monthly, air temperatures for the St. John's and the neighbouring Torbay Airport stations have been obtained for recent years from the published monthly records of meteorological observations in Canada and for earlier St. John's records directly from the Office of the Meteorological Branch of the Department of Transport at Torbay. Also, since air temperatures are available for Torbay-St. John's back to 1872 but sea temperatures only since 1950, a comparison with Torbay mean air temperatures has been made during the 1950-62 period based on anomalies of the

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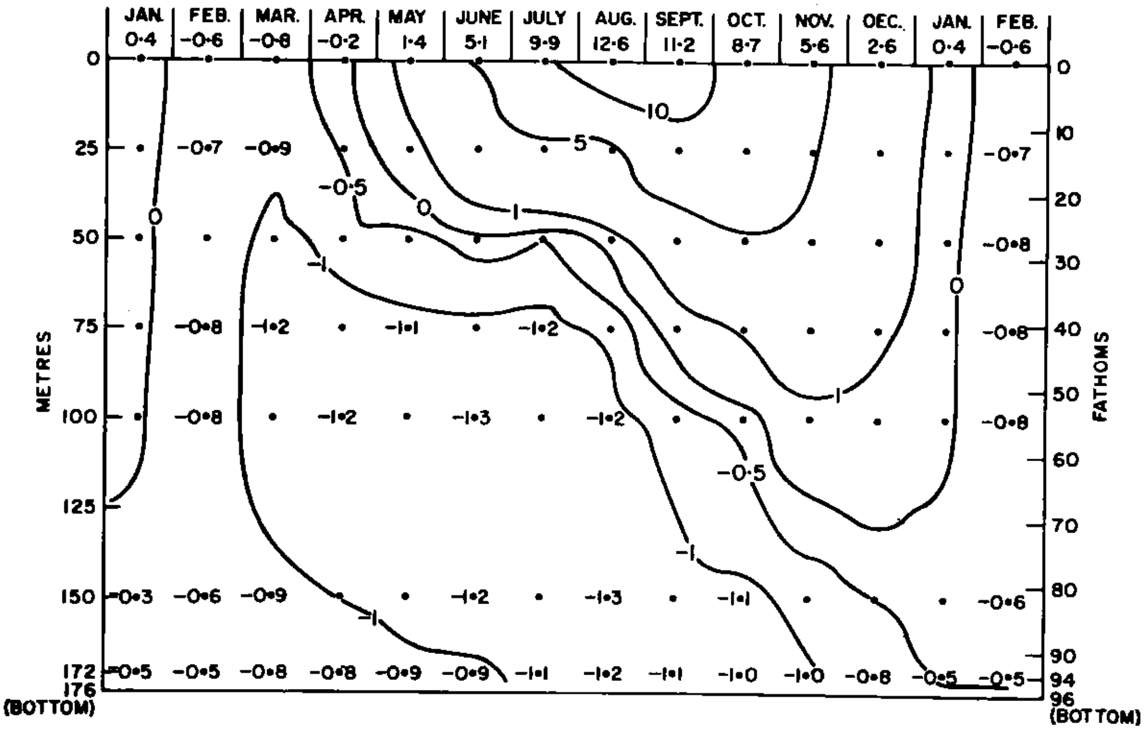

Fig. 1. Average sea temperatures (°C) at Station 27, 2 nautical miles off Cape Spear, near St. John's, Newfoundland. (Average mid-monthly temperatures at the depths indicated, for 1950-62. Position of station, 47°31'50"N, 52°35'10"W, 176 m).

average air temperature during this period and, based on the 1872-1962 average air temperature, anomalies of air temperature Torbay-St. John's back to 1872. The recent records of air temperature on which the 1950-62 average is based are from Torbay Airport, about 5 km from St. John's, and complete daily records of mean temperatures are available for Torbay for 1942-62. Consequently the 1942-62 mean air temperatures used are Torbay temperatures. Since 1942 there have been 9 years when complete records of mean daily temperature for both Torbay and St. John's are available. Comparison of the average temperature for those 9 years shows the St. John's yearly (and also the December-April and May-November) average temperature to be 0.56°C (1.0°F) higher than that of Torbay and the St. John's mean temperatures prior to 1942 have been reduced by this amount to convert them to the Torbay level before calculating anomalies.

In practice both for Station 27 and the air temperatures the mean monthly temperatures have been used and the mean yearly temperatures calculated directly from these without allowance for the differing number of days in the months. For air temperature summaries for comparison with the averages for Station 27, because air temperatures can be expected to have a delayed effect on water temperatures, averages have been made for the whole year and from December of the previous year to November of the year under consideration. Also to compare with the Station 27 January-May and June-December averages air temperature averages have been made from December (of the previous year) to April, the coldest air months, and from May to November.

Temperatures on the same date are needed for comparison and Station 27 could usually be occupied only at varying dates on the outward and inward passages of research vessels. Hence mid-monthly temperatures at the various standard levels were obtained from graphs of temperatures throughout the year at each level.

Temperatures of 25 m water columns have been used in obtaining averages. These water column temperatures have been obtained by averaging the shallower and deeper temperatures of each 25 m column. Thus temperatures at the surface and at 25 m have been averaged to give an average temperature for the 0-25 m column and similarly temperatures were derived for the 25-50 m and each additional 25 m column. A mid-monthly temperature at the 125 m level was interpolated. The average temperatures of the 25 m water columns were used in calculating the average yearly temperatures in the various water columns of Fig. 2-4. For some purposes such as development of pelagic eggs the surface and upper-layer temperatures may be of most importance whereas for adult inshore cod of the east coast over most of the June-December period the 25-50 and 50-100 m levels are most important. Anomalies in temperature are therefore provided for various portions as well as the whole of the water column.

ANOMALIES OF WATER TEMPERATURE AT STATION 27

In Fig. 2-4, apart from the greater amplitude of the anomalies at the surface and in the shallower water columns, the various portions of the water column at Station 27 usually have similar relative temperature anomalies and trends.

For the whole year (January-December) all portions of the water column (Fig. 2) had higher than average temperatures for 1951-53 and 1958, and lower than average temperatures in 1954, 1957 and 1959. For 1960-61 temperatures were somewhat higher than average in the shallower water columns and slightly below average in the water columns including the deepest water. Temperatures in 1955-56 were below average in the shallower and slightly above average in the deeper water columns. The year 1950 was generally slightly below average. The general trend at the shallower levels was that of higher than average temperatures in the years at the beginning and end of the period with an intervening period of lower than average temperatures. Over the whole period there was a slight downward trend which was more evident at the deeper than at the shallow levels.

The January-May anomalies (Fig. 3) provide the same general year by year picture as for the whole year, the most noticeable yearly difference being the distinctly below average temperatures in 1961. There was also a slight but definite downward trend in temperatures with no significant recovery toward the end of the period.

In June-December (Fig. 4) temperatures at the shallower levels were equally high toward the beginning and end of the period with low temperatures in intervening years and no declining trend. In the deeper water a declining trend is evident. The yearly temperatures for this period, however, usually followed the same trends as those of January-May (Fig. 3) with the notable exception that temperatures in 1961 were well above average from June to December and well below average from January to May. The relative differences at different levels between the anomalies in these colder and warmer months in 1961 are responsible for the yearly temperatures in this year being above average at the shallower depths and average or slightly below average when the deeper parts of the water column are included.

Also 1960 was well below average, except in the surface layer, in June-December and average or slightly above average in January-May. Over the whole year this results in somewhat above average temperatures in 1960 in the surface layer and below average temperatures in the deeper and whole water columns.

ANOMALIES OF AIR TEMPERATURE AT TORBAY-ST. JOHN'S

Years 1950-1962

For the period, both for January-December and December-November air temperatures there was a fairly close agreement with temperatures of the upper layers of the sea (Fig. 2). For the whole water columns, also, there was some agreement with air temperatures but the pattern of agreement was not so close as for the surface layers. Air temperatures showed a slight downward trend during the period.

In most years December-April air temperatures showed a close agreement with the average temperatures of the surface and of all water columns in January-May (Fig. 3).

For May-November air temperatures generally followed the same yearly trend as water temperatures in June-December at Station 27 (Fig. 4). Agreement was best with temperatures at the surface and at the upper water levels. Although in December-April air temperatures showed a definite downward trend over the period, for May-November air temperatures held level with equally high levels at the beginning and end and low temperatures in the middle of the period.

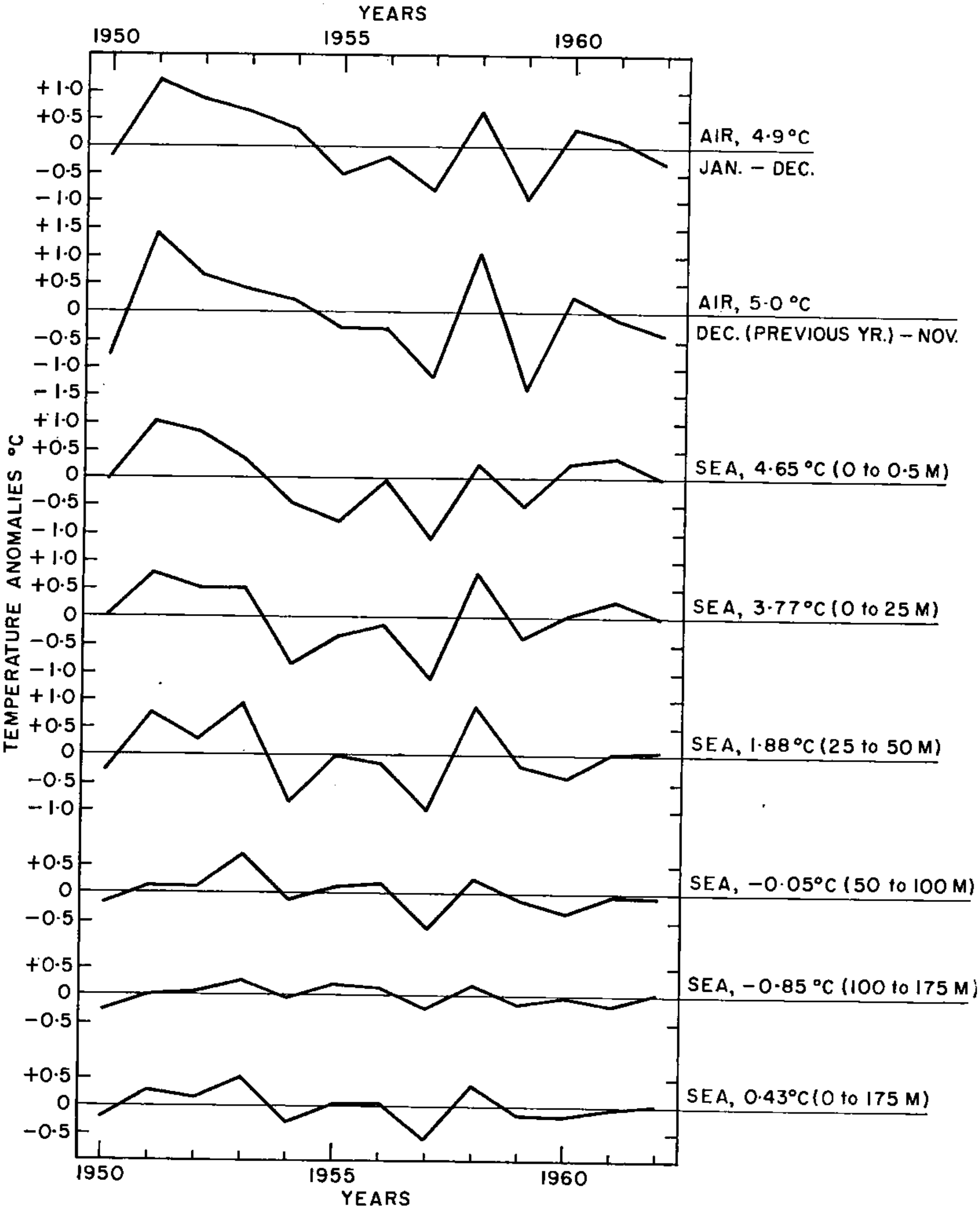

Fig. 2. Anomalies of yearly sea-surface and water column temperatures at Station 27 and of air temperatures at Torbay-St. John's, from average yearly sea and air temperatures, respectively, for 1950-62.

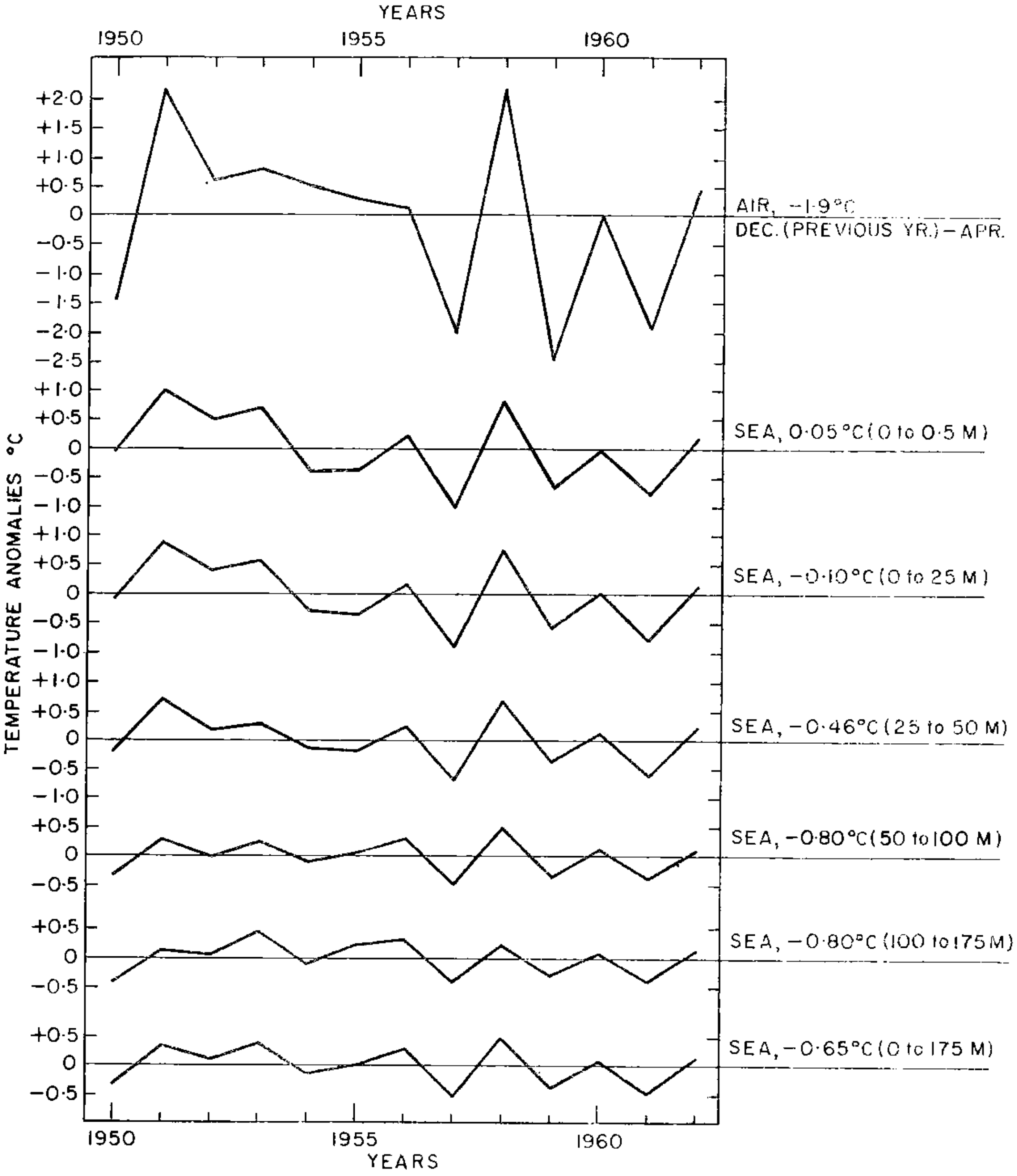

Fig. 3. Anomalies of yearly January-May sea-surface and water column temperatures at Station 27 and of December (of previous year) — April air temperatures at Torbay-St. John's, from average temperatures during these periods for 1950-62.

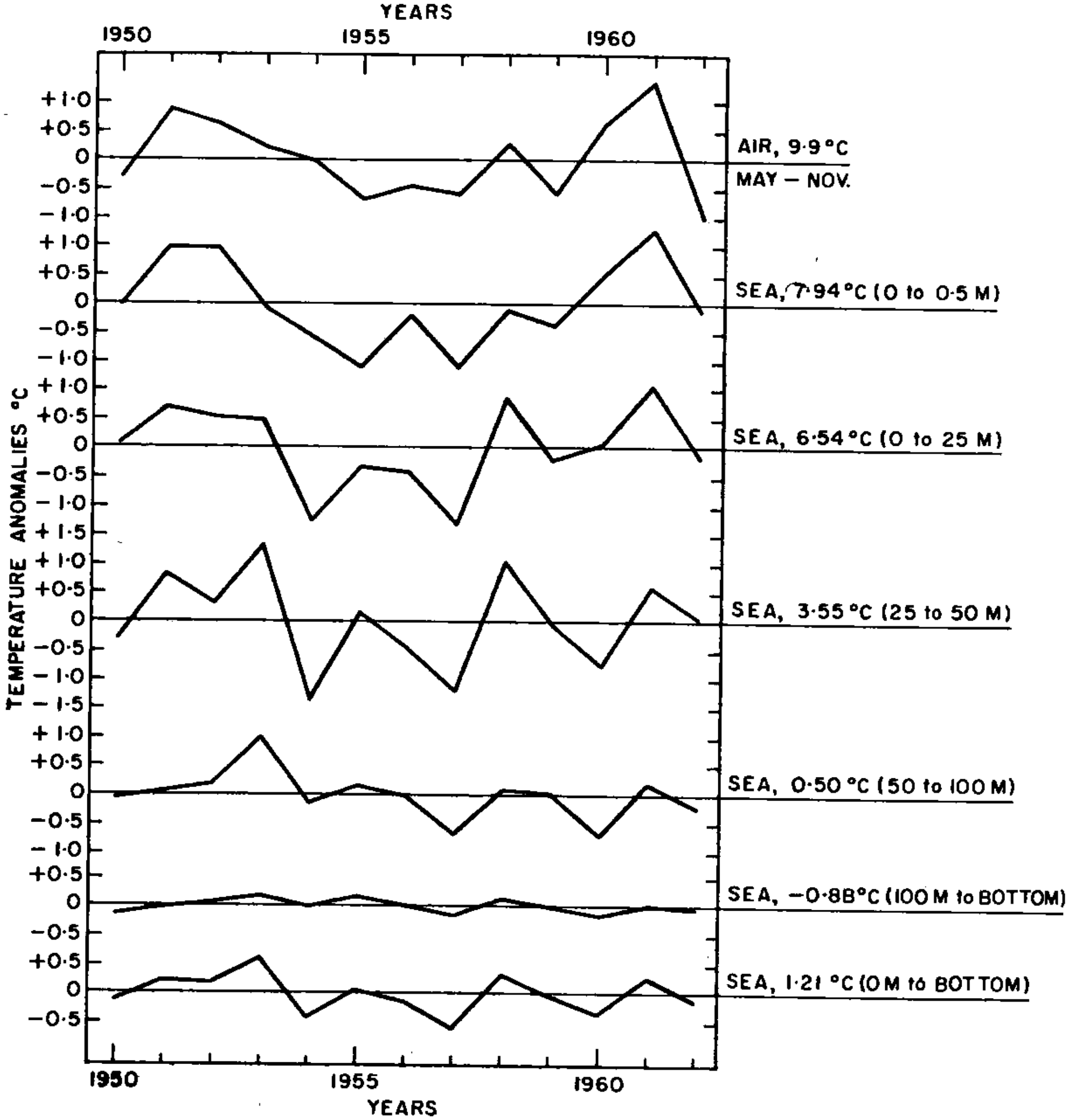

Fig. 4. Anomalies of yearly June-December sea-surface and water column temperatures at Station 27 and of May-November air temperatures at Torbay-St. John's from average temperatures during these periods for 1950-62.

In air temperatures as in the sea, 1961 had higher than average temperatures during the warmer months (Fig. 4) and lower than average temperatures during the colder months (Fig. 3).

In comparing sea and air temperatures it is better to follow trends in a series of years than to compare within individual years above or below the average line. Sea temperatures at Station 27 are limited in a downward direction at about -1.8°C whereas the lower values for air temperatures are much more variable. Also in a station so close to shore the prevalence of onshore and offshore winds will have a great influence regardless of the air temperature. Station 27 is also taken relatively infrequently compared with daily mean air temperatures.

Years 1872-1962

With all the possibilities for disagreement it is surprising how well the air and sea temperatures for 1950-62 followed the same pattern. Thus it appears worth while to study the pattern of air temperatures of Torbay-St. John's back to 1872 as being generally representative of sea temperatures, at least in the surface layers (Fig. 5). Mean yearly air temperatures rose from a low level in the 1880's and showed only a very slight decline from 1890 to the mid-1920's although there were many fluctuations. Temperatures have been generally above average since the 1930's and were highest in the early 1950's.

December-April air temperatures rose until about 1890, remained approximately the same until the early 1900's and then gradually fell until the 1920's. Temperatures have risen again to above average since the late 1920's with the highest temperatures of the period in the early 1950's.

May-November temperatures fell from the 1870's to the early 1900's and then gradually rose to above average in most of the period since the early 1920's. Temperatures in the 1930's were the highest of the period.

DISCUSSION AND CONCLUSIONS

Air and Sea-surface Temperature Trends in the North Atlantic

Many authors including Ahlmann (1949), Jespersen (1949) and Taylor et al. (1957) have shown gradually increasing annual air temperatures in areas bordering the North Atlantic since the latter, and often, especially for winter temperatures, the earlier part of the nineteenth century. The greatest increase has been during the colder part of the year.

Smed (1949) for surface temperatures in various areas of the North Atlantic, 1876-1939, demonstrated that a temperature increase began about the mid-1920's.

Goedecke (1952) for most of the Stations on the Norwegian Coast and in the area between Scotland, Iceland and Norway showed sea-surface temperatures declining at some stations slightly, and at others steeply, from the 1880's to the late 1910's and early 1920's and beginning to rise rapidly in the later 1920's or early 1930's. A decline occurred in the late 1930's and early 1940's followed by a further rise continuing to at least 1950. In the southern North Sea surface water temperatures probably declined from the 1880's to the early 1910's with a slow rise to about 1930 and a more rapid rise thereafter to at least 1950 after a decline in the late 1930's and early 1940's.

Stefánsson (1954) has shown increases in mean sea-surface temperatures off northern Iceland dating from the beginning of the twentieth century, with a more rapid increase beginning in the 1920's and a decline in the 1940's.

Hermann (MS, 1961) has reported for West and South Greenland sea-surface temperatures (April-September and April-October respectively) declining slightly in a series of fluctuations from 1876-80 to the early 1920's and thereafter increasing rapidly to a peak in the late 1920's and early 1930's and declining to a lower but still above average level in the intervening period to 1956-60.

Air and Sea-surface Temperature Trends in the Eastern Canadian Area

For areas more closely related to the St. John's area, Thomas (1955) found for the southeastern Atlantic Coast of Canada annual air temperatures declining from the late 1890's to the early 1920's and from then increasing to the 1950's but with a recession from the late 1930's to the early 1940's. The decrease to a low in the 1920's and the increase to a high in 1950 were both greater in winter than in summer.

Both winter and summer trends in these Nova Scotian area air temperatures are generally similar to those for the colder and warmer periods at Torbay-St. John's (Fig. 5). For the warmer months, however, in the Nova Scotian area there was a slight decline in temperature between the early 1900's and about 1918 with a rise thereafter whereas in the Torbay-St. John's data (for a longer series of months) the rise began about 1903. As a result the Nova Scotian yearly temperatures show a definite decline from the 1900's to the early 1920's but the Torbay-St. John's yearly temperature curve is relatively level or shows only a very slight decline during this period.

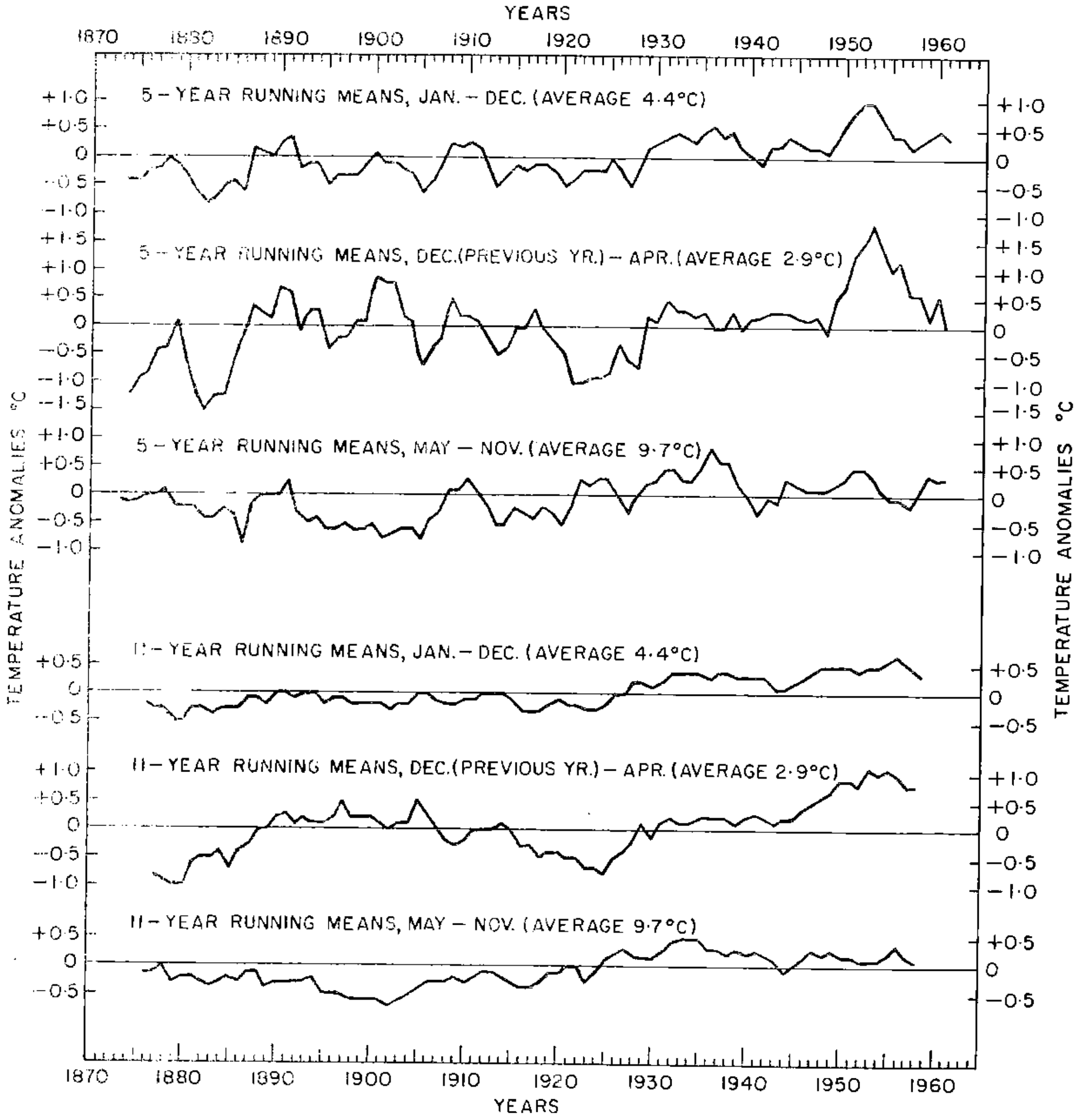

Fig. 5. Five-year and eleven-year anomalies of running means of air temperatures at St. John's-Torbay from the averages for 1872-1962. (The running means are attributed to the median year.)

Torbay air temperatures, 1942-54 were similar in trend and yearly pattern to those of Sydney and Sable Island with a fairly good but lesser resemblance to the air temperatures at Halifax and Yarmouth. In the recent period 1940-54 there were differences between air temperature trends in different years between the group of stations from Torbay, Newfoundland south to Yarmouth, Nova Scotia and the group from Belle Isle northward along the Labrador and Baffin Island coasts.

Temperatures of the surface water at St. Andrews, New Brunswick have been observed since 1922 and have shown a gradual, although fluctuating increase since the late 1920's with highest temperatures between 1949 and 1954 (Lauzier, 1958; Hachey, 1961). The general trends over the short period since 1950 are similar at St. Andrews and at Station 27 (Fig. 2) but anomalies of individual years are not always in agreement.

Riehl (MS, 1956) used all available data to compute monthly and yearly means of sea-surface temperatures of the North Atlantic, 1887-1936, summarizing the data by 5° lat, 5° long rectangles. Because Riehl's important manuscript is not generally available for comparison his graphs relative to the rectangles nearest to the Newfoundland and Newfoundland bank areas, and from which water passes from or enters this area have been reproduced in comparison with air temperatures at St. John's (Fig. 6). Although data on the number and location of observations in each rectangle are not available there is enough agreement in pattern within each group of the two different types of temperature pattern as to allow some confidence to be placed in the data.

In the area 45-50 (Fig. 6) which includes St. John's the sea temperature pattern was usually very similar to that of the St. John's air temperatures. Sea-surface temperatures in 45-50, 45-45 and 45-40 (of which the two former receive the full impact of the Labrador Current and the latter extends eastward from Flemish Cap and is beyond the influence of the colder part but is affected by the warmer part of the Labrador Current) show differences in pattern from those in areas between 40 and 45°N (40-40 to 40-65). In 45-50 surface temperatures, after remaining fairly level for the 1890-1910 period, fell strongly in 1911-16. In 45-45 temperatures were below average and generally declining from the early 1900's to at least 1916 with rising temperatures in the 1920's. In 45-40 the decline began still earlier in the late 1890's and temperatures declined to a low point in the early 1900's. Temperatures gradually rose from this point reaching levels strongly above average in the 1920's and 1930's. Temperature trends in this offshore rectangle are intermediate between those for 45-45 and those of the rectangles between 40 and 45°N.

Especially in the seaward rectangles between 40 and 45°N (40-40 to 40-55) sea-surface temperatures rose strongly from the 1890's to the 1930's. In rectangles 40-60 and 40-65 including part of the coasts and continental shelves of Nova Scotia, Maine and New England the rise in temperature since the 1890's was less and there was a severe drop in temperature to a low for the period in 1917 with below average temperatures in 1916-19. There was another severe low in 40-65 in 1922-24. The year 1917 is however, missing from all the other sea-surface graphs of Fig. 6 but it was a year of higher than average air temperatures at St. John's.

Brown (1963) for the sea area 42-44°N, 50-55°W (in the northern part of 40-50, and immediately south of the St. John's area, 45-50, of Fig. 6) has extended the period of analyses of sea-surface and air temperatures from the 1880's to 1959. For this area both sea and air temperatures showed a downward trend from the 1890's to the 1912-21 period, a warming trend till 1937 (information lacking, 1940-45), a rising trend to 1950-54 and a decline from this to 1959. These trends are most similar to those in 45-45 of Fig. 6. For the more southern part of 40-50 (40-42°N, 50-55°W) Brown found an increasing trend of sea and air temperatures from 1890 (as in Riehl, 40-50, Fig. 6) to the early 1950's with a falling tendency from 1951-52 to 1959.

Interrelationships of Trends in Air and Sea Temperatures at St. John's, and in other Eastern Canadian Localities and Neighbouring Sea Areas

The air temperature trends for the Nova Scotian area (composite of Sydney, Sable Island, Halifax and Yarmouth) and also for Sable Island separately (Thomas, 1955, Fig. 1 and 2) showed a declining trend from the 1890's to the early 1920's similar to Riehl's (1956) data for the northern area 45-45 (Fig. 6). In this same period the sea areas 40-55, 40-60 and 40-65 of Fig. 6, closest to the Nova Scotian area, showed rising surface temperatures.

Lauzier and Hull (MS, 1961), however, showed an extremely close relation in trend between 10-year running means of surface water temperatures from the 1920's to the 1950's at St. Andrews, N.B. and of air temperatures for the same period at Sable Island and Halifax.

Lauzier (1952) found that surface water temperatures at St. Andrews and at the Sambro Lightship, off Halifax, followed the same trends and were closely related in yearly pattern.

Lauzier and Hull (1962) showed that, for the period 1950-60, yearly surface water temperatures at St. Andrews followed a significantly downward trend similar to that at the Lurcher Lightship off southwestern Nova Scotia, and at the Sambro Lightship. On the other hand surface temperatures at Port Borden, Prince Edward Island and at Entry Island, Magdalen Islands (both in the southern part of the Gulf of St. Lawrence), and also in Halifax Harbour had trends more similar to those at Station 27, with higher temperatures at the beginning and toward the end and lower temperatures in the middle of the period.

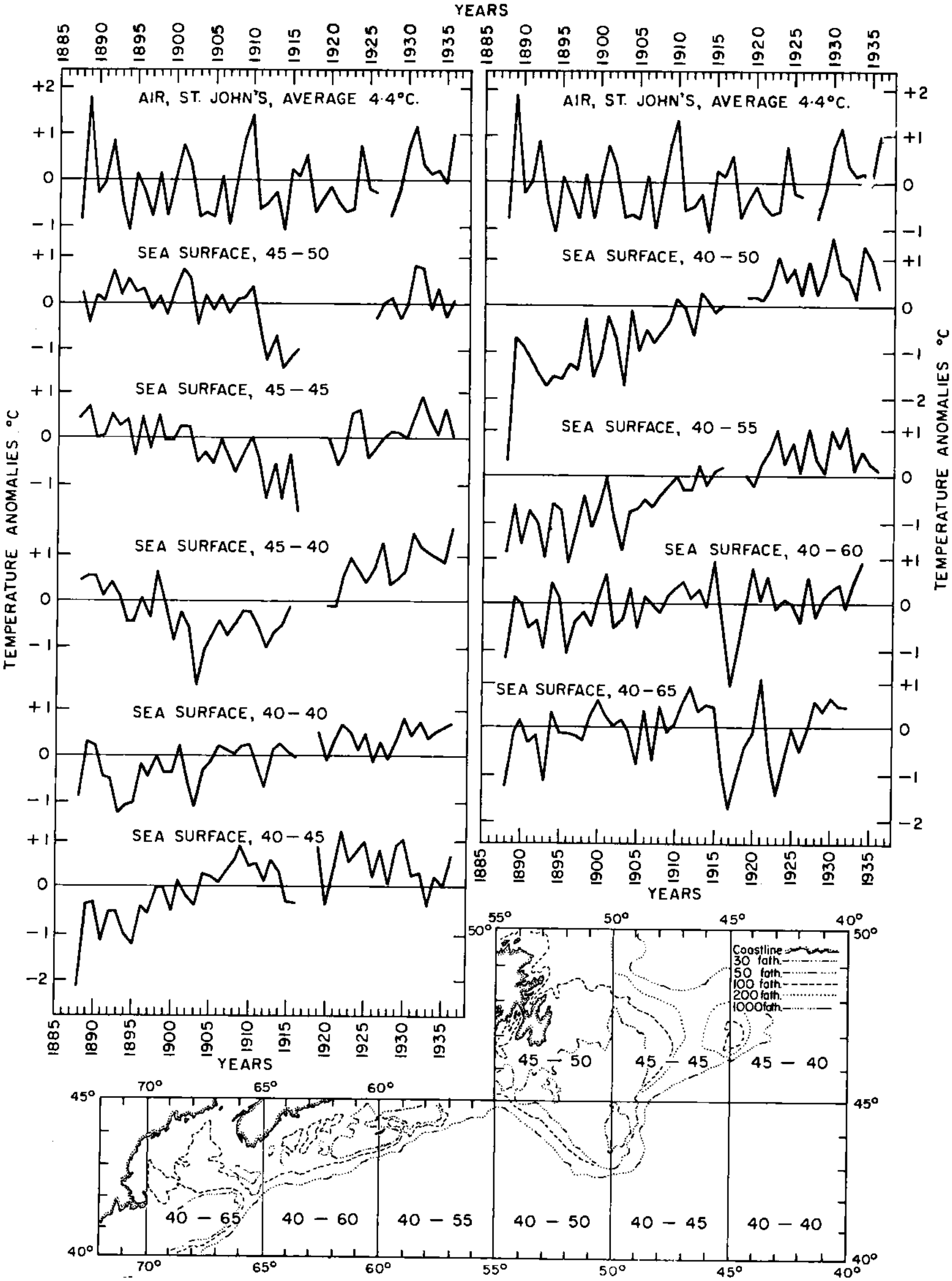

Fig. 6. Anomalies of yearly air temperatures at St. John's (converted to Torbay level) compared with anomalies of average sea-surface temperatures in 5° rectangles to the east and south (after Riehl, MS, 1956). (Each 5° rectangle is designated by the latitude and longitude coordinates of its southeast corner. The anomalies of yearly air temperatures were obtained by comparison with the average air temperature at St. John's (converted to Torbay) for 1888-1936.)

Thus in the earlier decades of the twentieth century there was a much lesser trend toward lower yearly temperatures in the St. John's than in the Nova Scotian coastal air temperatures, with an unexpected relationship of Nova Scotian air temperatures with distant rather than local sea-surface temperatures. More recently there was agreement in almost every year in the air temperature trends between St. John's-Torbay and Nova Scotian coastal stations particularly those of Sable Island and Sydney which are most surrounded by water. Also since the 1920's sea-surface temperatures at St. Andrews have been closely related in trend to air temperatures at Sable Island on the Scotian Shelf and to sea-surface temperatures off Halifax. During the period 1950-60, however, trends in sea-surface temperatures in the southern part of the Gulf of St. Lawrence were more like those at Station 27 off St. John's than at St. Andrews. In recent years as in former years, also, there is a close relationship in trend year by year between air temperatures at Torbay-St. John's and surface temperatures of the neighbouring sea area. This relationship is naturally closer with sea temperatures at Station 27 near St. John's than with the larger 45-50 area of Fig. 6.

No complete explanation can be offered at present for these alternating agreements and disagreements in regional air temperatures and with local air and sea-surface temperatures. The yearly average, however, is a composite of the warmer and the colder periods of the year which, as seen in Fig. 2-5, may have different trends and degrees of divergence from the yearly average. The relative degrees of seasonal divergence, as influenced by the nearness of a continental land mass and of resulting more extreme summer and winter temperatures, may result in different yearly trends.

Riehl's surface temperature data for 40-60 and 40-65 include not only part of the Scotian Shelf which is considerably under the influence of the southward flow from the Labrador Current and the Gulf of St. Lawrence, but also more seaward areas occupied by slope and Gulf Stream water. It is very likely that temperatures of the actual Scotian Shelf water declined in the latter part of the nineteenth and the early part of the twentieth centuries as did air temperatures in this area and sea temperatures in the area affected directly by the Labrador Current. The rise shown in Riehl's data during this period in 40-55 and 40-60 may have been due to most of his temperatures for these rectangles being from the offshore slope and Gulf Stream water where the temperature trend was evidently upward at this time. In this regard it may be noted (Fig. 6) that the rise in sea-surface temperatures during this period was considerably greater in 40-55 which included only a small portion of Shelf and still greater in 40-50 and 40-45 which are less subject to land influences as compared with 40-60 and 40-65 which include more shelf and coast.

Brown's (1963) results (in which, for the latter part of the nineteenth and the early parts of the twentieth centuries, the Labrador-Current-type downward trend was present in the northern part of rectangle 40-50, dominated by bank water and bank-related slope water, and the Gulf Stream type upward trend in the southern part of the same rectangle dominated by the more seaward slope water and the Gulf Stream), provide additional evidence that differing trends existed in these contrasting water types. Riehl's yearly trends for the whole rectangle were strongly upward during this period. It is also evident from Brown's results, compared with those of Riehl for the 40-50 rectangle, that 5° lat, 5° long rectangles are too large for studying temperature trends in areas where highly contrasting water bodies and water temperatures exist. The water of highly differing origins and temperatures in different parts of the rectangle may have different trends and also the averages from the whole rectangle are unlikely to be derived from an equal number of records from all types of water.

ACKNOWLEDGEMENTS

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REFERENCES

AHLMANN, HANS W. 1949. Introductory address [to symposium on climatic changes in the Arctic in relation to plants and animals]. *Rapp. Cons. Explor. Mer,* 125: 9-16.

BROWN, P.R. 1963. Climatic fluctuation over the oceans and in the tropical Atlantic. *Unesco, 1963. Changes of Climate, Proc. Rome Symp. Unesco and World Meteor. Org.,* p. 109-123.

GOEDECKE, ERICH. 1952. Das Verhalten der Oberflächentemperatur in der Deutschen Bucht während der Jahre 1872-1950 und der Zusammenhang mit dem der Nordwest-Europäischen Meere. *Ber Dtsch. Wiss. Komm. Meeresforsch.,* 13 (1): 1-31.

HACHEY, H.B. 1961. Oceanography and Canadian Atlantic waters. *Bull. Fish. Res. Bd. Canada,* 134: 1-120.

HERMANN, FREDE. MS, 1961. Some considerations about correlations between the West Greenland stock of cod and environmental factors. *Annu. Meet. int. Comm. Northw. Atlant. Fish 1961.* Doc. No. 34, Serial No. 898, p. 1-8.

JESPERSEN, PAUL. 1949. On changes in the distribution of terrestrial animals in relation to climatic changes. *Rapp. Cons. Explor. Mer.,* 125: 36-39.

LAUZIER, L. 1952. Recent water temperatures along the Canadian Atlantic coast. *Fish. Res. Bd. Canada, Atl. Prog. Rep.,* 53: 5-7.

1958. Surface sea water temperatures along the Canadian Atlantic coast, 1954-1957. *Ibid.,* 71: 8-12.

LAUZIER, L.M., and J.H. HULL. MS, 1961. Long-term variations of surface water temperatures. *Ann. Rep. (mimeo). Fish. Res. Bd. Canada, Biol. Sta., St. Andrews, N.B. for 1960-61,* App. No. 92, p. 211-214.

1962. Sea temperatures along the Canadian Atlantic coast 1958-1960. *Fish. Res. Bd. Canada, Atl. Prog. Rep.,* 73: 11-15.

RIEHL, HERBERT. MS, 1956. Sea surface temperatures of the North Atlantic, 1887-1936. *Univ. Chicago, Dept. Meteorol., Proj. NR 082 -120, Office Naval Res.,* p. 1-9.

SMED, JENS. 1949. The increase in the sea temperatures in northern waters during recent years. *Rapp. Cons. Explor. Mer,* 125: 21-25.

STEFÁNSSON, UNNSTEINN. 1954. Temperature variations in the North Icelandic coastal area. *Rit Fiskid.,* 2 (2): 1-27.

TAYLOR, CLYDE C., HENRY B. BIGELOW, and HERBERT W. GRAHAM. 1957. Climatic trends and the distribution of marine animals in New England. *Fish. Bull., U.S.,* 57(115): 293-345.

THOMAS, M.K. 1955. Climatic trends along the Atlantic Coast of Canada. *Trans. Roy. Soc. Can.,* Ser. 3, 49: 15-21.

H-3

LONG-TERM TEMPERATURE VARIATIONS IN THE SCOTIAN SHELF AREA.

By

L.M. Lauzier[1]

ABSTRACT

Surface water temperature observations at St. Andrews, N.B. during the last four decades are compared with other temperature series, surface and bottom temperatures, over the Scotian Shelf and along the Atlantic Seaboard. Short- and long-term temperature variations are generally uniform over the area. Study of temperature trends is extended back to 1880, based on the relationship between air and water temperature variations. Long-term temperature variations from the Scotian Shelf area follow some of the ocean temperature fluctuations.

INTRODUCTION

Bjerknes (1959, 1963), Brown (1963), Neumann (1960), Rodewald (1963) and Smed (1948 to 1962) have shown that the fluctuations of the marine climate are far from being uniform throughout the North Atlantic. However, the variations in fluctuations are linked together and could be explained by theories which provide an interim answer to some of the problems of interactions between sea and air.

The variability of the fluctuations may be expected to increase in the coastal areas (over the Continental Shelf) of the Western North Atlantic, where the interchange of properties between the atmosphere and the sea is more variable than over the open ocean, and where the continental drainage plays an important part in the replacement of the waters as well as in their stratification. Another important characteristic of the coastal waters, over the Continental Shelf, is their large annual amplitude and year-to-year variability as compared to the waters of the open ocean.

Temperature trends of the Canadian Atlantic waters have been studied previously by Hachey and McLellan (1948), McLellan and Lauzier (1956), Lauzier and Hull (1962) and Rodewald (1963) who considered the surface temperatures and also by Bailey (1953), McLellan (1955), and Lauzier and Trites (1958) who showed changes in temperatures at depths. Climatic trends in coastal areas adjacent to ICNAF Subarea 4 (Bay of Fundy, Scotian Shelf and Gulf of St. Lawrence) have been considered by Templeman and Fleming (1953), Templeman (1955), Rodewald (1956), and Taylor *et al.* (1957).

Our task here is to investigate the fluctuations of the marine climate of part of the southern end of the ICNAF area, the Scotian Shelf area (Fig. 1), as reflected by long-term changes in either surface water or air temperatures and to show the variations of the marine climate at depth, mainly on some of the fishing areas.

DATA

Twice daily observations of surface water temperatures at St. Andrews, N.B., which began in 1921, are the basis of the longest continuous series of water temperature along the Canadian East Coast. This 43-year series is considered here as a reference point for comparison with other series of shorter durations. The annual mean temperature is derived from the twelve monthly means. Unless otherwise indicated, other water temperature series were obtained from the records at the Biological Station of the Fisheries Research Board of Canada in St. Andrews, N.B.

The meteorological data from Halifax, N.S. and Sable Island, N.S. come from Longley (1954) and from the Meteorological Records published by the Meteorological Service of Canada.

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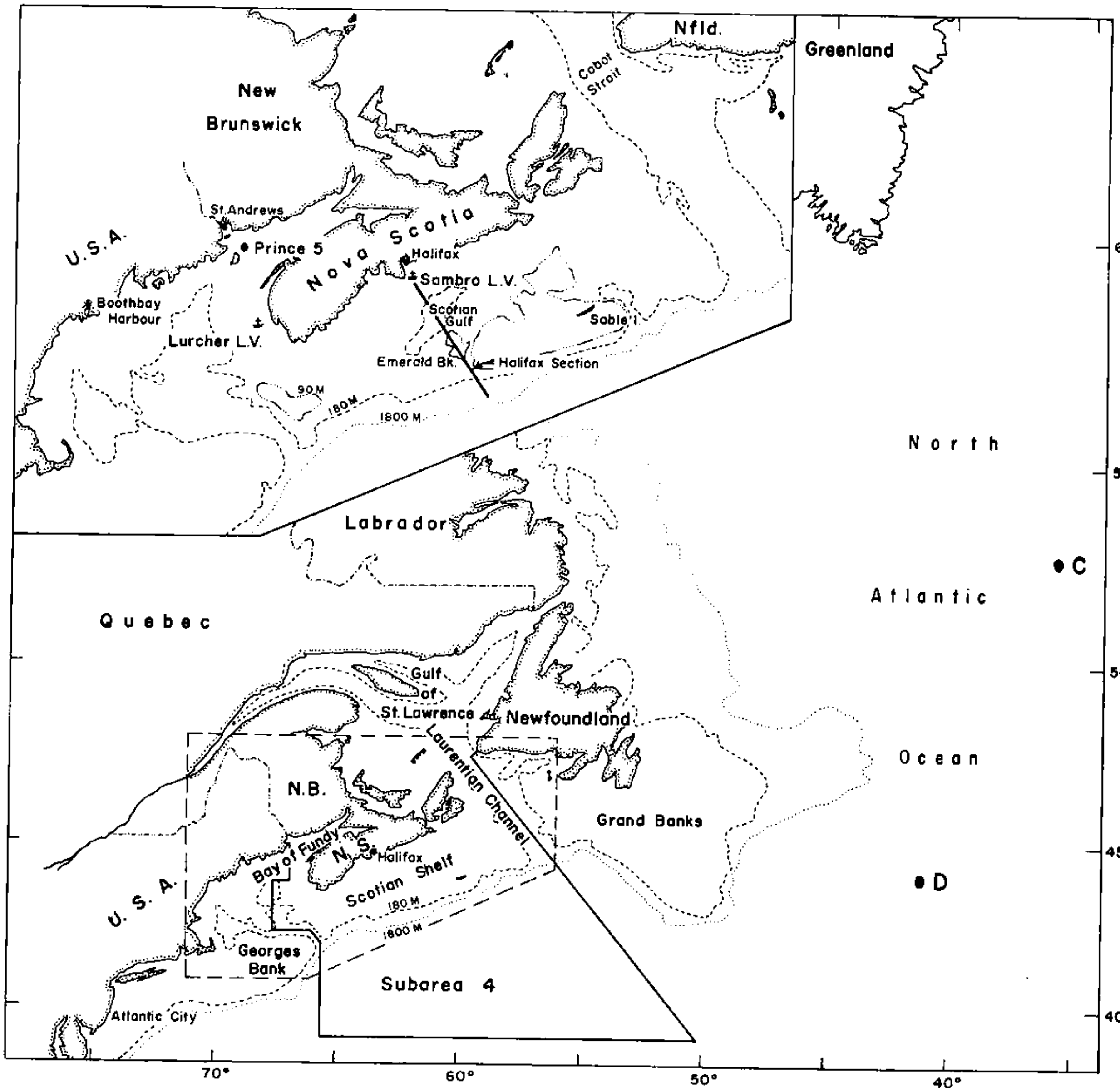

Fig. 1. ICNAF Subarea 4 and details of Scotian Shelf.

LONG-TERM VARIATIONS

Surface water temperatures

The St. Andrews series is represented in Fig. 2 showing both the year-to-year variations and the long-term fluctuations. The annual mean temperature for St. Andrews is 7.0°C. The lowest and the highest annual temperatures were 5.4°C in 1923 and 8.5°C in 1951 respectively. We see that the temperature was below the average in 10 of the first 15 years of the series and that it was above the average in 10 out of the last 15 years of the series. The 10-year moving average, eliminating short period variations, indicates an upward trend of the surface temperatures from the 1920's to the 1950's with a secondary maximum and minimum in the middle 1930's and early 1940's respectively.

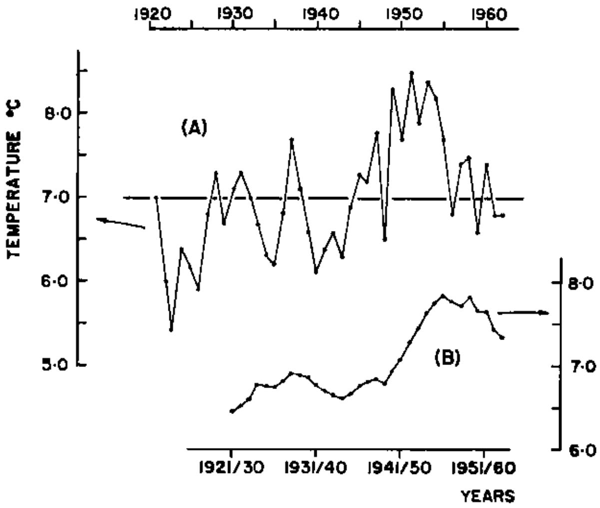

Fig. 2. Surface water temperatures at St. Andrews, N.B.; (A) annual means, (B) ten-year moving averages of annual means credited to the last year of the period.

The 10-year averages increased from 6.4°C for 1921-30 to 7.8°C in 1946-55. One important feature of this series is the reversal of the trend from the middle of the 1950's to the present time, the 10-year average for 1954-63 is 7.2°C.

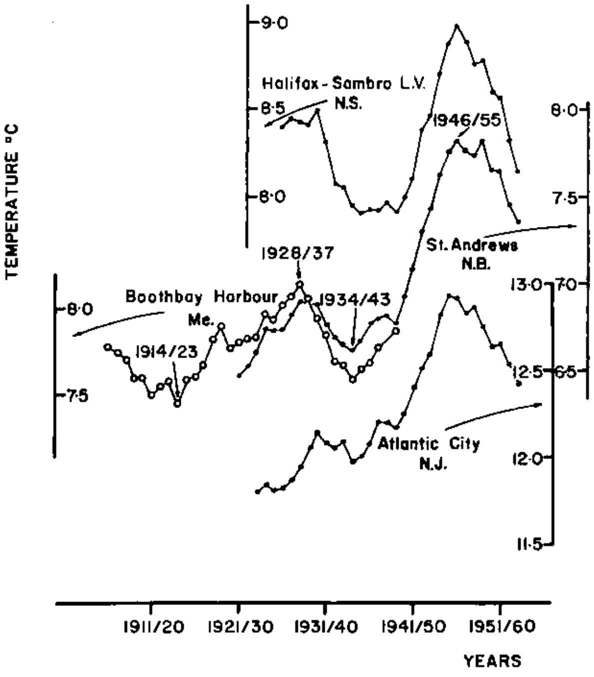

Fig. 3. Surface water temperatures at Halifax-Sambro L.-V., N.S.; St. Andrews, N.B.; Boothbay Harbour, Me.; Atlantic City, N.J. Ten-year moving averages of annual means credited to the last year of the period.

Other surface temperature series, two of them taken outside the Scotian Shelf, are represented as 10-year moving averages in Fig. 3. They are: Halifax Harbour - Sambro Light-vessel, 1926-62; Atlantic City, N.J., 1924-62 and Boothbay Harbour, Maine, 1906-48. The St. Andrews curve is repeated for comparison and adjoined to the Boothbay Harbour series. Atlantic City data to 1958 have been published by U.S. Coast and Geodetic Survey (1960) and the unpublished data from recent years were obtained through the kindness of the Director of the Survey. Boothbay Harbour data were listed in Taylor *et al.* (1957). Halifax Harbour data for the period 1926-35 have been adjusted to the Sambro Light-vessel level, based on the relationship Halifax-Sambro for the years following 1936. The similarity between the temperature series implies that the warming trend from the 1930's to the 1950's followed by cooling from the middle of the 1950's is a widespread phenomena over the Continental Shelf from at least the Laurentian Channel to New Jersey Coast.

The adjoining of St. Andrews and Boothbay Harbour series allows us to visualize a water temperature series for a relatively long period, for almost 6 decades. These combined curves suggest that the St. Andrews series commenced when the warming trend had already started. From Fig. 3, it seems that the general warming started around 1920, reached a secondary maximum and minimum in the middle 1930's and early 1940's respectively and thereafter progressed to a peak attained in the middle 1950's. The secondary maximum seems to be more pronounced in Halifax-Sambro area than at the other three stations.

Shorter temperature series of surface water in the Gulf of St. Lawrence (Lauzier and Marcotte, 1964) indicate local short-term variations superimposed to the long-term variations generally accepted for continental Shelf waters. The warming seemingly continued until 1960 in part of the Gulf of St. Lawrence.

Air temperatures

It is our intention here to use air temperatures as comparative series because the periods of

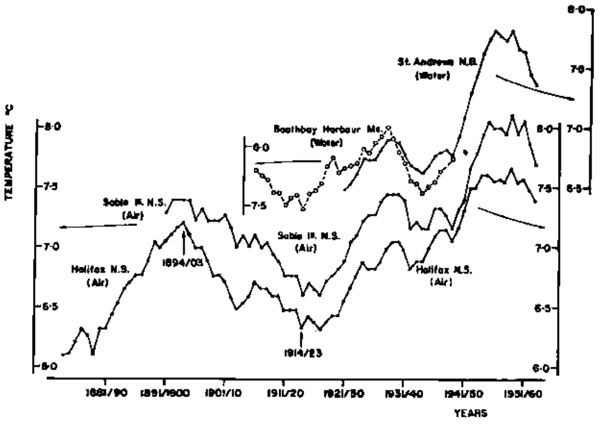

Fig. 4. Surface water temperatures at St. Andrews, N.B. and Boothbay Harbour, Me. Air temperatures at Sable Island and Halifax, N.S. Ten-year moving averages of annual means credited to the last year of the period.

observations are longer than those of the water temperatures. Air temperature series from Sable Island, 1891-1962, seems to be the ideal series because of the oceanic location of the Island, 90 miles south of Nova Scotia, almost at the edge of the Continental Shelf. Halifax, N.S. temperature series, one of the longest in Eastern Canada, started in 1874. Figure 4 shows Halifax and Sable Island air temperature variations as ten-year moving averages along with the St. Andrews-Boothbay Harbour curve repeated from Fig. 3.

Because of the close relationship between the three curves during the last six decades, we are probably justified in assuming that the longer air temperature records tell us approximately what the trends of water temperatures were between 1875 to 1905. The temperature curves in Fig. 4 indicate a warming period from at least the 1880's to the beginning of this century, a cooling period during the first two decades of this century. A long warming period from the 1920's to the 1950's was momentarily interrupted by a secondary minimum in the early forties. The last eight years are those of a cooling period.

Bottom temperatures

Bottom water temperature series from points on the Scotian Shelf and vicinity are much shorter and discontinuous as compared to those of surface temperatures. These series are compared, on a quarterly basis, to St. Andrews series (Fig. 5). Quarterly deviations of the St. Andrews surface temperatures are shown in curve C. In all curves of Fig. 5, short-term variations are more apparent than long-term fluctuations. The important point here is to show the general features of the bottom temperature series as compared to the reference series, from which the long-term fluctuations are inferred.

Bay of Fundy-Gulf of Maine Area

The bottom temperature series at Prince 5 station is the longest in our records. Located on the north side of the Bay of Fundy (Fig. 1), this station (depth: 90 m) has been visited once a month since 1924. Because of the vigorous tidal mixing in the Bay of Fundy, reducing the stratification to a small value, a very close relationship is expected in the variations between St. Andrews surface temperatures and Prince 5 station bottom temperatures, as shown by curves A and C of Fig. 5. The long and short periods of warming and cooling are approximately the same for both series.

At Lurcher Light-vessel, daily bottom (at 95 m) temperature observations commenced in 1950. The annual range of bottom temperatures is less at Lurcher than at Prince 5 station, and the average summer temperature gradient is also less at Lurcher than at Prince 5 station showing a greater oceanic influence on the temperature variations at Lurcher. Temperature trends of the bottom waters, at Prince 5 and at Lurcher, shown in curves A and B of Fig.5, are very similar. However, the cooling period of the 1950's seemed to have started earlier at Lurcher than at Prince 5 station and at St. Andrews. The rate of cooling during the 1950's and the beginning of the 1960's is somewhat more pronounced within the bottom waters at Lurcher and Prince 5 than for the surface waters at St. Andrews.

Halifax-Emerald Bank area

The waters of this area have a different temperature structure than those of the Bay of Fundy-Gulf of Maine area. The temperature stratification is such that a minimum temperature layer located at an average depth of 50-60 m persists during most of the year, except during the winter. Under such

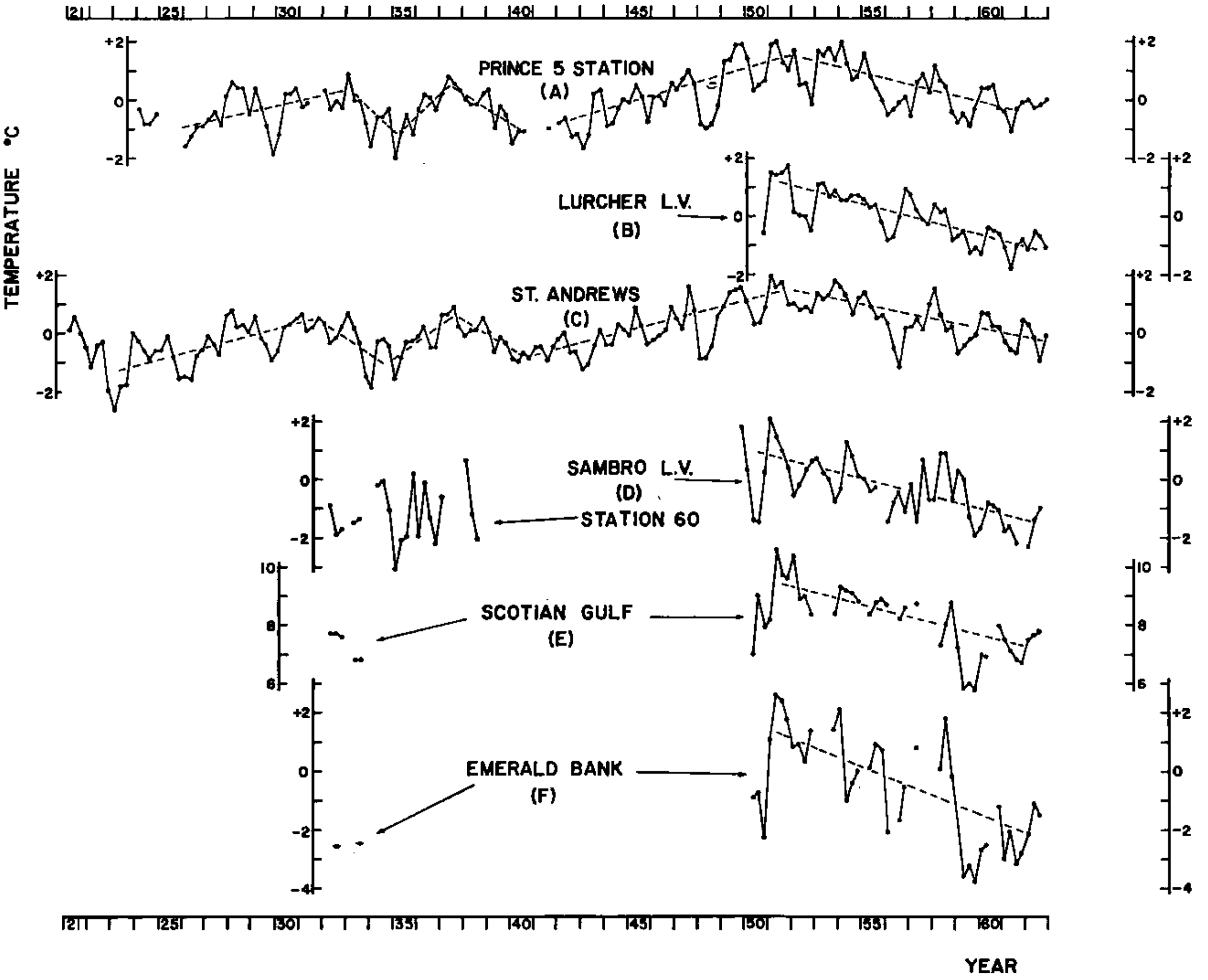

Fig. 5. Quarterly deviations of water temperatures: (A) Prince 5 Station, bottom temperatures average 1924-1960; (B) Lurcher L.-V, bottom temperatures, average 1950-1959: (C) St. Andrews, surface temperatures, average 1921-1960: (D) Sambro L.-V., bottom temperatures, average 1949-1959: (F) Emerald Bank, bottom temperatures, average 1950-1959. Maximum temperatures within bottom layer of Scotian Gulf, curve (E). The dash lines represent temperature trends.

conditions the bottom waters, where the depth of water is greater than 60 m, are those of a relatively warm layer as compared to the mid-depth layer. These waters generally have a higher salinity than those of the Bay of Fundy area, at the same depth, indicating a greater oceanic influence in their formation, (a greater slope water component in their mixture). The annual amplitude of temperature of bottom waters, at depths greater than 60 m, is much reduced as compared to the waters of the Bay of Fundy area. It is on the average 2.7°C at Sambro Light-vessel (at a depth of 85-90 m) as compared to 6.3°C at Lurcher and 8.1°C at Prince 5 station.

In 1949, twice daily bathythermograph (BT) cast observations commenced at Sambro Light-vessel to be continued to the present time. Through the courtesy of Mr R.E. Banks of Naval Research Establishment, the unpublished bottom temperature data for Sambro Light-vessel were put at the author's disposal. Quarterly deviations of bottom temperatures at Sambro are shown in Fig. 5 (curve D). As for Lurcher, the cooling trend in the fifties seemed to have started earlier than at St. Andrews and at Prince 5. A slight warming in 1957 and 1958 is noticeable at Sambro

Light-vessel. The general cooling trend of the 1950's was of the same order of magnitude at Sambro and at Lurcher but the short-term variability seemed to be greater at the former. During the 1930's, bottom temperatures were observed during frequent cruises at Station 60, which is located alongside Sambro Light-vessel. These temperatures were approximately 1.4°C lower than those of the 1950's at Sambro. Because of the large variations of the deviations during the thirties, it is difficult to assess the extent of the cooling and warming, if any, during that period which would correspond with those observed at St. Andrews and at Prince 5 station.

A series of seasonal cruises on the Scotian Shelf covering the Halifax Section from the coast southward over the Scotian Gulf and Emerald Bank commenced in 1950. The maximum temperatures recorded in the deep layer of the Scotian Gulf are shown in curve E of Fig. 5. The deviations from seasonal averages of the bottom temperatures on Emerald Bank are shown in curve F of Fig. 5. These two series show a cooling trend during the 1950's comparable to the trend already described for the other series. On Emerald Bank, however, the variability of deviations seems to be greater than at the other points and the cooling trend seems to be more intense, 3.2°C per 10 years, as compared to 2.0°C at Sambro Light-vessel.

The observations of temperatures in the 1930's at the same locations as in the 1950's (Scotian Gulf and Emerald Bank) indicate only that the temperature level was then lower than at the peak (about 1951) but approximately the same as in 1961, almost in line with the St. Andrews series.

Laurentian Channel

Lauzier and Trites (1958) have considered the long-term trends in the deep waters of the Laurentian Channel. Their study included data up to 1957. More observations have been taken every year since then. A total of 17 cruises has been made between 1958 and 1962 in the Cabot Strait area where the Laurentian Channel is the only entrance of deep warm waters to the Gulf of St. Lawrence. In Fig. 6, the temperatures of two isohalines, 33.0 and 34.0^{o}/oo and of the core of the deep layer (maximum temperature) are plotted against time. For comparison, annual temperatures at St. Andrews have been included in Fig. 6. The general warming from the 1920's through the 1930's until the 1950's has been observed in the deep layers of the Laurentian Channel. However, the warming from the 1930's to the 1940's is minimum, 0.3°C, for the 33.0^{o}/oo water and maximum, 0.9°C, for the core of the deep layer. Frequent temperature observations during the 1950's indicate that these waters, while warmer than in previous years, stayed warm longer than those of the Scotian Shelf. The deeper the waters, the later the peak temperature occurred in the 1950's. The 33.0^{o}/oo water experienced a definite cooling in the last ten years, while the 34.0^{o}/oo water did not show any trend and large variations at the core make it difficult to detect any appreciable trend during the last 10 years.

The definite lag in reaching a peak temperature is reflected in the warming and cooling of some of the surface waters in the Gulf of St. Lawrence (Lauzier and Marcotte, 1964).

General features

The comparison of surface and bottom temperature variations and trends for different areas of the Continental Shelf for periods of varying lengths leads us to believe that the water masses on the Continental Shelf from the Laurentian Channel to the Bay of Fundy have been subjected to long-term variations of temperatures of fairly uniform character. Furthermore because of the close relationship between trends of air and water temperature variations, we are probably justified in assuming that the longer air temperature records tell us approximately the trends of water temperatures over a longer period than that of actual sea temperature measurements.

To summarize: the long-term trends of water temperature in the Shelf part of ICNAF Subarea 4, from 1880 to 1962, were as follows: a warming period for the first 20 years, a cooling period from about 1900 to the beginning of the 1920's, a warming period between approximately 1922-24 and 1953-55 with secondary maximum and minimum centered in the middle 1930's and the beginning of the 1940's respectively. The trend from 1953-55 to 1962 exhibits a fairly intense cooling, except in the very deep waters of Cabot Strait area.

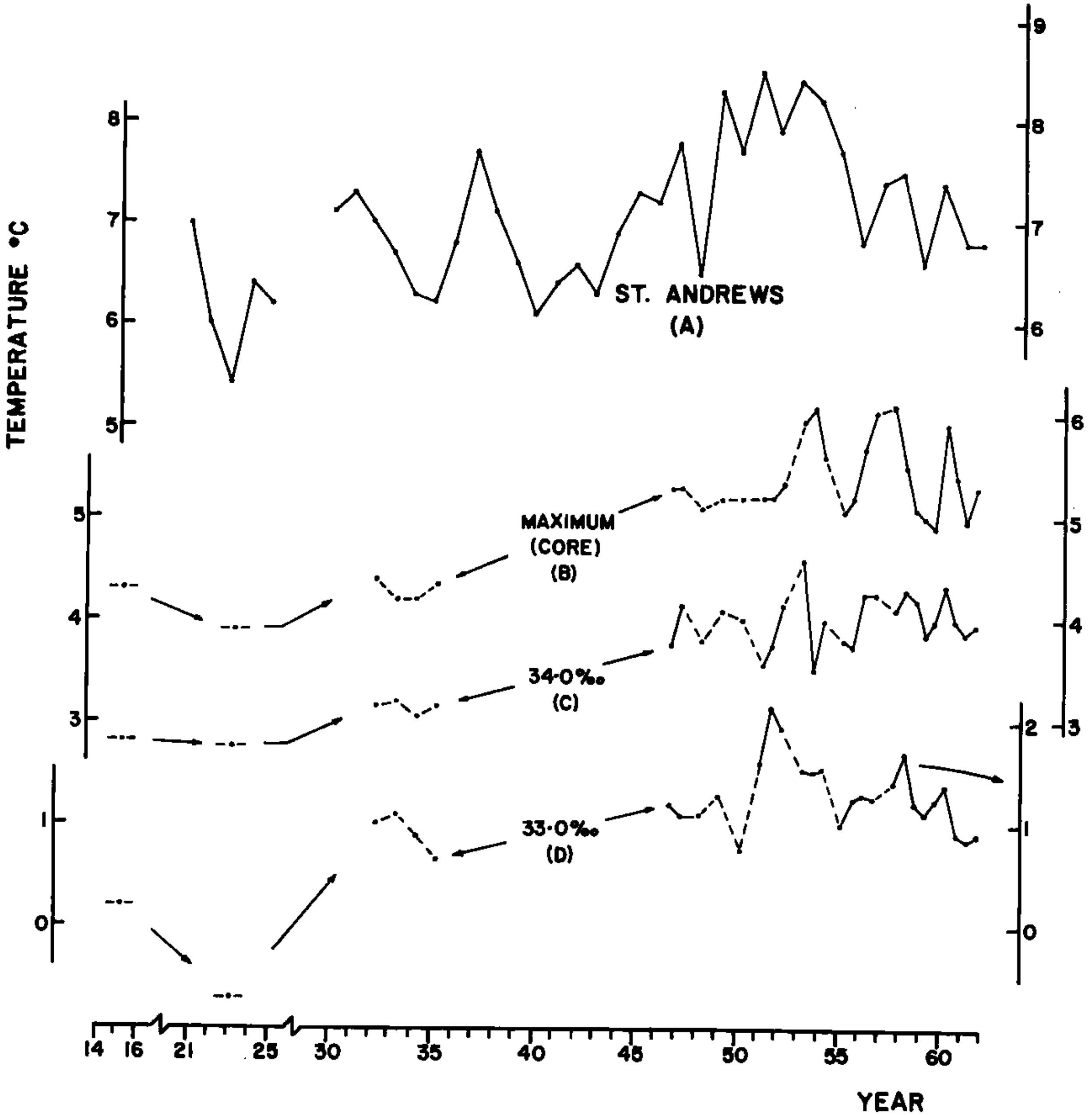

Fig. 6. Temperature variations of surface water at St. Andrews, N.B. (annual means) curve (A), and of waters of the deep layer in Cabot Strait, Laurentian Channel, (semi-annual means) at the core, curve (B); at isohaline 34.0°/oo, curve (C); at isohaline 33.°/oo, curve (D).

DISCUSSION

We cannot explain the long-term variations of temperatures described previously. We should point out however the difference in the temperature variations of the Scotian Shelf area as compared to those of the surrounding Northwest Atlantic and also some of the problems related to the hydrography of the Scotian Shelf area.

Northwest Atlantic

The temperature trends of the waters over the Scotian Shelf have striking similarities with those of the surface waters northeast of the Grand Banks and just north of the Gulf Stream. However, these trends are different from those of the waters in the main North Atlantic gyre.

The surface waters located over the northeast corner of the Grand Banks (45-50°N, 45-50°W) have experienced an intense cooling from 1890 to approximately 1915-25, followed by warming until the 1950's (Riehl, 1956 and Schell, 1957). Temperature data from Weatherships C and D, east of this area, indicate a cooling trend during the 1950's (Rodewald, 1963). For an area located just north of the Gulf Stream (42-44°N, 50-55°W), Brown (1963) shows a cooling trend from approximately 1890 to the period 1912-21 followed by a warming trend until 1937. An increase of temperature during the late 1940's and early 1950's was followed by a fall of temperature of nearly 2.5°C in the late 1950's (Brown, 1963). From the northern half of the main North Atlantic gyre, surface temperature data indicate a warming trend, with a maximum change along the Gulf Stream, from 1890 to 1950, followed by a cooling tendency during the 1950's (Riehl, 1956; Bjerknes, 1959; Brown, 1963).

The most successful explanation of climatic variations of the North Atlantic surface waters emphasized the effect of changes in the atmospheric circulation (intensification of westerlies) on the internal adjustment of the water masses of two large vortices, associated with the Bermuda-Azores High and Icelandic Low respectively. Processes involved in the variations about the normal heat balance of the surface waters of various regions were also given some attention.[2]

Scotian Shelf area

During the last 17 years we have experienced general warming followed by cooling superimposed on alternation of warm and cool years (Fig. 2). Should the problems of warm and cool years be investigated further before we are able to give a sound explanation to the long-term fluctuations? An analogy between the short-term variations and the long-term fluctuations would be fruitful. More information on the circulation, water mass production and heat budget is essential. Little is known about the first two and less about the last one.

Short-term changes in annual temperatures seem to be associated with variations in intensity of the westerlies along the Canadian Atlantic coast. This relationship indicates that lower temperatures are associated with stronger westerlies in 1948, 1959 and 1961, and that higher temperatures are associated with weaker westerlies in 1949, 1951 and 1953. Stronger westerlies may a) maintain a certain amount of upwelling along the coast, keeping the surface temperature at a low level during the summer, and somewhat higher level in the winter; b) bring over the water, during the winter, cold dry air masses increasing then heat loss to the atmosphere which would counteract the warming effect of upwelling. The resulting surface cooling may increase vertical mixing on the Shelf area as well as to the east and therefore increase the production of the intermediate temperature layer that would occupy a large volume during the spring and summer. Hachey (1937) has considered the effect of upwelling on the Scotian Shelf during the summer. Such relationship or association may only indicate a small scale phenomenon. We still have to know more about the circulation at the surface and at depths, over and beyond the continental Shelf. In our opinion a very important aspect of the problem is the production of water masses. We know from previous studies that the water masses in the area possibly result from the mixing of Labrador water, Slope water, and low salinity "inshore" waters. Water masses could be identified but the mixing mechanism is still unknown. Finally the consistency of property distributions within a "component" water mass like the Slope Water and the Labrador water may be questionable. If they vary from year-to-year, from a cold period to a warm period, how are these variations going to affect the mixing mechanisms and the resulting "mixture"?

SUMMARY

1. Long-term surface temperature variations at St. Andrews, N.B. show a warming trend from the 1920's to the 1950's with a secondary maximum and minimum in the middle 1930's and early 1940's respectively. A cooling trend has been observed from the middle 1950's to the present time.

2. Trends of surface water temperatures at St. Andrews, N.B. are representative of surface temperature variations over a large area of the Atlantic Seaboard from, at least, Halifax, N.S. to

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[2] This over-simplification does not do justice to the work of Bjerknes (1959, 1963), Neumann (1960) and Rodewald (1963). The readers are therefore encouraged to study their contribution, as well as the contribution by Lamb and Johnson (1959) to the general subject of climatic variations, and the account by Malkus (1962) of large scale interactions between sea and air.

Atlantic City, N.J. Temperature variations at Boothbay Harbour, Me. are used as an extension in retrospect of temperature trends from the 1920's to 1905.

3. Bottom temperature variations and trends on the Scotian Shelf, in the Bay of Fundy area, and deeper layer temperature variations in the Laurentian Channel, are similar to those of surface temperatures at St. Andrews with minor differences. This similarity indicates that the temperature fluctuations occurred within the water masses as well as at the surface.

4. Air temperature trends at Halifax and Sable Island, N.S. are closely related to the trends of surface water temperatures observed at St. Andrews, N.B. and Boothbay Harbour, Me. during the last 6 decades. Trends of air temperatures from longer series starting around 1875 are taken as indicative of trends of water temperatures between 1875 and 1905.

5. In general, the long-term trends of water temperature in the Shelf part of ICNAF Subarea 4, from 1880 to 1962 were as follows: a warming period for the first 20 years, a cooling period from about 1900 to the beginning of the 1920's, a warming period between approximately 1922-24 and 1953-55 with a secondary maximum and minimum centered in the middle 1930's and the beginning of the 1940's respectively. The trend from 1953-55 to 1962 exhibits a fairly intense cooling.

6. No explanation for the temperature trends on the Scotian Shelf is offered. Comparison is made between the trends on the Shelf and the large scale fluctuations over the North Atlantic.

REFERENCES

BAILEY, W.B. 1953. Seasonal variations in the hydrographic conditions of the Bay of Fundy. *Fish. Res. Bd. Canada MS Rept. Biol. Sta.*, No. 551, 17 p. Unpublished.

BJERKNES, J. 1959. The recent warming of the North Atlantic. *In* B. Bolin. *The atmosphere and the sea in motion.* Oxford Univ. Press. p. 65-73.

1963. Climatic change as an ocean-atmosphere problem. *In* WMO-UNESCO Rome Symposium. *Changes of climate.* UNESCO, Paris, 297-321.

BROWN, P.R. 1963. Climatic fluctuation over the oceans and in the tropical Atlantic. *In* WMO-UNESCO Rome Symposium. *Changes of climate.* UNESCO, Paris. 109-123.

HACHEY, H.B. 1937. Ekman's theory applied to water replacements on the Scotian Shelf. *Proc. N.S. Inst. Sci.*, 19(3): 264-276.

HACHEY, H.B., and H.J. MCLELLAN. 1948. Trends and cycles in surface temperatures of the Canadian Atlantic. *J. Fish. Res. Bd. Canada*, 7(6): 355-362.

LAMB, H.H., and A.I. JOHNSON. 1959. Climatic variations and observed changes in the general circulation. *Geogr. Ann., Stockh.*, 41: 94-134.

LAUZIER, L.M., and J.H. HULL. 1962. Sea temperatures along the Canadian Atlantic Coast, 1958-1960. *Fish. Res. Bd. Canada, Atlantic Prog. Rept.* No. 73: 11-15.

LAUZIER, L.M., and A. MARCOTTE. 1964. Températures des eaux de surface à Grande Rivière, P.Q., 1938-1962. Comparaisons avec d'autres stations côtières. In preparation.

LAUZIER, L.M., and R.W. TRITES. 1958. The deep waters in the Laurentian Channel. *J. Fish. Res. Bd. Canada*, 15(6): 1247-1257.

LONGLEY, R.W. 1954. Mean annual temperature and running mean temperatures for selected Canadian Stations. *Met. Serv. Canada, Tech. Cir.* No. 2481, Toronto.

MALKUS, J.S. 1962. Interchange of Properties between sea and air. Large scale interactions. *In* M.N. Hill. *The Sea. Ideas and Observations on Progress in the study of the Seas.* Interscience Publishers. New York. 88-294.

MCLELLAN, H.J. 1955. Change in bottom temperatures on the Scotian Shelf. *J. Fish. Res. Bd. Canada*, 12(3): 375-386.

MCLELLAN, H.J., and L. LAUZIER. 1956. The prediction of water temperature. *Canad. Fisherm.* 43: 11-12.

NEUMANN, G. 1960. Some meteorologically.important relationships between the ocean and atmosphere. *Trans. N.Y. Acad. Sci. Ser. 11.* 22(8): 615-633.

RIEHL, H. 1956. Sea surface temperature of the North Atlantic 1887-1936. *Univ. Chicago*, 9 p. Chicago. Unpublished.

RODEWALD, M. 1956. Die rezente Erwarmung der Atlantischen Kustengewasser Nordamerikas. (The recent rise in temperature in the coastal waters on the Atlantic coast of North America). *Sonderdruck aus der Deutschen Hydrographischen Zeitsohrift*, 9(4): 182-186.

1963. Sea-surface temperatures of the North Atlantic ocean during the decade 1951-1960, their anomaly and development in relation to the atmospheric circulation. *In* WMO-UNESCO Rome Symposium. *Changes of climate*. 97-107. UNESCO, Paris.

SMED, J. 1948 to 1962. Monthly anomalies of surface temperature. *Ann. biol., Copenhague*, Vol. 3 to 17.

SCHELL, I.I. 1957. Gaining a better understanding of the representativeness of sea surface temperature observations and of the density of these observations required for research purposes. *Tufts Univ. Meteorological Studies Rept.* 57-2, 19 p. Unpublished.

TAYLOR, C.C., H.B. BIGELOW and H.W. GRAHAM. 1957. Climatic trends and the distribution of Marine Animals in New England. *Fish. Bull., U.S.*, 57: 293-345. (Fish. Bull. No. 115).

TEMPLEMAN, W. 1955. Groundfish stocks of the western North Atlantic Trans. *Twentieth North American Wildlife Conf.* 454-476.

TEMPLEMAN W., and A. FLEMING. 1953. Long-term changes in hydrographic conditions and corresponding changes in the abundance of marine animals. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 3: 79-86.

UNITED COAST AND GEODETIC SURVEY. 1960. Surface water temperature and salinity, Atlantic Coast. *C. & G.S. pub.* 31-1, 76 p. Washington.

H-4

EFFECT OF LONG-TERM TEMPERATURE TRENDS ON OCCURRENCE OF COD AT WEST GREENLAND

By

Paul M. Hansen[1] and Frede Hermann[1]

ABSTRACT

The seasonal variation in temperature at different depths and different localities off the West Greenland coast is illustrated by selected hydrographic stations and compared with available information about the occurrence of cod at different seasons.

OCCURRENCE OF COD AT WEST GREENLAND

As is well known the occurrence of cod has been periodical at West Greenland. The two best known cod periods are the period from about 1845 to 1851 and the present cod period which started about 1920 and still continues.

In the first period both English and Danish vessels were fishing cod at the West Greenland banks and coastal waters. The stock of cod decreased however rather suddenly from 1849 and the fishery stopped. In the long period from about 1850 to 1920 there were only small local stocks of cod in some fjords and at some localities in South Greenland the cod appeared for a short time only during the summer. Faroese and Danish fishery expeditions in 1906, 1908 and 1909 found almost no cod on the West Greenland banks.

In 1917 the cod appeared in greater shoals at Frederikshåb at 62°N. In 1922 the cod occurred north to Sukkertoppen at 66°N and in 1928 the northern limit of the stock of cod had reached Disco Bay at 69°N. In the early 1930's the cod reached as far north as Upernavik district at about 73° N.

After about 1950 the northern limit of the cod stock had again moved southward and only small quantities of cod are now caught north of 69°N. Figure 1 showing the yield of the Greenlanders cod fishery gives a good illustration of how suddenly the stock of cod has increased in the 1920's.

VARIATION OF SEA TEMPERATURE OFF WEST GREENLAND

Figure 2 gives the variation of the surface temperature anomalies for West Greenland and South Greenland respectively presented as five-year running means. Figure 3 shows the areas West Greenland (A_1) and South Greenland (B) as established by Smed (1947-62).

The most pronounced feature in both curves is the strong and sudden increase of temperature in the 1920's. In the late 1930's the temperature decreased again and in the post-war years the temperature has been about 0.5° lower than its maximum value about 1930. In the late 1950's and the beginning of the 1960's the temperature has again been increasing.

The increase of the stock of cod occurred almost simultaneously with the rise in temperature, and it seems reasonable to assume that it is the climatic improvement which has made it possible for the cod to extend its northern limit further northward at West Greenland. The strong decrease of the cod fishery experienced in late years north of 69°N may be a consequence of the drop of temperature after about 1940.

It is worth mentioning that a drop in temperature of only about 0.7°C from the value in 1946-50 would have brought the temperature back to the levels for the years before 1920 when almost no cod was found in the Greenlandic area. We have possibly been very near a catastrophe for the West

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[1] Greenland Fisheries Investigations, Charlottenlund, Denmark.

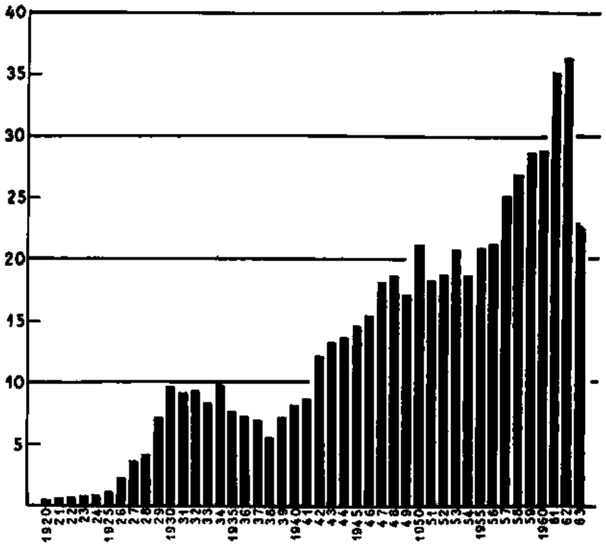

Fig. 1. Yield of Greenlanders cod fishery in thousand tons 1920 to 1963 (1963 estimated from catch until November).

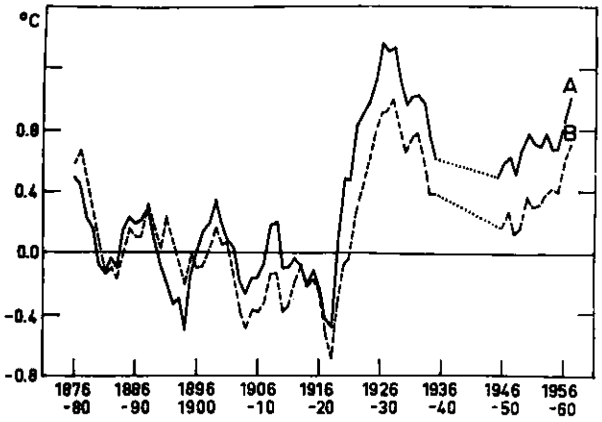

Fig. 2. Five years running means of surface temperature anomalies.
Curve A: for Smed's area A_1 mean April - September.
Curve B: for Smed's area B mean April - October.

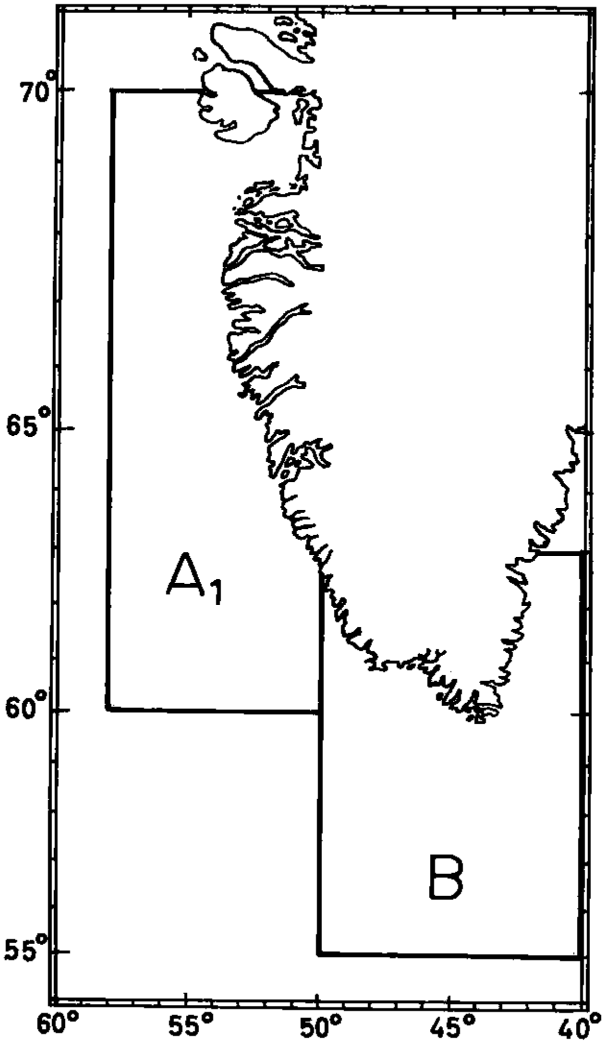

Fig. 3. Location of areas A_1 and B.

Greenland cod population, but fortunately the temperature now seems to be increasing again.

It must be borne in mind that in this paper five-year means of surface temperatures were used. The year-to-year fluctuations in surface temperature are to a high degree averaged out and it is probable that these averages represent fairly well the variation of temperatures also in the deeper layers where the cod lives.

Subsurface temperature observations are rather few in the years before 1920, but they indicate that a considerable warming of the deeper layers has occurred. This has been discussed by Ad. S. Jensen (1939).

VARIATION IN ICE CONDITIONS OFF WEST GREENLAND

Direct measurements of sea temperature are only available from West Greenland waters for the past 87 years, but information on the amount of the Polar ice (Storis) carried by the East Greenland Polar Current to West Greenland is available for a considerably longer period. Speerschneider (1931) collected information about Storis from log books of ships visiting Greenland and since 1901 the Danish Meteorological Institute has published maps of the distribution of ice in West Greenland waters. Since there is assumed to be a close connection between sea temperature and the presence of Storis a consideration of the ice conditions can be expected to yield information concerning climatic changes in the sea.

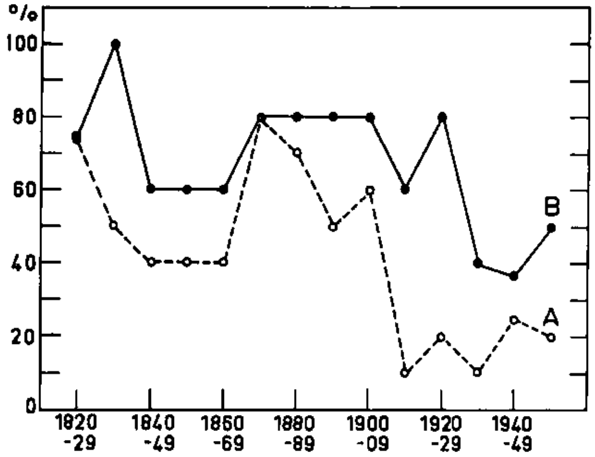

Fig. 4. Frequency of years in which the Storis reached as far north as Godthåb: (A broken line) and to Fiskenaesset (B full line).

Speerschneider (1931) produced in tabular form a summary of the maximum extension of ice along the west coast of Greenland. On the basis of this summary and the material published in "Nautisk Meteorologisk Årbog" and from unpublished information from the Danish Meteorological Institute, Fig. 4 has been drawn. The points for curve A give, for each decade, the percentage of the year in which Storis reached at least to the neighbourhood of Godthåb (64°N), while those for curve B give the analogous curve for Fiskenaesset (63°N). The most striking features in the curves are the strong decrease in the frequency of Storis off Godthåb from about 1910 and off Fiskenaesset from about 1930. Furthermore, there seems to have been a period with relatively favourable ice conditions from about 1840 to 1870.

It is remarkable that the rich cod period from about 1845 to 1851 lies in this interval where favourable ice conditions make it probable that the sea temperatures were also relatively favourable.

REFERENCES

HANSEN, PAUL M., and F. HERMANN. 1953. Fisken og Havet ved Grønland. *Skr. Danm. Fisk.-og Havunders.*, No. 15.

HANSEN, PAUL M. 1949. Studies on the biology of Cod in Greenlandic waters. *Rapp. Cons. Explor. Mer.*, 123, Copenhagen.

HACHEY, H.B., F. HERMANN and W.B. BAILEY. 1954. The waters of the ICNAF Convention area. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 4; Part 4.

JENSEN, A.S. 1939. Concerning a change of climate during recent decades in the arctic and subarctic regions, from Greenland in the West to Eurasia in the East, and contemporary biological and geo-physical changes. *Kgl. Danske Vid. Selskab. Biologiske Medd.* XIV, 8. København.

SMED, J. 1947-62. Monthly anomalies of the surface temperatures in the sea. *Ann. biol., Copenhague*, Vol. II to XVII.

SPEERSCHNEIDER, C.L.H. 1931. The state of ice in Davis Strait 1820-1930. *Publ. d. danske Met. Inst. Medd.*, No. 8., København.

H-5

VARIATION OF THE TEMPERATURE OF THE SURFACE WATER IN AREAS OF THE NORTHERN NORTH ATLANTIC, 1876-1961

By

Jens Smed[1]

ABSTRACT

For a number of areas covering most of the region 50°N-67°N, 0°-58°W the variation of the surface temperature from year to year during the period 1876-1961 is illustrated. Regional differences with regard to magnitude of temperature changes are considered.

Since 1876 observations of surface temperatures have been made regularly in the northern North Atlantic by Danish and Icelandic commercial vessels. The data for the years 1895-1961 have been published in the annual publications of the Danish Meteorological Institute (1896-1963) in the form of half-monthly or monthly means for one degree squares. Based on the data for the years 1876-1915, Ryder (1917) published monthly means of surface temperature in one degree squares over this period. The mean values for this 40-year period will in the following text be called the normal values.

For each month of the period 1876-1961 and for each one degree square the difference of the monthly mean from the normal value for the month has been calculated and for each month these anomalies have been averaged over each of the areas shown in Fig. 1. Finally, for each area and year, a yearly anomaly was calculated by averaging the monthly anomalies. These monthly and yearly anomalies for the areas in Fig. 1 were published in the Annales Biologiques (Smed, 1947-64).

For the various areas, the yearly anomalies have been plotted in Fig. 2 and 3. A conspicuous feature of these figures is the preponderance of positive anomalies from about the middle of the 1920's in all areas except the southeasternmost one, area N.

The main tendency of the temperature variation becomes still more conspicuous in Fig. 4 where the yearly anomalies have been smoothed out by calculation of 5-year overlapping means. From Fig. 4 it appears that there is a decrease of temperatures from the start of the observations in the 1870's to a minimum in the 1880's. From this minimum there is an increase to a maximum which is reached at the end of the 1880's or in the 1890's. Then comes a long period of fluctuations. The main tendency during this period is towards slightly lower values. The minimum is reached at about 1920. From this time there is for most areas a rapid increase to a maximum which in the western areas was already reached in the late 1920's or in the 1930's, whereas in the eastern areas it seems to have been reached in the 1940's. The ensuing decrease lasts until about 1950 when it is followed by a slight increase.

It might be mentioned here that a study (Smed, 1943) of the observations of the salinity of the surface water during the years 1902-39 in a number of areas of the northern North Atlantic showed during this period a variation of the salinity rather parallel to the variation of temperature illustrated above.

With regard to the two southernmost areas, E and N, the above general picture of the variation of temperature is only partly valid. For these areas the high temperatures in the late 1880's have not later been reached. The somewhat diverging course of temperature in these areas, especially in area N, appears from Table 1 also.

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[1] ICES Hydrographic Service, Charlottenlund, Denmark.

TABLE 1. ANOMALIES OF SURFACE WATER TEMPERATURE (°C) IN THE AREAS A_1 TO N IN THE PERIODS INDICATED.

Area Period	A_1	B	C	D	E	F	G	H	I	J	K	L	M	N
1876-1900	0.1	0.1	0.3	0.2	0.3	0.1	0.1	0.1	0.0	0.0	0.1	0.1	0.2	0.3
1901- 25	0.0	-0.2	-0.2	-0.2	-0.3	-0.4	-0.3	-0.2	0.0	-0.2	-0.1	-0.2	-0.3	-0.2
1926- 50	0.7	0.3	0.6	0.3	0.0	0.2	0.4	0.3	0.7	0.4	0.3	0.3	0.2	-0.1
1951- 61	0.7	0.3	0.8	0.4	0.3	0.3	0.8	0.6	1.1	0.7	0.5	0.6	0.3	0.0

Table 1 compares the temperature anomalies, for the various areas, averaged over the 25-year periods 1876-1900, 1901-25 and 1926-50 and finally over the recent shorter period 1951-61. The table shows that, averaged over the period 1876-1900, the temperature is normal or slightly above in all areas, the average anomalies varying from 0.0° to 0.3°. From this period to that of 1901-25 a decrease takes place, varying from 0.0° in area I to 0.6° in area E, so that for the last mentioned period the average temperature is normal or slightly below in all areas.

From the period 1901-25 to that of 1926-50 Table 1 shows a rise of temperature in all areas. The increase differs considerably from one area to another, however, and the geographical distribution of the values shows a clear picture. The increase is small in the southernmost areas N and E, 0.1° and 0.3°, respectively. It is somewhat higher, *viz.* 0.4° -0.6°, in the central areas (B, D, F, H, J, K, L, M). And the increase is high, *viz.* 0.7° -0.8°, in the northernmost areas (A_1, C, G, I). Averaged over the period 1926-50 the temperature is above normal in all areas except the two southernmost ones, N and E.

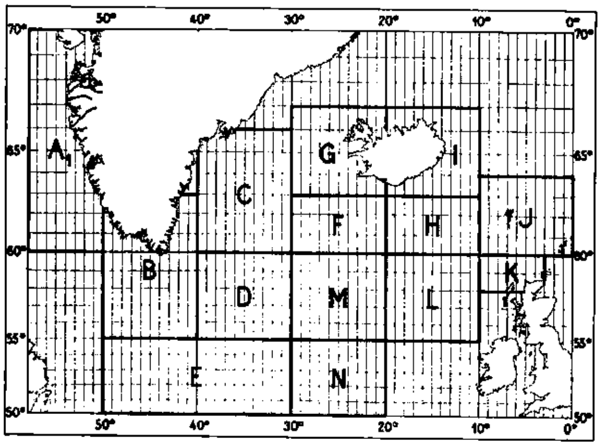

Fig. 1. Location of areas.

Table 1 shows furthermore that the temperature has continued to increase although somewhat slower, from the period 1926-50 to the recent period 1951-61, except in the two areas to the west and south of Greenland, A_1 and B, where the average temperature has remained constant. The greatest increase, 0.4°, took place in the areas surrounding Iceland, G and I.

Comparing the period of lowest temperatures, 1901-25, to that of highest temperatures, 1951-61, we find a temperature rise from about 0.5° in the south (excepting the area N where the rise is 0.2° only) to about 1° in the north.

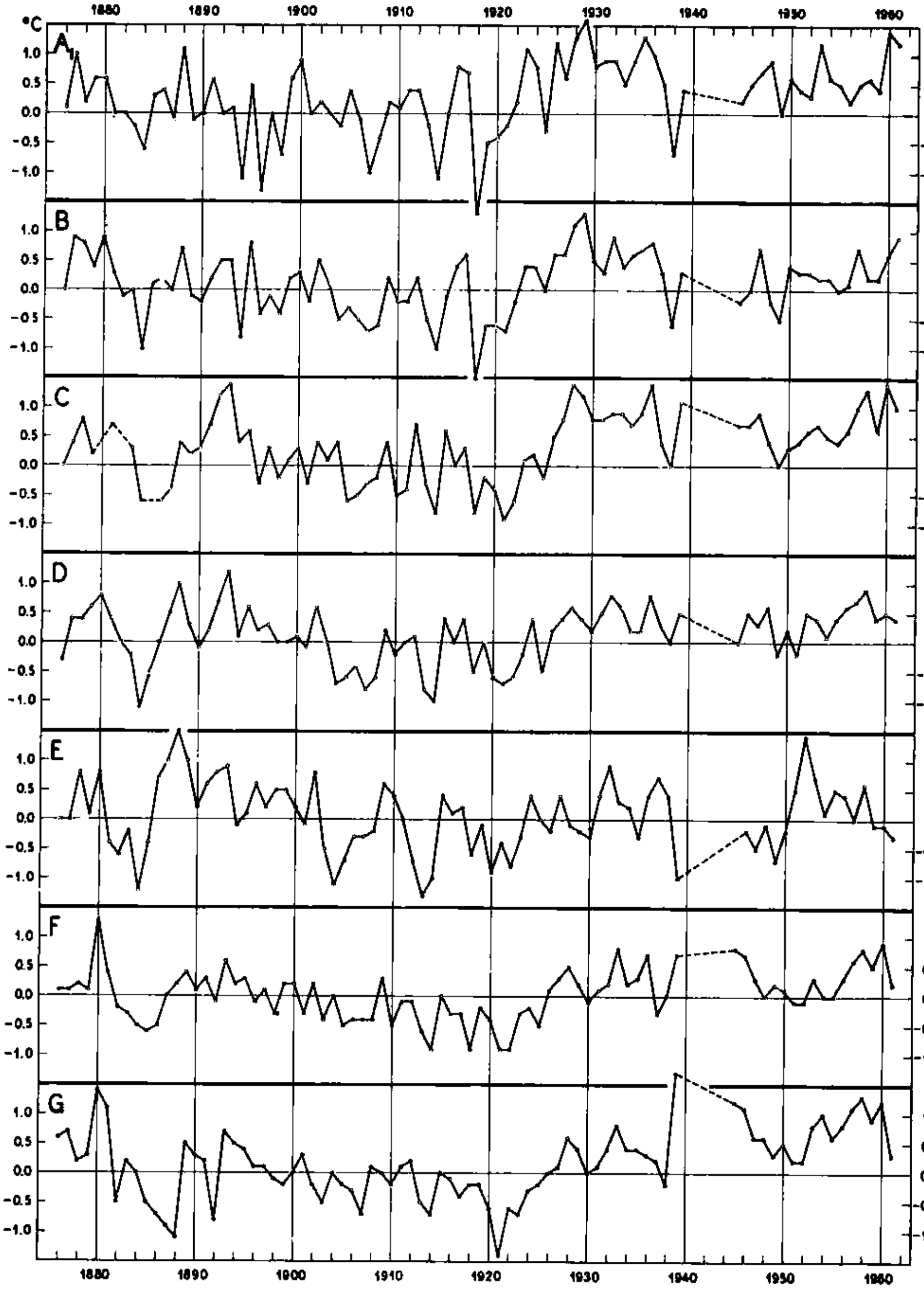

Fig. 2. Yearly anomalies of the temperature of the surface water in the areas A_1 to G.

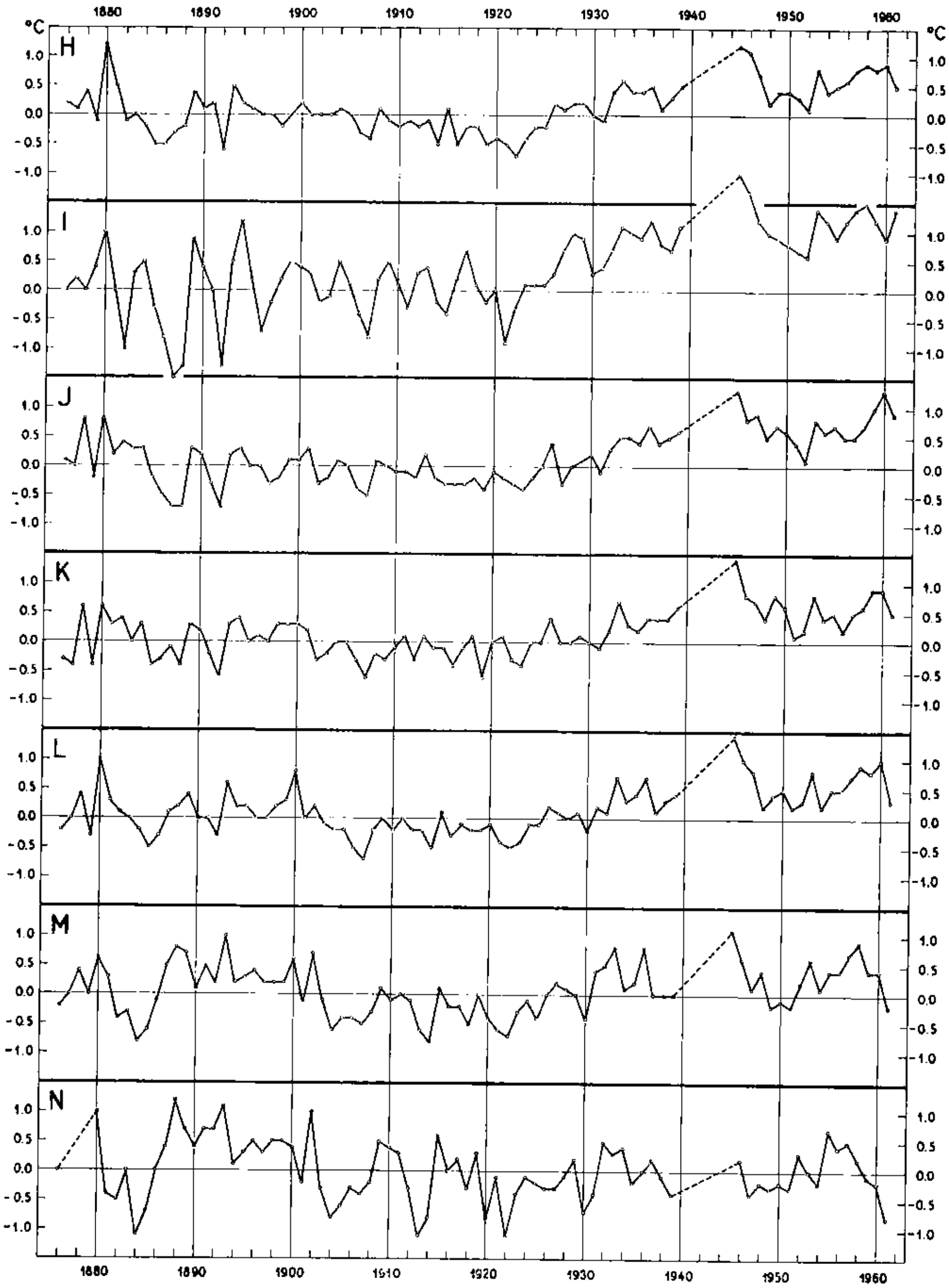

Fig. 3. Yearly anomalies of the temperature of the surface water in the areas H to N.

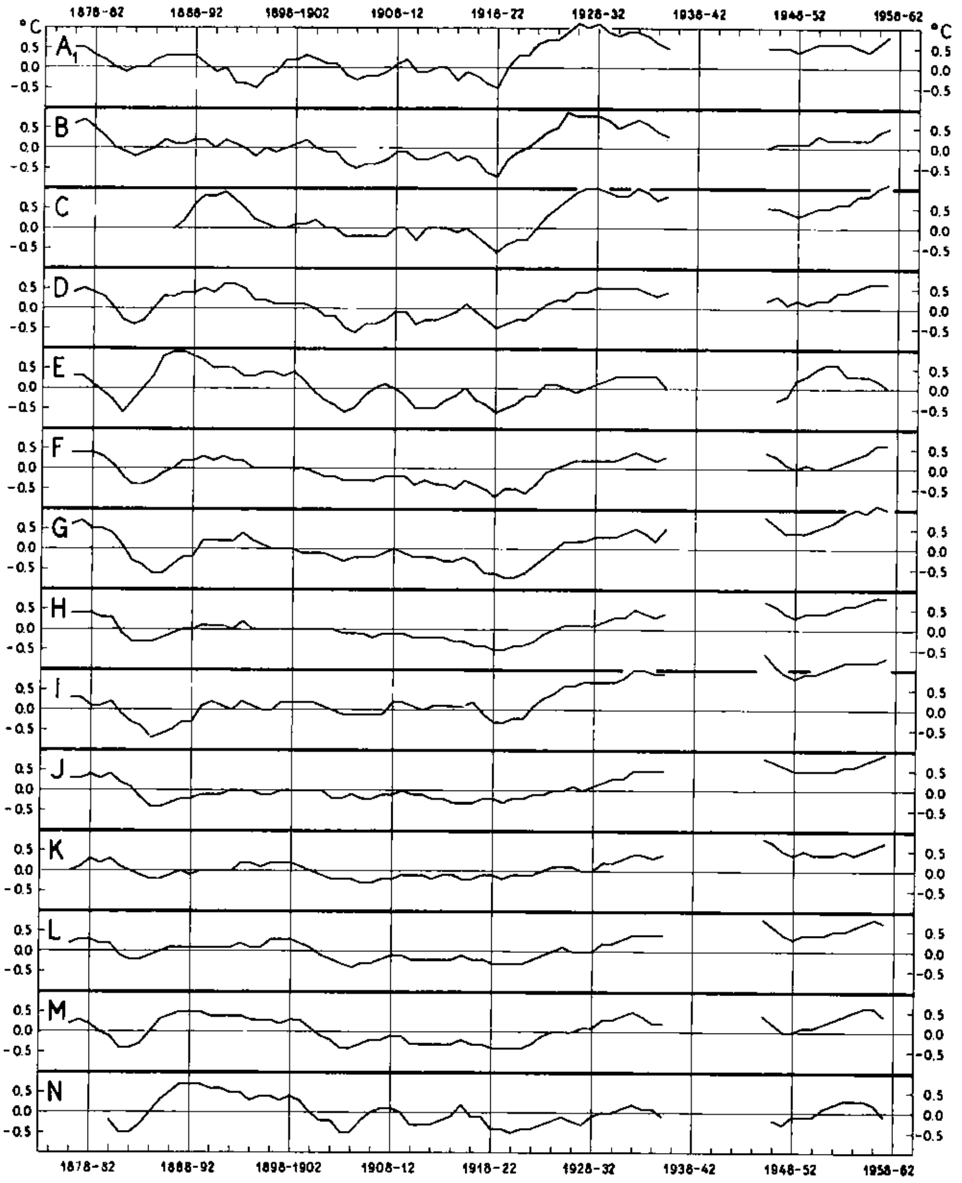

Fig. 4. Overlapping 5-year means of anomalies of surface water temperature in the areas A_1 to N.

REFERENCES

DANISH METEOROLOGICAL INSTITUTE. 1896-1963. *Observations météorologiques nautiques,* 1895-1898. *Nautical-Meteorological Annual,* 1899-1939, 1945-61.

RYDER, C. 1917. Monthly mean temperatures of the surface water in the Atlantic, North of 50° N. Lat.—Appendix to the *Nautical-Meteorological Annual* of the Danish Meteorological Institute.

SMED, J. 1943. Annual and seasonal variations in the salinity of the North Atlantic surface water. *Rapp. Cons. Explor. Mer,* 112: 77-94.

1947-1964. (Articles in the *Ann. biol., Copenhague,* Vols. 2-17 and 19).

H-6

LONG-TERM VARIATIONS OF OCEANOGRAPHIC CONDITIONS AND STOCKS OF COD OBSERVED IN THE AREAS OF WEST GREENLAND, LABRADOR AND NEWFOUNDLAND

By

A.A. Elizarov[1]

ABSTRACT

Variations of oceanographic conditions along West Greenland, Labrador and Newfoundland coasts are considered. These variations are assumed to reflect relaxation or strengthening of the polar water masses. Water temperatures are used as the indicator of fluctuations in the oceanographic conditions. Commercial productivity of the sea and relative fluctuations of fish stocks in the area are also considered. Izhevsky's method for estimating relative indices of variations of cod stocks gave good results for the Labrador and Newfoundland areas.

Annual variations of temperature conditions in the sea are considered, in many papers, to be the main cause of fluctuations in the groundfish yield. Hermann (1953) showed that an increase of water temperature in the area of Fyllas Bank is related to an increase of the yield of the West Greenland cod and a fall of water temperature results in decrease of the yield.

Kislyakov (1961), having studied the variations of hydrological conditions and annual fluctuations of the cod yield in the Norwegian and Barents Seas, concluded that the highest and lowest intensity of currents is correlated with productive and nonproductive years respectively. The increase in intensity of currents is related to a rise of water temperature, the fall to a decrease of temperature.

Thus fluctuations in the yield of cod are related to annual variations of temperature. In the present case we deal with both causal and mediate relationships. Undoubtedly, water temperature directly influences the formation of fish resources of the sea. A rise of temperature hastens growth and development of eggs and larvae, intensifies the processes of albumen metabolism of different aged fish, and influences the formation of food conditions for fish. The role of water temperature as the indicator of the oceanographic regime of the sea should, however, be noted to be more significant.

Izhevsky (1961) showed first that heat supply in the seas of Northern Europe and the inland seas of the USSR appears to be the indicator of a number of physical processes which finally determine the commercial productivity of the sea. It will be shown below that the same is true of the fishing areas of the Northwest Atlantic.

Fishing areas of the Northwest Atlantic are located meridionally and are influenced by the system of regular warm and cold currents — the Labrador, West Greenland and North Atlantic. Variations of mean temperatures in the active layer of the sea in the areas of Newfoundland and Labrador are related to the strengthening or weakening of the intensity of the Labrador current, as well as to the increase or decrease of the outflow of cold polar water masses (Elizarov, 1962). The polar water moving southward along the continental slope interacts with the relatively warm water masses of the temperate latitudes of the Atlantic Ocean. A decrease or increase of the inflow of polar water masses causes a corresponding extension or reduction of the relatively warm water masses of Atlantic origin. An increase or decrease in the intensity of the West Greenland current and its warm component causes variations in temperature and hydrochemical regimes on fishing banks themselves and on the continental slope.

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[1] All-Union Research Institute of Marine Fisheries and Oceanography, Moscow, USSR.

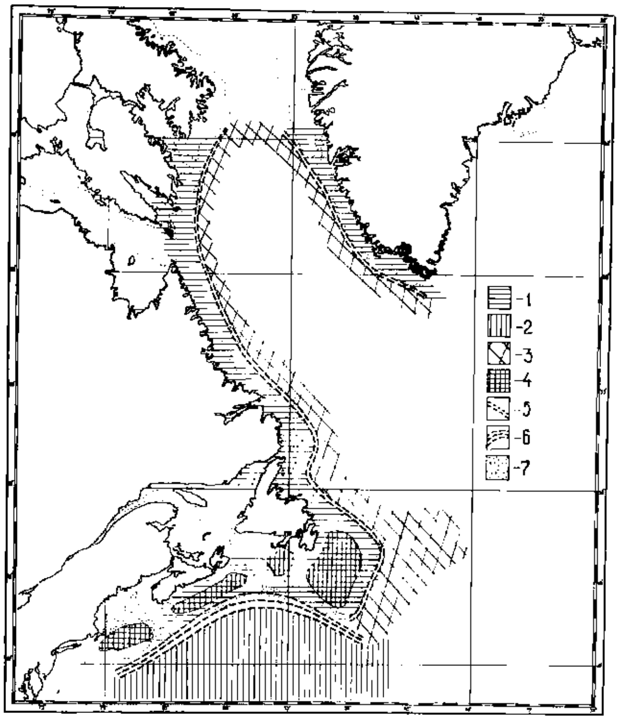

Fig. 1. Water masses and fronts: 1-polar waters, 2-tropical waters, 3-water of moderate latitudes of the Atlantic, 4-bank waters, 5-secondary polar front, 6-polar front, 7-waters of slope.

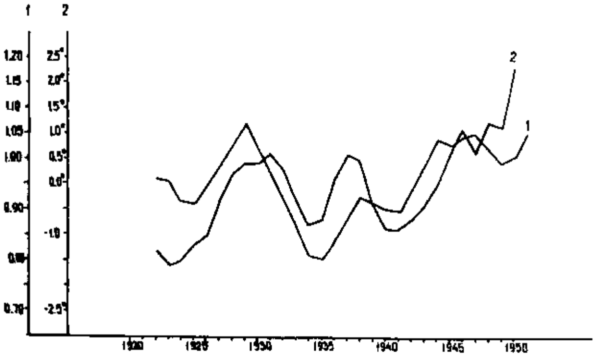

Fig. 2. Long-term variations of the discharge and water temperature (in three-year sliding average). 1-Discharge of St. Lawrence, 2-water temperature on the sea surface in St. Andrew's, Canada.

The analysis of data obtained during long-term observations showed that variations in water temperature and salinity in the areas of West Greenland, Labrador and Newfoundland had a high correlation coefficient (over 0.60). The correlation decreases in the inshore waters where the influence of continental discharge and transport of water out of the Hudson and Belle Isle Straits is found. Over the long term there is a correlation between the St. Lawrence River discharge and the sea surface temperatures at St. Andrews, N.B. (Fig. 2), indicating that a warm climate is associated with greater river flow. Thus during warm periods, higher salinities are found in offshore waters due to the wide distribution of the Atlantic water masses, and lower salinities are found in inshore waters resulting from increase of river discharge. An increase in the amount of Atlantic water as indicated by a rise of temperature in the 0-200 m layer, is associated with a corresponding rise of salinity in all the areas investigated. The fact that the variation of temperature in the area is closely connected with fluctuations in the supply of the upper productive layers with biogenic elements proves to be very important.

As shown by Adrov (1962), enrichment of the water masses of the West Greenland banks with nutrient salts takes place due to an influx of relatively warm deep Atlantic waters flowing up along the slope. In the Frederikshaab area (West Greenland) the correlation coefficient between temperature and phosphorus was 0.67, and between temperature and silicate 0.65. Thus, in a warm year, nutrient salts in the productive layer increase and *vice versa*. Observations of the distribution of biogenic elements over the Newfoundland and Labrador Banks in March-April of 1960 showed that the content of phosphorus and silicates increased, in general, from west to east, *i.e.* from the area of the cold, low salinity polar waters towards the warmer, high salinity waters of the Atlantic origin (Ponomarenko and Istoshina, 1962). The above fact does not mean that waters of Atlantic origin are richer with biogenic elements than the Arctic ones. The Atlantic water masses represent deep waters (their core is located between 200-400 m) which tend to rise into the upper layers near the continental slope. The core of the polar water transported by the Labrador current moves near the surface of the sea, is heated from the top and in the process of photosynthesis partially loses its saturation with nutrient salts.

On the basis of the data obtained during surveys conducted in March-April 1960, a direct relation was found between water temperature and content of phosphorus on different sections of the Grand Newfoundland Bank. On the northern slope of the Bank where the surface heat and the development of phytoplankton has not begun the correlation coefficient for the 0-1000 m layer was 0.94.

On the sections farther to the south along the main stream of the Labrador current the correlation decreases gradually. The correlation coefficient for the 100-500 m (and 100-1000 m) layer did not however drop below 0.60.

Thus, temperature conditions in the fishing areas of the Northwest Atlantic are indicative of the oceanographic phenomena and processes. As a rule, a warm year is characterized by the following conditions which are of great importance for the yield:

1. General increase of heat supply in the sea.

2. Rise of near-bottom temperatures on the shelf.

3. Increase in salinity in the larger part of the area (excluding coastal waters).

4. Increase in river discharge and corresponding growth by providing the coastal zone with biogenic elements.

5. Extension of the relatively warm Atlantic water, which involves an increase of biogenic elements, in the productive layers near the fringe of the shelf.

Quite opposite processes are characteristic of a cold year.

As mentioned previously, definite temperature conditions are related to a definite level of the cod yield. Hermann's data and ours are compared with the stronger year-classes of West Greenland cod (ICNAF, 1951-1960) in Fig. 3. In general, productive years correspond to the maximum temperatures and the nonproductive years to minimum temperatures. The year 1941, an extremely warm one, represents the only exception as the 1941 year-class did not distinguish itself in the fishery.

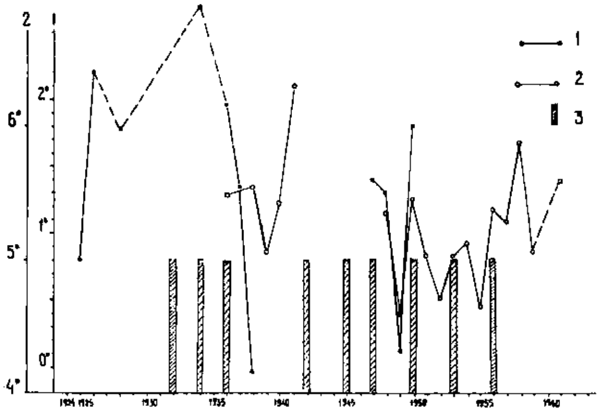

Fig. 3. Strong year-classes of cod in the area of West Greenland (indicated with columns) and mean water temperatures by months
1-in near-bottom layer on the Fyllas Bank in June, according to Hermann.
2-in the 0-200 m layer on the standard section southwest of the Cape Farwell in July, according to Elizarov.

From this correlation an estimate of the year-class size can be made by knowing the oceanographic conditions for the year. The water temperature of the active layer of the sea (0-200 m) estimated on the basis of standard hydrological sections with reduction to a definite date can be assumed as the index of oceanographic conditions for the year.

A similar method was first worked out and used by Izhevsky (1961) for the seas of Northern Europe. The results showed that there was good agreement between the estimated and actual values of catch.

Analogous results were obtained by us for the fishing areas of Labrador and Newfoundland. Water temperature on standard sections in the areas of Labrador and Newfoundland estimated with the help of equations of the relationship of these sections with the Kola meridian section (Elizarov, 1962) are assumed as basis of curves 1 and 2 (Fig. 4). It was taken into account when estimating that cod at age 6-9 was the base of fishing. The high level of 1954-1956 is due to large cod catches per hour of trawling in the area of Newfoundland Banks (Fig. 5). Decline of fishing conditions in the Labrador and Newfoundland areas are shown in Fig. 4. Table 1 shows the data on fishing of cod in the area of Newfoundland Banks. In 1958 the greatest decline in cod stocks was observed.

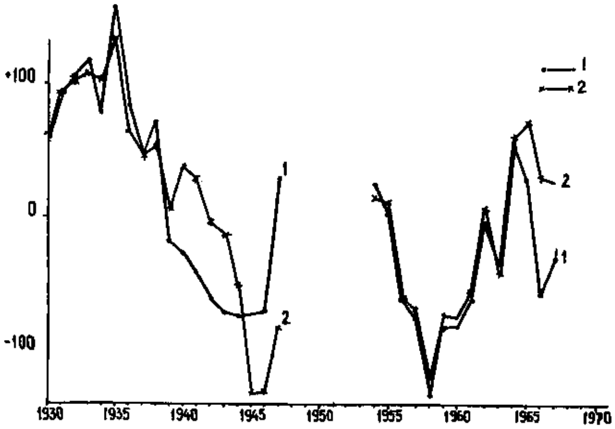

Fig. 4. Fluctuations of cod stocks estimated by means of the index of water regime (mean temperature of the 0-200 m layer): 1-in the area of Labrador, 2-in the area of Newfoundland.

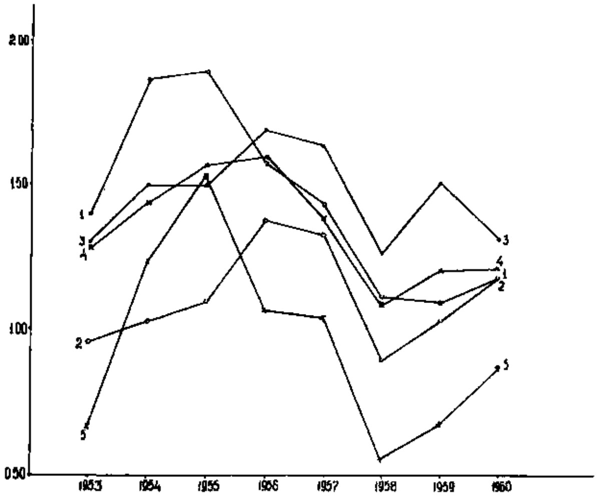

Fig. 5. Mean catches per hour of trawling in the Newfoundland area.
1,2-catches of medium and large-size Spanish trawlers:
3,4-catches of medium and large-size Portuguese trawlers:
5-catches of Canadian trawlers.

During the first half of 1961 the Soviet fleet in the areas of Newfoundland and Labrador fished mainly for cod, catch per unit of fishing effort reached maximum values (to 1,750 kg per hour of trawling).

TABLE 1. CATCHES OF COD IN THE AREA OF NEWFOUNDLAND

Years	Catch of cod ('000 tons)	(as % of the total catch of groundfish)
1957	454	73.7
1958	293	54.8
1959	433	59.9
1960	509	72.9

Thus, there is a good coincidence between cod stocks, estimated with the help of indices of the water conditions, and catches per hour of trawling.

CONCLUSIONS

1. Variations observed in intensity of the currents of the Northwest Atlantic cause changes both in temperature and hydrochemical regimes in the zones of the shelf and continental slope. A decrease of the polar water outflow and a corresponding rise of water temperature is related to an increase of salinity in the offshore part of the area (excluding coastal sections) and a rise of biogenic elements. Increase of river discharge is characteristic of periods of warm years in the onshore areas.

2. Fluctuations of water temperature are closely related to variations of other elements of the regime which, in total, determine the commercial productivity of the sea. In addition, water temperature appears to be one of the elements of the water situation which directly regulates the intensity of biological processes. Thus water temperature can be used as the indicator of annual fluctuations of oceanographic conditions.

3. Analysis of the data concerning water regime and reproduction of cod obtained over a long

period of time showed that the increase of the cod yield in the Northwest Atlantic coincides, as a rule, with the warm years, and decrease of the yield to the regime of cold years.

4. Correlations existing between variation of oceanographic conditions and the level of reproduction of groundfish permit us to calculate relative fluctuations of fish stocks with the help of indices of the water regime. Izhevsky (1961) summarized for each year the temperature conditions under which each year-class in the fishery was produced. Application of this method for the Labrador and Newfoundland areas gave good results: variations of cod stocks estimated by relative indices with the help of the water regime conformed to the actual variations of cod catches per hour of trawling.

REFERENCES

ADROV, M.M. 1962. Hydrological investigations off West Greenland, collection of Soviet fishery investigations in the Northwest Atlantic. Issued by *Ryb. Khoz.*

ELIZAROV, A.A., 1960. Results of Soviet oceanographic investigations in the Labrador and Newfoundland areas. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 10: 95-101.

1962. On year to year fluctuations of the Labrador and West Greenland Currents intensity and on possibility of forecast of the year temperature conditions in fishing areas of the northwest part of the North Atlantic. Oceanology *5*. Issued by the Academy of Sciences of the USSR, Moscow.

HERMANN, F. 1953. Influence of temperature on strength of year classes. *Ann. Biol.*, 9 (1952).

ICNAF. 1951-1960. International Commission for the Northwest Atlantic Fisheries. *Annu. Proc.*, Vol. 1-10, 1951-60.

IZHEVSKY, G.K., 1957. On early determination of type of the Barents Sea regime. *Ryb. Khoz.*, 12. Moscow.

1961. Oceanographic bases of formation of sea commercial productivity. *Pischpromizdat.* Moscow.

KISLYAKOV, A.G. 1961. Relationship between hydrological conditions and variations of cod year-classes abundance. Transactions of conferences of Ichthyology Commission of AN USSR, Vol. 13, Moscow.

PONOMARENKO, L.S., and M.A. ISTOSHINA, 1962. Hydrochemical studies in Newfoundland area of Northwest Atlantic; collection of Soviet fishery investigations in Northwest Atlantic. Issued by *Ryb. Khoz.*, Moscow.

WILLIAMS, G.R. 1961. Cyclical variations in world-wide hydrological data. *J. Hydraul. Div. Proc. Amer. Soc. Civil Engrs.*, 87; 6; part 1.

H-7

VARIATION IN RECRUITMENT OF COD (*GADUS MORHUA* L.) IN SOUTHERN ICNAF WATERS, AS RELATED TO ENVIRONMENTAL CHANGES

By

W.R. Martin[1] and A.C. Kohler[2]

ABSTRACT

Long-term trends and annual variations in recruitment of cod to the commercial fisheries of the southern ICNAF area are negatively correlated with sea surface temperatures during the first year of life. This recruitment-temperature association is described for New England, Western Nova Scotia and Gulf of St. Lawrence areas. Similarities between cod and haddock in the occurrence and distribution of dominant year-classes suggest that environmental conditions during the early pelagic life of these species have important effects on recruitment. The association of temperature and recruitment is interpreted to mean that temperature and water transport are limiting factors in the survival of cod eggs and larvae for recruitment to fisheries.

INTRODUCTION

Effects of long-term climatic changes on the abundance of cod in the northern part of the ICNAF area, off West Greenland, have been described in a series of published papers including Jensen (1939), Hansen (1949), and Hermann (1953). The most recent conclusions concerning the importance of high water temperatures in the production of large year-classes of cod at West Greenland are reported by Hansen and Hermann (1964) and by Hermann, *et al.*, 1964).

As a corollary to the positive correlation between year-class survival and temperature observed for ICNAF Subarea 1, year-class strength and resultant fishing success might be expected to be negatively related to temperatures at the southern end of the cod range. This paper examines the hypothesis that weak year-classes are associated with above-average temperatures during early development and strong year-classes with below-average developmental temperatures in ICNAF Subareas 4 and 5.

Sea temperature observations have been taken twice daily since 1921 by the Fisheries Research Board of Canada, at St. Andrews, N.B. Lauzier (1964) has shown that annual variations and trends in the average temperature observed at St. Andrews are representative of changes in the marine climate over the continental shelf adjacent to Nova Scotia and New England. These environmental data are examined in relation to long-term series of statistics and year-class observations for landings of cod from ICNAF Subareas 5 and 4. Annual landings of cod from New England grounds (Subarea 5) for the whole 42-year period of temperature observations are available in ICNAF Statistical Bulletins (Anon., 1952-63). More detailed information on landings by year-classes, and in some cases on landings in relation to fishing effort, has been collected since 1946 by the Biological Station at St. Andrews, N.B., from representative grounds in Subarea 4.

Results of analyses are reported in four sections, and interpretations are considered in the Discussion. The locations of places and areas mentioned in the text are shown in Fig. 1.

TEMPERATURE AND RECRUITMENT VARIATIONS

New England

Annual data on St. Andrews mean water temperatures and landings of cod from Subarea 5 are presented for the period 1921 to 1962 in Table 1. The long-term trend is from low temperatures and

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[1] Fisheries Research Board of Canada, Ottawa, Ontario, Canada.

[2] Fisheries Research Board of Canada, Biological Station, St. Andrews, N.B., Canada.

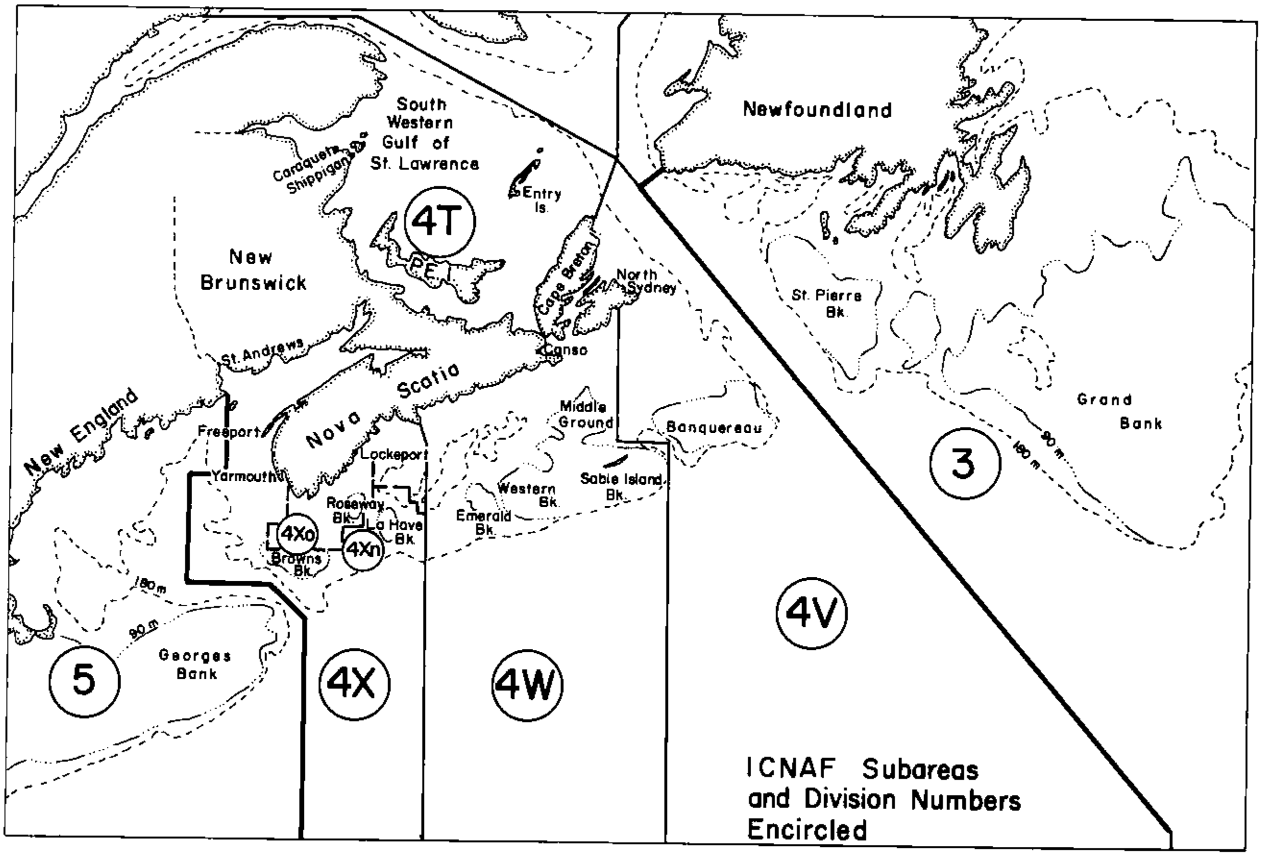

Fig. 1. Chart of the southern ICNAF area.

high landings in the late 1920's to high temperatures and low landings in the early 1950's. Recently the trend has been reversed; lower temperatures and higher landings have been observed.

Age-composition data for Subarea 5 cod landings were not available to provide an assessment of the association between temperatures and the size of year-classes produced at these temperatures. However, an attempt to learn something about this relationship has been made by calculating correlation coefficients between temperatures and total cod landings made up to 7 years later. The results are tabulated in Table 2 and a sample plot of the data for a time lag of 4 years is shown in Fig. 2. It is noted that the highest correlations (-.72 and -.75) are for landings made 3 to 4 years following the year of the temperature measurements. Schroeder (1930) has described the fast growth of Subarea 5 cod and the dominance of 3- and 4-year-old fish in catches for tagging experiments. If year-class strength is determined at the egg-larval stage of development, and landings are in fact largely 3- and 4-year-old fish, the best correlations would be expected for a 3 to 4 year time lag between temperature observations and landings. The high correlations, even with a lag of 7 years, when very few cod are left in the fishery, probably result from the high auto-correlation observed in the temperature series.

Consideration has been given to the possibility that the high correlations result from common trends rather than a causal relationship between temperature and cod catches. To eliminate the effect of possible trends, straight lines have been fitted to both the temperature and cod landings data; and secondly, third degree polynomials have been fitted to these data. Landings and temperatures have been calculated as deviations from the respective "trend" lines, and correlation coefficients have been calculated between landings and temperature residuals. The resultant correlation coefficients are shown in columns 3 and 4 of Table 2. Correlation coefficients between temperatures and landings 4 years later have been reduced by about -.40, but they are still significant. This would be expected if there is a good relationship between temperature and strength of year-classes.

TABLE 1. ANNUAL COD LANDINGS FROM ICNAF SUBAREA 5 AND ANNUAL MEAN SEA SURFACE TEMPERATURES AT ST. ANDREWS, N.B. (LANDINGS IN METRIC TONS, ROUND, FRESH).

Year	USA	Canada	Other	Total	Mean sea surface temp.°C
1921	32859			32859	7.0
1922	31632			31632	6.0
1923	31274			31274	5.4
1924	33469			33469	6.4
1925	35193			35193	6.2
1926	41122			41122	5.9
1927	42807			42807	6.8
1928	40749			40749	7.3
1929	43294			43294	6.7
1930	48380			48380	7.1
1931	39082			39082	7.3
1932	36154			36154	7.0
1933	37491			37491	6.7
1934	32404			32404	6.3
1935	36178			36178	6.2
1936	36373			36373	6.8
1937	46387			46387	7.7
1938	37445			37445	7.1
1939	31897			31897	6.6
1940	28297			28297	6.1
1941	32257			32257	6.4
1942	29172			29172	6.6
1943	31226			31226	6.3
1944	33549			33549	6.9
1945	33702			33702	7.3
1946	35160			35160	7.2
1947	27533			27533	7.8
1948	29374			29374	6.5
1949	28867			28867	8.3
1950	24251			24251	7.7
1951	19077			19077	8.5
1952	14886			14886	7.9
1953	11226	4		11230	8.4
1954	12237	0		11237	8.2
1955	12457	20		12477	7.7
1956	13238	8		13246	6.8
1957	13160	21		13181	7.4
1958	16252	64		16316	7.5
1959	16218	132		16350	6.6
1960	14282	148	USSR	14430	7.4
1961	17669	241	55	17965	6.8
1962	18226	7935	?	26161	6.8

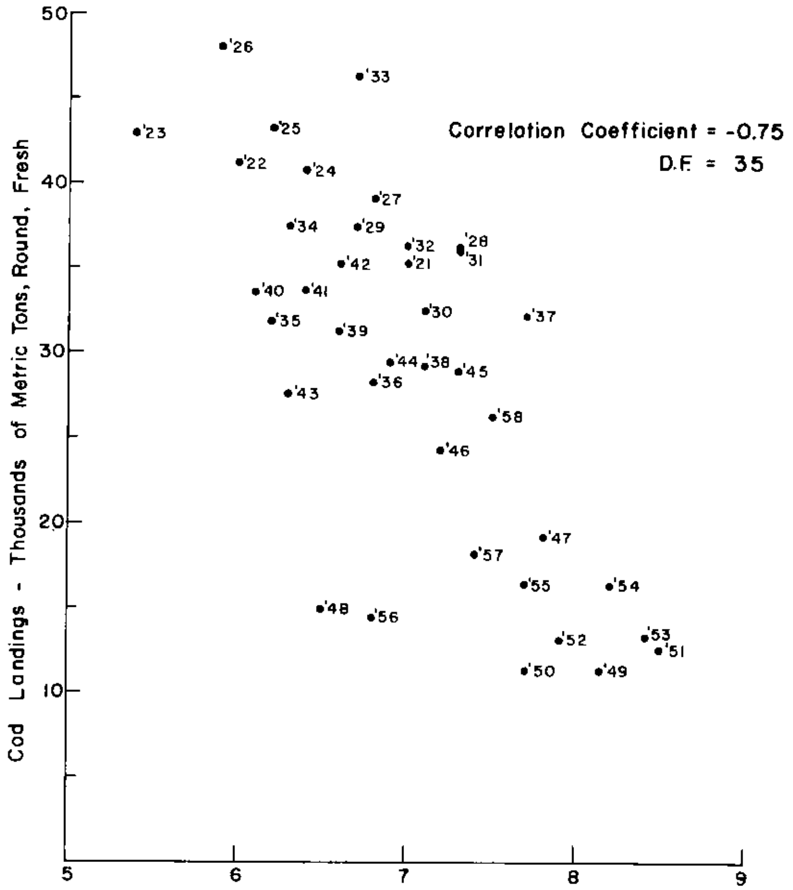

Fig. 2. Relationship of annual mean sea surface temperatures at St. Andrews, N.B., and Subarea 5 cod landings 4 years later. Years for temperature data are shown.

TABLE 2. CORRELATIONS BETWEEN ICNAF SUBAREA 5 COD LANDINGS AND TEMPERATURE DATA (TABLE 1). CORRELATIONS ARE GIVEN FOR TEMPERATURE AND LANDINGS 0 TO 7 YEARS LATER.

Lag (years)	Correlation coefficient	Correl. coeff. eliminating possible linear trend	Correl. coeff. eliminating possible third degree polynomial trend
0	-.40[a]	.00	.03
1	-.53[a]	-.12	-.08
2	-.65[a]	-.23	-.18
3	-.72[a]	-.30	-.25
4	-.75[a]	-.38[a]	-.34[a]
5	-.68[a]	-.33[a]	-.31
6	-.65[a]	-.34[a]	-.33[a]
7	-.63[a]		

[a] significant at 95% level

The dangers in concluding that low temperatures are the cause of high landings of cod in ICNAF Subarea 5 are fully appreciated. Changes in effort and landings for the haddock fishery in Subarea 5 (Graham, 1952) parallel the cod landings data in Table 1 for the years up to about 1945. There have been changes in market preference for haddock over cod, and changes in gear and depths fished. The long-term increase in fishing effort by otter trawlers may have been an important factor affecting the trend toward decreased landings of cod. However, it is difficult to understand how this trend in fishing practices could account for the recovery from very low landings in the 1950's. Changes in landings appear to be more closely related to fluctuations in environmental conditions.

The significant negative correlations between annual mean temperatures and landings of cod from ICNAF Subarea 5 are consistent with the hypothesis that small year-classes are associated with above-average temperatures, and large year-classes with below-average temperatures, at the southern end of the cod's geographic range in the western North Atlantic.

Western Nova Scotia

Cod data for western Nova Scotia (unit areas o and n of ICNAF Division 4X) are only available for a shorter period (1946 to 1962). However, the availability of information on fishing effort in relation to landings, and on age composition of landings, permits a more precise assessment of the temperature-year-class strength relationship during this limited time series.

Cod landings from the 4Xo-n area are shown in Table 3. Most of the catch has been taken by Canada. Both Canadian and United States 4Xo-n landings follow the same long-term trend toward lower landings that we have observed for Subarea 5.

TABLE 3. COD LANDINGS FROM UNIT AREAS O AND N OF ICNAF DIVISION 4X (IN METRIC TONS, ROUND).

Year	USA	Canada	Total
1946	1254	10139	11393
1947	1295	8285	9580
1948	1276	8203	9479
1949	802	7622	8424
1950	895	9386	10281
1951	833	8230	9063
1952	1036	9233	10269
1953	460	6924	7384
1954	660	8009	8669
1955	505	7341	7846
1956	305	6938	7243
1957	183	7815	7998
1958	467	6669	7136
1959	107	6246	6353
1960	425	6127	6552
1961	627	6519	7146
1962	335	7277	7612

Most of the Canadian catch has been taken by baited longlines fished from inshore boats. Sampling of landings by this fishery has been carried out at Lockeport, N.S. Abundance has been measured by average landings per tub of longline gear (each containing eleven 50-fathom (91.4 m) lines with about 50 baited hooks per line). Sampling of the landings for age composition has provided a breakdown of these abundance data by year-classes (Table 4).

The relative strength of year-classes has been measured by totalling catches per tub over ages 3 to 7 for each of the year-classes 1944-51. The figures thus obtained have been correlated with sea temperatures during the year of spawning and early development. The St. Andrews temperatures listed in Table 1 have been used as an index of temperature changes in the 4Xo-n area.

TABLE 4. RELATIVE STRENGTH OF YEAR-CLASSES OF COD FROM THE 4XO-N AREA AS MEASURED BY NUMBERS OF FISH LANDED PER TUB OF TRAWL AT EACH AGE.

	Age												
Year	2	3	4	5	6	7	8	9	10	11	12	13	14
1947	1	6	11	4	4	5	5	1	–	1	–	–	–
1948	1	5	9	8	2	2	2	3	1	1	1	–	–
1949	2	8	8	7	8	–	1	2	1	–	–	–	–
1950	2	8	11	6	5	5	–	–	1	1	–	–	–
1951	1	10	8	8	3	2	3	–	–	2	–	–	–
1952	1	4	15	10	6	4	2	2	1	–	–	–	–
1953	–	3	8	10	5	2	1	1	1	–	–	–	–
1954	–	3	9	7	7	3	1	1	1	1	–	–	–
1955	–	6	9	7	5	4	2	1	1	1	–	–	–
1956	–	1	12	5	4	3	3	1	–	1	1	–	–
1957	–	1	2	9	2	3	2	3	2	–	1	1	1
1958	–	3	6	5	7	1	1	1	1	–	–	–	–

Year-class	Total numbers per year-class for ages 3 to 7
1944	29
1945	26
1946	35
1947	34
1948	46
1949	27
1950	26
1951	20

Although based on only 6 degrees of freedom, a significant correlation coefficient of -.75 was calculated. The correlation does not necessarily imply cause and effect. However, the high negative correlation is again consistent with the hypothesis that small year-classes are associated with above-average developmental temperatures and large year-classes with below-average temperatures at the southern end of the cod's distribution in the Northwest Atlantic area.

Southwestern Gulf of St. Lawrence

The cod fishery in the southwestern Gulf of St. Lawrence has been studied since 1946. The development of a Canadian dragger fishery and European otter-trawler exploitation of this stock have substantially increased landings of Division 4T cod. The greatly increased fishing effort obscures any effect that climatic changes may have had on landings.

Our examination of the temperature-cod recruitment relationship is based on mean surface temperatures taken daily during the months of May to October at Entry Island (Lauzier, 1953; Lauzier and Hull, 1961), and on sampling of Canadian cod landings for age composition at fishing ports in northern New Brunswick. The average temperatures and the year-classes which were dominant in landings for more than one year are listed in Table 5.

Temperatures were observed to be below the average annual temperature of 11.9°C during 8 of the 21 years. Five dominant year-classes of cod were observed in this period, and 4 of these year-classes were spawned in below-normal sea temperature years.

These rather superficial observations concerning the relationship between temperatures and cod abundance are again consistent with the hypothesis that large year-classes are associated with below-normal developmental temperatures in ICNAF Subareas 4 and 5.

TABLE 5. COMPARISON OF MEAN SURFACE TEMPERATURES (°C) FOR MAY TO OCTOBER AT ENTRY ISLAND AND DOMINANT YEAR-CLASSES OF SOUTHWESTERN GULF OF ST. LAWRENCE COD.

Year	Mean surface temperature °C	Temp. below average (11.9°C)	Dominant year-class	Year	Mean surface temperature °C	Temp. below average (11.9°C)	Dominant year-class
1937	12.2			1948	11.2	X	
1938	12.1			1949	12.2		
1939	11.3	X		1950	11.8	X	X
1940	11.3	X		1951	12.8		
1941	10.5	X	X	1952	12.6		
1942	12.9			1953	12.0		
1943	11.4	X		1954	11.4	X	X
1944	11.9			1955	11.9		
1945	12.1			1956	11.7	X	X
1946	11.9			1957	11.9		
1947	12.3		X				

Distribution of Dominant Year-Classes

It is of interest to examine the relationship of the dominant year-classes of cod observed off Western Nova Scotia and in the Western Gulf of St. Lawrence to dominant year-classes observed in adjacent areas and in a related species, haddock (*Melanogrammus aeglefinus* L.).

Sampling of Canadian landings for age composition has been carried out at representative fishing ports in Nova Scotia, New Brunswick and Prince Edward Island since 1946. The age-composition data, assigned to area fished, are on file at St. Andrews. The Gulf of St. Lawrence data have been published by Kohler (1964). The dominant year-class for each annual set of samples from each fishing ground is the one having the greatest individual percentage in the sample and is listed for cod in Table 6. The general pattern of distribution of dominant year-classes is summarized by groups of fishing grounds which roughly correspond with the distribution of stocks of cod in ICNAF Subarea 4 (Martin, 1953) in Fig. 3.

Similar treatment of haddock samples to show dominant year-classes is summarized in Table 7 and Fig. 4. The haddock data have been extended to Georges Bank (Subarea 5) by adding observations by Graham (1953-1961) and to St. Pierre and Grand Banks (Subarea 3) by adding information reported by Templeman (1953-1961). Table 7 also includes data for Browns Bank and Inshore Lockeport (Hennemuth, Grosslein and McCracken, 1964; Kohler, 1958; and Wise, 1957).

An examination of Fig. 3 and 4 shows that dominant year-classes commonly extend over a broad geographic range. It is particularly noteworthy that the largest year-classes are dominant over a wide area as well as remaining for several years in the fishery. In most cases dominant year-classes are distributed over contiguous areas rather than in a discontinuous distribution pattern. In some cases a dominant year-class appears in only one area, but these are the exceptions rather than the rule. Some dominant year-classes are found only in inshore areas and others are confined to offshore banks; some are found on western grounds, and others have an easterly distribution.

It is of special interest that cod and haddock year-classes are often dominant for the same years and the same areas. The 1943 and 1952 year-classes were particularly strong in both species and in both cases were distributed from Cape Breton to Georges Bank. The 1945, 1948, and 1950 year-classes were dominant in both species and they had similar distributions over the western part of the area. The 1947 and 1949 year-classes were dominant in both species and were distributed over eastern Nova Scotia grounds. The similarities in the occurrence and geographic distribution of dominant year-classes in these two species suggest that common factors are operating during very early stages of development in the determination of year-class survival for recruitment to fisheries. This appears reasonable in view of the late winter and early spring spawning of Nova Scotian populations of both species (Grosslein, 1962; Templeman, 1962), and the common pelagic life of eggs and larvae.

TABLE 6. DOMINANT YEAR-CLASSES OF COD IN COMMERCIAL LANDINGS. DATA ARE TAKEN FROM FILES OF THE GROUNDFISH INVESTIGATION, FISHERIES RESEARCH BOARD OF CANADA, BIOLOGICAL STATION, ST. ANDREWS, N.B. DASHES INDICATE NO DATA.

Year	Freeport grounds	Yarmouth grounds	LeHave Bk.	Roseway Bk.	Lockeport grounds	Western Bk.	Sable Is. Bk.	Middle Ground	Banquereau	Canso grounds	N. Sydney grounds	SW Gulf St. Lawrence
1946	'43	'43	'43	-	'43	'39;'42	-	'38;'39	'39	'41	'39	'35
1947	'44	'43;'44	'43	'43	'43	'39	'43	'39;'41	'39	'39;'41	'39	'41
1948	'45	'43;'44	'43	'43	'44	'43	'39	'43	'39;'43	'43	'41	'41;'42
1949	'45	'45;'46	'43	'44	'43;'45	'39	'39;'43	'41;'43	'43	'43	'41	'41
1950	'47	'45	'43;'45	'46	'46	'43	-	'43	'43	'43	'43	'41
1951	'48	'48	'43	'46	'43;'46	'43	'41	-	'43;'45	'46	'43	'46
1952	'48	'48	'48	-	'47;'48	-	'49	'47	'43;'47	'47;'48	'43;'47	'47
1953	'48	'50	'48	-	'48	-	-	-	'47	'47;'49	'47	'47
1954	-	-	'50	-	'50	-	'46	-	'49	'47	'47	-
1955	'52	-	'50	'52	'52	'47	-	-	-	'49	-	'50
1956	-	-	'51	'52	'52	'49	'49;'51	-	'52	-	'52	'50
1957	-	-	-	-	'52	'49	-	'49	'49	-	'49	'50
1958	-	-	-	-	'54	'49;'55	-	'52	'52;'55	-	'49;'52	'53
1959	-	-	-	-	'54;'55	'52	'53	-	'54	-	'52	'54
1960	-	-	'54	-	-	'55	-	-	'55	-	'54	'54
1961	-	-	'56	-	'56	'52	'56	-	-	-	'56	'56
1962	-	-	'57	-	'58	-	-	'58	'56	-	'56	'56;'57

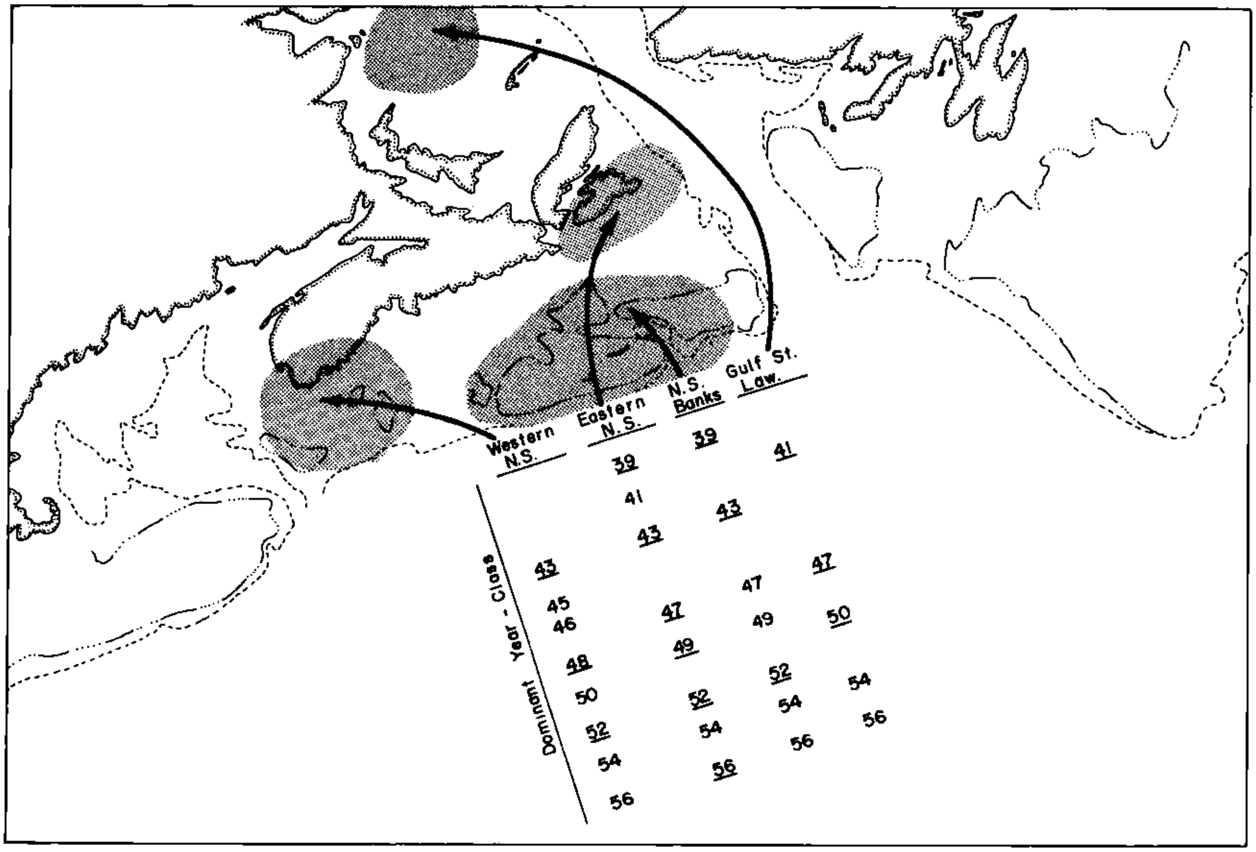

Fig. 3. Dominant year-classes in cod landings for the years 1946-1962. Extra strong year-classes are underlined.

The early summer spawning stocks of Gulf of St. Lawrence cod and St. Pierre Bank haddock produce dominant year-classes which differ from one another and often from the dominant year-classes found on Nova Scotia Grounds.

DISCUSSION

Many papers have been written on variations in year-class strength for cod and other species in the North Atlantic area, with interpretations of the importance of temperature, water transport, wind direction and intensity, and planktonic food as factors affecting year-class survival.

Frost (1938) and Dickie (1955) have examined the relationship between year-class strength and temperature for Subarea 3 cod and Division 4X sea scallops, respectively. In both cases the apparent effect of temperature on survival was interpreted as the effect of water transport on both temperature and transport of pelagic eggs and larvae.

Colton and Temple (1961) and Steele (1963) have written two of the most recent papers on the relation between water circulation and the transport of fish eggs and larvae in ICNAF Subarea 5 and Division 4X. They contend that most haddock and pollock eggs and larvae are swept away from spawning areas, and that only a small fraction is retained in the counter-clockwise eddy of the area to settle and produce year-classes which are large enough to support commercial fisheries.

Carruthers, *et al.* (1951), Chase (1955), and Hill and Lee (1958) have described the apparent relation of wind to brood strength of haddock and cod through its effect on surface-water transport.

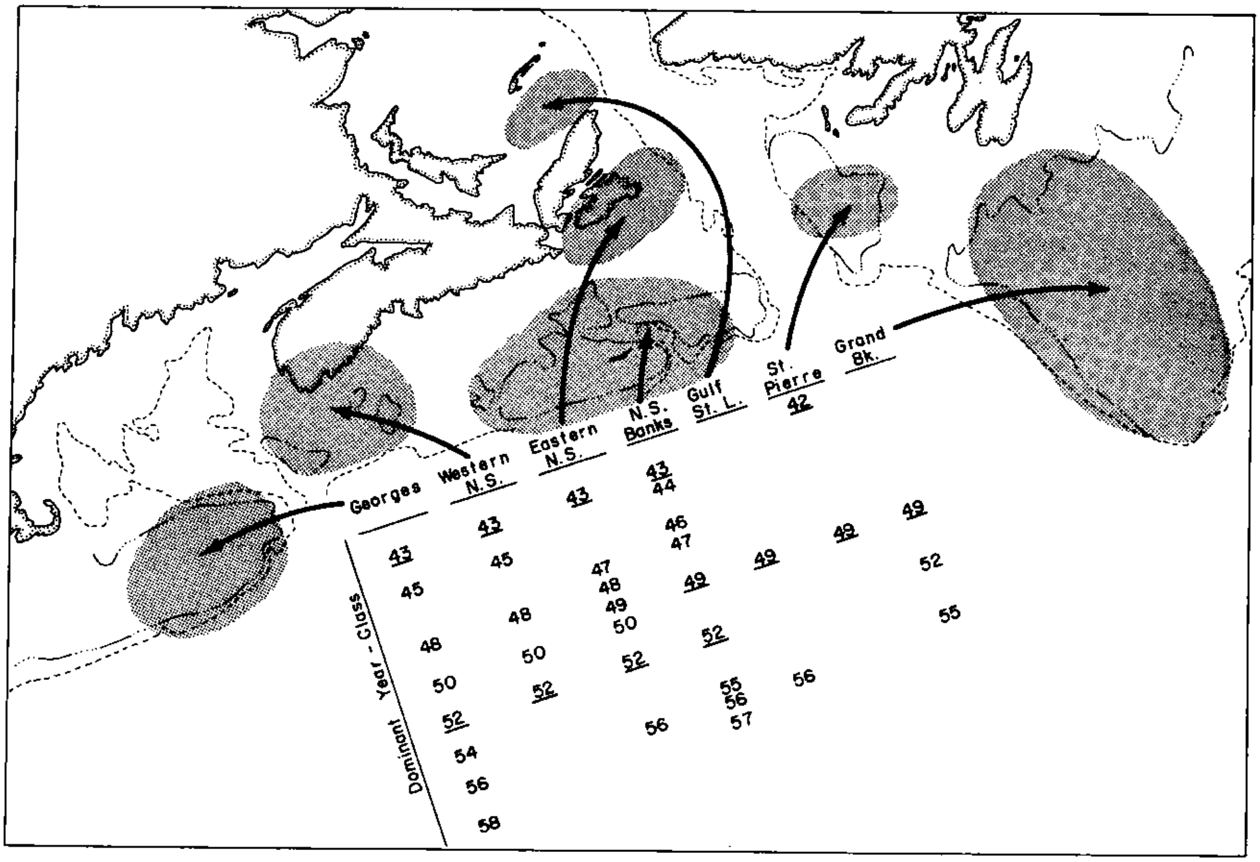

Fig. 4. Dominant year-classes in haddock landings for the years 1946-62. Extra strong year-classes are underlined.

Poulsen (1930), Dannevig (1947), Wiborg (1957) and Corlett (1958) refer to the importance of availability of planktonic food for the survival of cod in the Northeast Atlantic area. In these papers the effects of physical factors, such as temperature and wind, on plankton and cod larvae production are discussed.

All of these physical variables, wind, water transport, and sea temperatures, appear to be interrelated and related in one way or another to abundance of plankton, including fish eggs and larvae. It is concluded therefore that the consistent negative correlations between temperature during early development and cod abundance do not necessarily imply cause and effect. Changes in sea temperatures may directly affect plankton production and year-class survival, or they may simply reflect the direct effects of changes in water transport on the distribution of plankton and fish eggs and larvae. The possible mechanics of these interpretations are considered further.

Temperature must be a limiting factor in the survival and well being of plankton crops, including fish eggs and larvae. The water temperatures of ICNAF Subarea 1 and Subarea 5 sometimes appear to be sufficiently extreme to drastically reduce the numbers of cod eggs and larvae in these subareas. Year-class strength is more variable at either end of the species range than in the central areas.

In southern waters, low temperature may prolong the spawning period and the pelagic life of larvae, thereby providing greater opportunities for suitable feeding conditions to permit good survival and growth of large lots of larvae.

TABLE 7. DOMINANT YEAR-CLASSES OF HADDOCK IN COMMERCIAL LANDINGS. DATA ARE TAKEN FROM GRAHAM (1953-1961), HENNEMUTH, GROSSLEIN AND MCCRACKEN (1964), KOHLER (1958), TEMPLEMAN (1953-1961), AND WISE (1957). DASHES INDICATE NO DATA.

Year	Georges Bank	Browns Bank	Freeport Grounds	Yarmouth Grounds	LaHave Bank	Roseway Bank	Lockeport Grounds	Emerald Bank
1946	'43	-	'39;'43	'43	;40	-	'39;'43	'41
1947	'43;'45	-	'43	'43	'40	'43	'43	'40:'41;'42
1948	'45	-	'43	'43	'43	'43	'43	-
1949	'45;'46	-	'43	'43	'43	'43	'43	'43;'44
1950	'48	-	'44;'45	'43	'43	'43	'43;'45	'43
1951	'48	-	'45;'47	'45	'43	-	'45	-
1952	'50	-	'46;'48	'46;'48	'46;'47	-	'46;'48	-
1953	'50	-	'48	'48;'49	'47;'48	'48	'48	'47;'48
1954	'50;'52	-	-	'48	'48;'49	'49	'48	-
1955	'52	-	-	-	'49;'50	'50	'50	-
1956	'52	'50	-	-	'50;'52	-	'50	'50;'52
1957	'52;'54	'52	-	-	'52	-	'52	'52
1958	'54	'52	-	-	-	-	'52	'52
1959	'56	'54	-	-	-	-	'52	'52
1960	'58	'54	-	-	-	-	'56	'55
1961	'58	'56	-	-	-	-	-	'56
1962	'59	-	-	-	-	-	-	'56;'57

TABLE 7. CONTINUED.

Year	Western Bank	Sable Is. Bank	Middle Ground	Banquer-eau	Canso Grounds	N.Syd-ney Grounds	SW Gulf St.Law.	St.Pierre Bank	Grand Bank
1946	'41	-	'40	'39	'40	-	'43	'39	-
1947	'41	'43	'43	'43	'43	'43	-	'42	-
1948	'43;'44	'44	'43	'43	'43;'44	'43	-	'42	-
1949	'44	'44	'44	'43	'43	'43	-	'42	-
1950	'44;'46	-	-	'44	-	'43	-	'42	-
1951	'46	'46	-	'46	'45	'46	'46	-	-
1952	'46;'47	'47;'49	'47;'49	'46;'47	'47	'47	'47	'47	-
1953	'47	'47	'48	'47	'48	'47	'48;'49	'46;'47	-
1954	'47;'49	'52	-	'49	'48	'49	'49	'49	'49
1955	'49	'52	'49	'49	'49	'48	'49	'49	'49
1956	'49;'52	'52	'52	'49	-	'50	'49	'49	'49
1957	'52	'51	'52	'50;'52	-	'52	'52	-	'49;'52
1958	'52	'55	'52	'52;'54	-	'52	'54	-	'52
1959	'52	'55	'55	'54;'55	-	'52	'54	-	'55
1960	'55	'56	-	'56	-	'56	'56	-	'55
1961	'56	-	-	-	-	-	'56	-	-
1962	'56;'57	'56;'57	-	'56;'57	'57	-	-	-	-

Sandström (1919), Trites and Banks (1958) and Bigelow (1928) have described the circulation of surface waters in the Gulf of St. Lawrence, Nova Scotia Banks, and Gulf of Maine areas, respectively. The pattern of circulation over each fishing area can account for the retention of sufficient pelagic eggs and larvae to permit adequate settling of young fish to bottom on grounds which are suitable for continued survival.

Hachey (1934), Day (1958), Bumpus (1960) and Colton and Temple (1961) refer to annual variations from the general circulation patterns. In some years, water transport appears to carry fish eggs and larvae from one fishing area to another, and often completely away from suitable bottom habitats. Annual variations in water transport are believed to be of great importance in the determination of year-class strength. The transport is presumably affected by relative contributions of major ocean currents, such as those of Labrador and the Gulf Stream, and by wind. Annual variations in water transport are probably reflected in the annual temperature changes observed at monitoring stations.

Trites and Banks (1958) have described the transport of water from east to west along the Nova Scotia coast, and from west to east over offshore Nova Scotia Banks. Net drift was observed to be 2 to 4 miles per day. Annual variations in the timing and duration of pelagic life of fish eggs and larvae could result in the annual variation in distribution of dominant year-classes illustrated in Fig. 3 and 4. Young fish may settle to bottom on inshore, western, offshore, or eastern grounds, or on combinations of these areas. Some year-classes are carried away almost completely during pelagic life, and this would appear to be particularly common for certain populations such as St. Pierre (Templeman, 1961) and Georges Bank (Colton and Temple, 1961) haddock.

Long-term trends and annual variations in recruitment of cod to the southern part of the ICNAF area are negatively correlated with water temperatures during the first year of life. The correlations are interpreted to mean that temperature has a direct effect on survival, and that temperature is an indirect measure of effects of wind and water transport on plankton, including cod eggs and larvae. Colder water could imply greater water transport from east to west, which would result in the appearance of strong year-classes on western grounds.

A continuation of the types of observations described in this paper, and the addition of oceanographic studies of water transport and zooplankton, together with laboratory experiments on factors affecting survival of cod eggs and larvae, are needed to provide a better understanding of the effects of the changing environment on recruitment to cod fisheries.

ACKNOWLEDGEMENTS

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REFERENCES

ANONYMOUS. 1952-1963. International Commission for the Northwest Atlantic Fisheries: *Second Annual Report* and *Statistical Bulletins*.

BIGELOW, H.B. 1928. Physical oceanography of the Gulf of Maine. *Fish. Bull., U.S.*, 40: 511-1027. (Document No. 969).

BUMPUS, D.F. 1960. Sources of water contributed to the Bay of Fundy by surface circulation. *J. Fish. Res. Bd. Canada,* 17 (2): 181-197.

CARRUTHERS, J.N., A.L. LAWFORD, V.F.C. VELEY and B.B. PARRISH. 1951. Variations in brood strength in the North Sea haddock in the light of relevant wind conditions. *Nature, London,* 168, 4269, p. 317-9.

CHASE, JOSEPH. 1955. Winds and temperatures in relation to the brood strength of Georges Bank haddock. *J. Cons.,* 21 (1): 17-24.

COLTON, JOHN B., and ROBERT F. TEMPLE. 1961. The enigma of Georges Bank spawning. *Limn. and Ocean.*, 6(3): 280-291.

CORLETT, J. 1958. Plankton in the western Barents Sea and the year-class strength of Arcto-Norwegian cod. *J. Cons.*, 23 (3): 354-356.

DANNEVIG, A. 1947. Extracts of observations made at the Fløde vig seafish hatchery, Orendal, Norway. *Ann. biol.*, 2: 101-105.

DAY, C.G. 1958. Surface circulation in the Gulf of Maine as deduced from drift bottles. *Fish. Bull, U.S.*, 141: 443-472.

DICKIE, L.M. 1955. Fluctuations in abundance of the giant scallop, *Placopecten magellanicus* (Gmelin) in the Digby area of the Bay of Fundy. *J. Fish. Res. Bd. Canada,* 12 (6): 797-857.

FROST, N. 1938. Some fishes of Newfoundland waters (with notes on the distribution of eggs and larvae). *Nfld. Dept. Nat. Res., Res. Bull.* 4, 16 p.

GRAHAM, H.W. 1952. Mesh regulation to increase the yield of the Georges Bank haddock fishery. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 2: 23-33.

1953-61. United States research reports. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, Vol. 4-11.

GROSSLEIN, M. 1962. Haddock stocks in the ICNAF Convention area. *Int. Comm. Northw. Atlant. Fish. Redbook, 1962,* Part III: 124-131.

HACHEY, H.B. 1934. The replacement of Bay of Fundy waters. *J. Biol. Bd. Canada,* 1: 121-131.

HANSEN, PAUL M. 1949. Studies on the biology of cod in Greenlandic waters. *Rapp. Cons. Explor. Mer.*, 123: 1-77.

HANSEN, P.M., and FREDE HERMANN. 1964. Effect of long-term temperature trends on occurrence of cod at West Greenland. *This symposium, Contribution No. H-4.*

HENNEMUTH, R.C., M.D. GROSSLEIN, and F.D. MCCRACKEN. 1964. Abundance, age composition of landings and mortality of haddock caught off southern Nova Scotia 1956-61. *Res. Bull. int. Comm. Northw. Atlant. Fish.*, 1: 43-73.

HERMANN, F. 1953. Influence of temperature on strength of cod year-classes. Conseil Perm. Intern. Explor. de la Mer. *Ann. biol.*, Vol. IX (1952): 31-32.

HERMANN, FREDE, PAUL HANSEN and Sv. HORSTED. 1964. The effect of temperature and current on the distribution and survival of cod larvae at West Greenland. *This symposium, Contribution No. B-14.*

HILL, H.W., and A.J. LEE, 1958. The effect of wind on water transport in the region of the Bear Island fishery. *Proc. Roy. Soc.*, (B) 148: 104-116.

JENSEN, A.S. 1939. Concerning a change in climate in recent decades in the arctic and subarctic regions, from Greenland in the West to Eurasia in the East, and contemporary biological and geophysical changes. *Kgl. Danske. Vid. Selskab. Biologiske Medd.* XIV, 8, København.

KOHLER, A.C. 1958. The validity of otolith age determination for haddock (*Melanogrammus aeglefinus* L.) from the Lockeport, N.S. area. *J. Fish. Res. Bd. Canada,* 15 (6): 1229-1238.

1964. Variations in the growth of Atlantic cod (*Gadus morhua* L.). *J. Fish. Res. Bd. Canada,* 21 (1): 57-100.

LAUZIER, L.M. 1953. Coastal station Data, Atlantic coast. *Fish. Res. Bd. Canada, MS Rept. Biol. Sta.*, No. 537.

1964. Long-term temperature variations in the Scotian Shelf area. *This symposium Contribution No. H-3.*

LAUZIER, L.M., and J.H. HULL. 1961. Temperatures along the Canadian Atlantic Coast 1950-1959. *Fish. Res. Bd. Canada,* MS Rept. (Ocean and Limn.), No. 39.

MARTIN, W.R. 1953. Identification of major groundfish stocks in Subarea 4 of the Northwest Atlantic Convention Area. *Annu. Proc. int. Comm. Northw. Atlant. Fish.,* 3: 57-61.

POULSEN, E.M. 1930. On the fluctuations in the abundance of cod fry in the Kattegot and the Bett Sea and causes of the same. *Rapp. Cons. Explor. Mer.,* 65 (4): 26-30.

SANDSTRÖM, W.J. 1919. The hydrodynamics of Canadian Atlantic waters. *In* Canadian Fisheries Expedition 1914-15, p. 221-343. *Dept. Naval Service, Ottawa.*

SCHROEDER, W.C. 1930. Migrations and other phases in the life history of the cod off southern New England. *Fish. Bull.,U.S.,* Vol. 46: 1-136.

STEELE, D.H. 1963. The pollock (*Pollachius virens* (L.)) in the Bay of Fundy. *J. Fish. Res. Bd. Canada,* 20 (5): 1267-1314.

TEMPLEMAN, W. 1953-61. Canadian research reports. Subareas 2 and 3. *Annu. Proc. int. Comm. Northw. Atlant. Fish.,* Vol. 4-11.

1961. Canadian research report 1960. Subareas 2 and 3. *Annu. Proc. int. Comm. Northw. Atlant. Fish.,* 11: 23-31.

1962. Divisions of cod stocks in the Northwest Atlantic. *Int. Comm. Northw. Atlant. Fish, Redbook, 1962,* Part III: 79-123.

TRITES, R.W., and R.E. BANKS. 1958. Circulation on the Scotian Shelf as indicated by drift bottles. *J. Fish. Res. Bd. Canada,* 15 (1): 78-89.

WIBORG, K.F. 1957. Factors influencing the size of the year-classes in the Arcto-Norwegian tribe of cod. *Rep. Norw. Fish. Invest.,* 11 (8): 124.

WISE, J.P. 1957. Growth rate of Browns Bank Haddock. *Res. Rep. U.S. Fish. Serv.,* No. 50, 13 p.

H-8

CHANGES IN THE HYDROGRAPHY OBSERVED ALONG THE EAST COAST OF THE UNITED STATES

By

D.F. Bumpus[1] and Joseph Chase[1]

ABSTRACT

Daily temperature and salinity measurements at lightships along the Atlantic seaboard of the United States over a period of seven years have revealed a number of short-term changes. These are compared with previous observations of longer periods in order to show the recent trends. The returns from drift bottles along this same coast have also indicated changes and may in some instances be associated with changes in the runoff from adjacent watersheds.

INTRODUCTION

This paper is being presented at the session in the ICNAF Environmental Symposium having to do with the effect of long-term trends. We shall discuss some changes in the hydrography off the east coast of the United States, changes which undoubtedly have their effects on the biota which we are not presently prepared to discuss. This is more of a warning to ecologists that, while the seasonal effect of the cycles of wind, temperature and river runoff continue to prevail in influencing the marine environment, relatively minor changes in these parameters may cause marked changes in the hydrography and circulation, at least off the east coast of the United States.

We shall limit our discussion to some of the data developed from our lightship program (Fig. 1) which was commenced in late 1955. Daily temperature measurements with a bathythermograph and surface salinity samples have been taken at 12 lightships off the east coast. Surface temperature observations have been made at some selected shore stations. In late 1958 we began to release two drift bottles daily at many of the lightships. Through these observations we have sensed some changes in the hydrography which may be pertinent.

RECENT TRENDS IN WATER TEMPERATURE OFF THE EAST COAST OF THE UNITED STATES.

The general upward trend in air temperatures covering, approximately, the hundred years ending about the middle of this century (Veryard, 1963; Mitchell, 1963) has been paralleled, to some extent, by rises in sea water temperatures (Bjerknes, 1959; Rodewald, 1956). More recently, downward trends have been recorded in air temperature (Mitchell, 1963) and in surface water temperatures in some areas (Rodewald, 1963; Lauzier and Hull, 1961).

A program of daily bathythermograph observations at lightships along the east coast of the United States was begun in 1956 under a contract between the US Fish and Wildlife Service and the Woods Hole Oceanographic Institution (Bumpus, 1957; Day, 1959 *a* and *b*, 1960, 1963; Chase, 1964). Although the data from this program do not yet constitute in themselves a long enough record for long-term climatological study, they do extend the previous record of Bumpus (1957*a*) of surface water temperatures. It is the purpose of this study to examine these records for trends and to compare them with records of air and water temperatures from stations on the coast.

New England.

Typical of the trends during this century is the curve of 5-year means of winter (December, January, February) air temperatures at Boston, Massachusetts, and New Haven, Connecticut, combined

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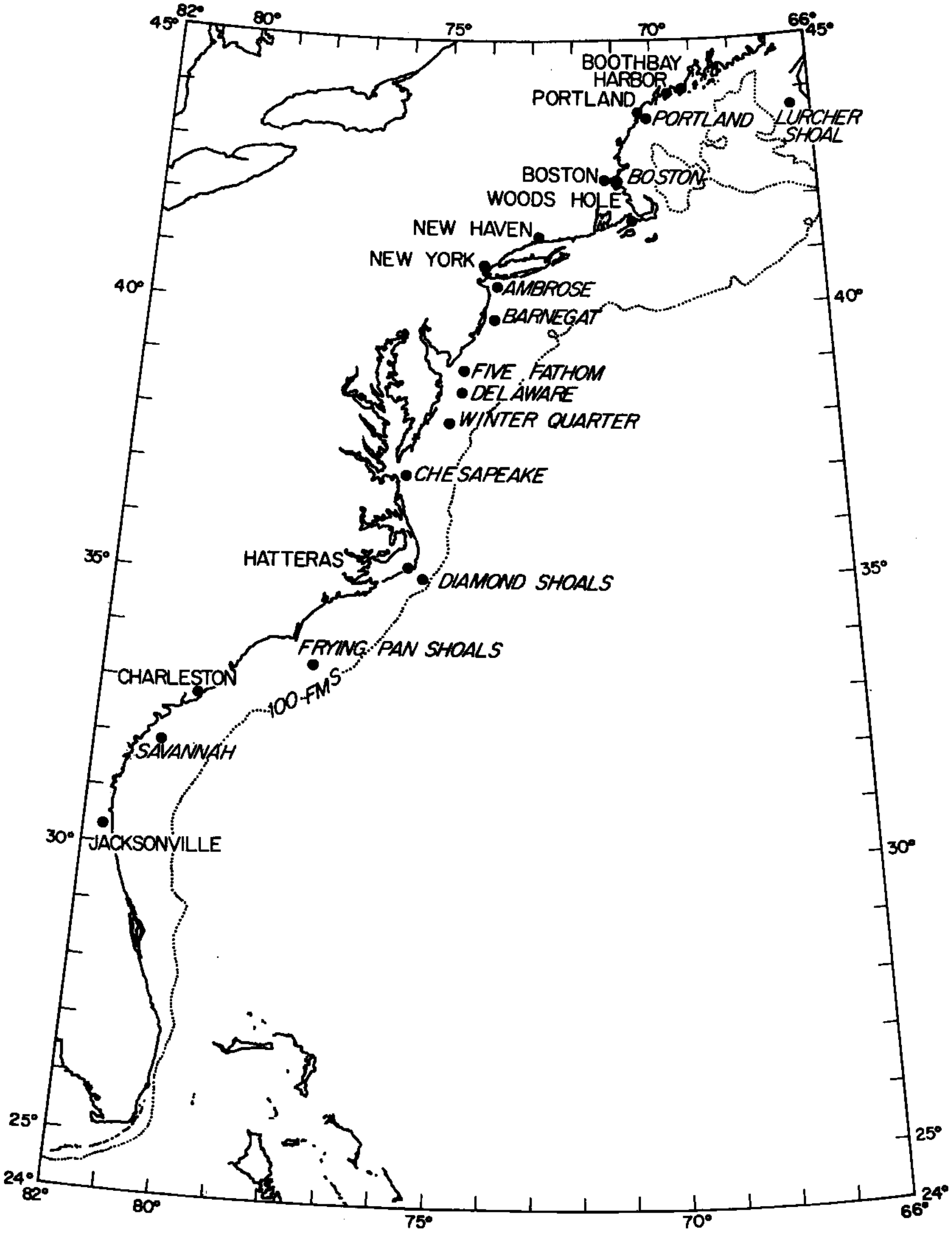

Fig. 1. East Coast of the United States.

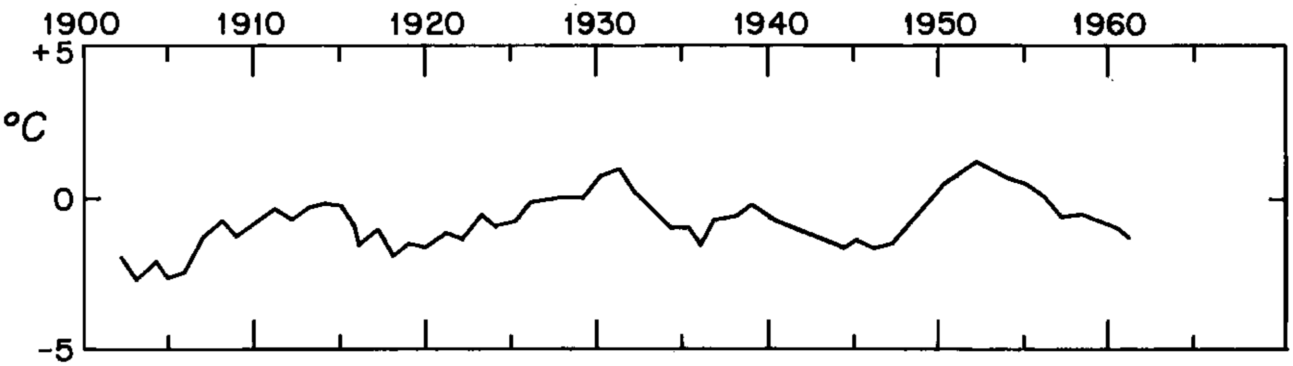

Fig. 2. Five-year means of winter (December, January, February) air temperature at Boston, Massachusetts and New Haven, Connecticut, combined.

(Fig. 2). The curve rises gradually to 1931. A second maximum occurred in 1952. The low values between the peaks and again in recent years are about normal for this century but higher than the general level of values for the last half of the nineteenth century. For the summer months over this same period there has been very little change in southern New England (Taylor, *et al.*, 1957). Water temperatures at Boothbay Harbor, Maine for February and for the year (Fig. 3) parallel the air temperatures of Fig. 2. The rise in February values is more than that of the winter air temperatures. The maxima of 1931 and 1953 occurred at about the same time as those in air temperature. The August record shows little long-term change although there was a prominent maximum in 1951. The drop during the past decade is clear in all three curves.

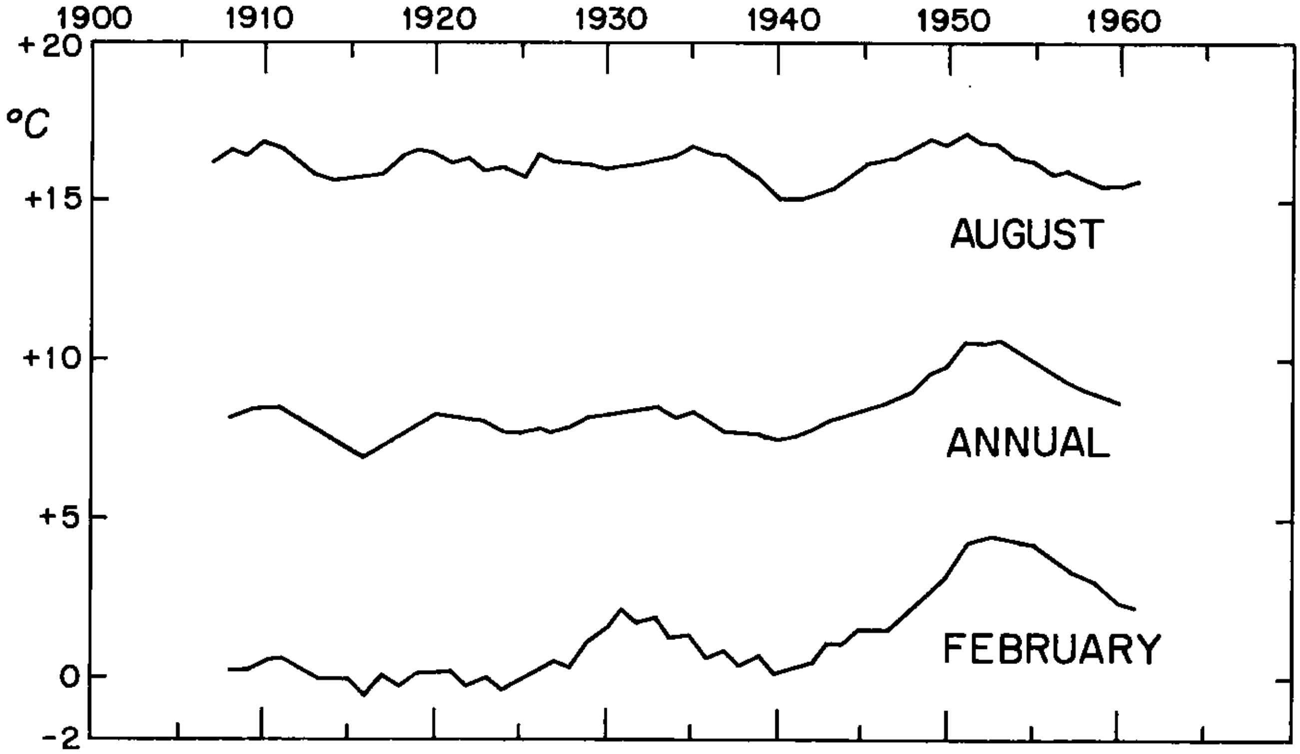

Fig. 3. Five-year means of water temperature at Boothbay Harbor, Maine for August, the year, and February.

Surface water temperatures have been recorded at Woods Hole, Massachusetts since 1880. The annual averages show a maximum near 1950. The level of an indicated maximum in the early 1930's is uncertain due to gaps in the record of observations. The change is in the winter data. Five-year means in February, for example, show a minimum of -1.3°C for the period 1901 through 1905 and a maximum of 2.1°C for 1949-53. The general level before the minimum was about 0°C. The highest February value since 1953 is 1.5°C (1960) and for the last three years the average is -0.7°C.

Typical of the warmer months is August with a five-year minimum of 20.3°C (1901-05) and a maximum of 22.2°C (1948-52). The average for the three years 1880, 1883 and 1885 (no data available for August of 1881, 1882 and 1884) is 22.2°C.

At Portland Lightship, which is well offshore and thus far removed from the local influence of cities (Duckworth and Sandberg, 1954; Swartz, 1956), there was also a rise in winter temperatures culminating in about 1950 and a small decline since then. Three-year means indicate a previous maximum about 1928. There is little change apparent in the summer temperatures since the beginning of observations in 1925.

At Boston Lightship, the old record comprises data for 1925 to 1941. The observations made since 1956 indicate no significant trends in any season and the values are about the same as those of the old record. There was a small maximum in the winter temperatures about 1932.

New York to Cape Hatteras

Rodewald (1956) noted the rise in January air temperatures at New York City from the decade ending in 1888 to a maximum for the decade ending in 1937 and the occurrence of another maximum in the decade ending in 1953. The gain in summer temperature over the same 65 years was less than half that of winter. From his examination of later values and of past trends he conjectured a return to lower winter values which has in fact been borne out by later observations along the coast.

At Hatteras, North Carolina, the air temperatures have undergone similar trends. There were winter maxima in 1929-34 and 1948-53. The principal minimum was in the years 1900-05.

There are six lightships along this stretch of coast which participate in the bathythermograph program. The southernmost of these, Diamond Shoals Lightship, is subject to so much variation in water temperature due to advection as to defy analysis of its data for climatic trend until a much longer record has been made. Three of the others, Barnegat, Five-Fathom Bank and Chesapeake Lightships, show a decrease in winter water temperatures in recent years after a maximum in about 1950. The records for the other two, Ambrose and Delaware (with Winter Quarter) Lightships are too irregular for complete analysis but at least these records do not contradict the general trends for the area. Chesapeake Lightship which has the longest temperature record (begins in 1928) experienced a marked winter maximum in about 1931-32 and another maximum near 1950. Apparently there were no significant trends in summer.

Cape Hatteras to Jacksonville

The air temperature record at Charleston, South Carolina (Fig. 4) shows maxima in winter five-year means in about 1933 and 1951 that are only slightly higher than maxima around 1882 and 1892.

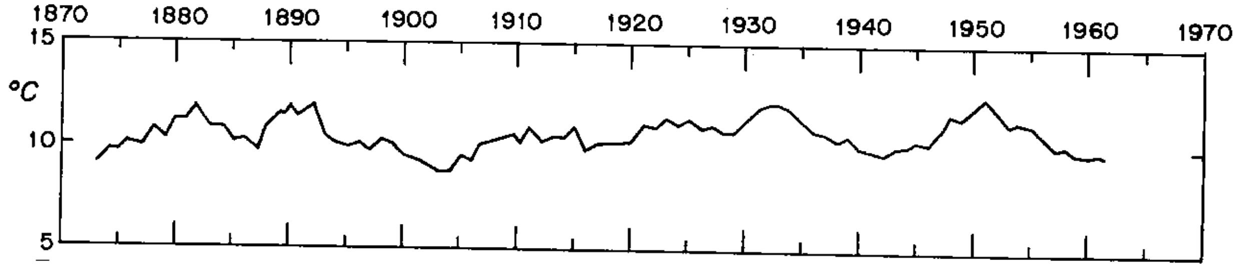

Fig. 4. Five-year means of winter (December, January, February) air temperature at Charleston, South Carolina.

The minimum centered about the winter of 1902-03 had a value of 8.7°C as compared with 12.3°C for the maximum centered about 1950-51. The summer temperatures show no significant trends.

At Jacksonville, Florida, the air temperature record reveals winter maxima and minima at nearly the same times as at Charleston and the summer data reveal no significant trends.

The two lightships off this part of the coast which participate in the bathythermograph program are Frying Pan Shoals and Savannah Lightships. Both have experienced a decline in winter surface water temperatures since 1956 (although the exceptionally low values for February and March of 1958 are probably due to advection of colder water rather than to climatic change). Both observation posts have previous records dating from 1947 which indicate maximum winter temperatures around 1950 and in addition a short record of observations at Frying Pan Shoals from 1930 through 1934 indicates a winter maximum there around 1932. Again no summer trends are apparent.

THE CIRCULATION

The general circulation in the Gulf of Maine at the surface comprises an anticyclonic gyre in the Gulf and a cyclonic eddy over Georges Bank (Bigelow, 1927) which develop during the spring months of the year and begin to deteriorate during the summer (Day, 1958). During the winter the southern side of the gyre and the Georges eddy appear to be absent. From Nantucket Shoals southwestward the surface circulation is southwesterly as far as Cape Hatteras where it turns offshore. South of Hatteras the surface circulation is northeasterly off the Carolinas, and reversing off Georgia and Florida being northerly during the winter and southerly during the late summer and autumn. However, through the use of drift bottles, we have noted certain departures from the norm.

Runoff effect in northern Gulf of Maine

The non-tidal drift at the surface from Lurcher Lightship near Yarmouth, Nova Scotia is northerly into the Bay of Fundy. During the whole year 1957 there were no exceptions to this rule except for the return of a few drift bottles in November which apparently were caught up in a back eddy and were found on the western coast of Nova Scotia south of their point of origin. However, during the first three months of 1958, the majority of those bottles which were recovered from Lurcher Lightship releases, were from the coast of Massachusetts having been carried at speeds as great as 13 km/day. Following this period, the circulation returned to normal (Bumpus, 1960). This remarkable change in the circulation was supported by the return of drift bottles released in Passamaquoddy Bay during this same period. It became quite obvious when one examined the runoff from rivers emptying into the Gulf of Maine that, for a period of nine months, the runoff was much below normal followed by a period, December 1957 and January and February 1958, when the runoff was substantially greater than normal, thus producing the dynamic impetus for a vigorous anticyclonic circulation around the perimeter of the Gulf of Maine. We have looked further into the drift bottle returns from Lurcher Lightship and discovered that it is not at all uncommon for drift bottles released at that location to be found on the shores of New England but we have not seen them make the traverse in such large numbers or at such great speeds as in early 1958. The year 1962 was an exception; a very small number crossed to New England in March of that year. Also 1957 was exceptional in that the circulation was persistently, except as noted for November, directed northerly into the Bay of Fundy where, as in other years (1959, 1960 and 1961), it was not uncommon for the current to send a branch westward across the southern end of the Bay of Fundy and so on southwesterly along the coast of New England.

Now if we look at this southwesterly flow at the location of Portland Lightship we find that during the first four months of the year the non-tidal drift is predominantly southerly but that during the remainder of the year it falters and many bottles will drift northerly into Casco Bay or even easterly across the southern end of Casco Bay.

However, during the latter part of 1958 and much of 1959, the runoff from New England rivers was much below normal and the drift bottle data exhibit the consequential weakening of the close inshore anticyclonic drift during that period.

The effect of the runoff can be graphically displayed by comparison of the departures from the mean of the runoff of the Pemigewasset River and the surface salinity as observed at Portland Lightship (Fig. 5). The relationship is remarkably good considering that the river is gagged many miles upstream and debouches into the sea south of the lightship.

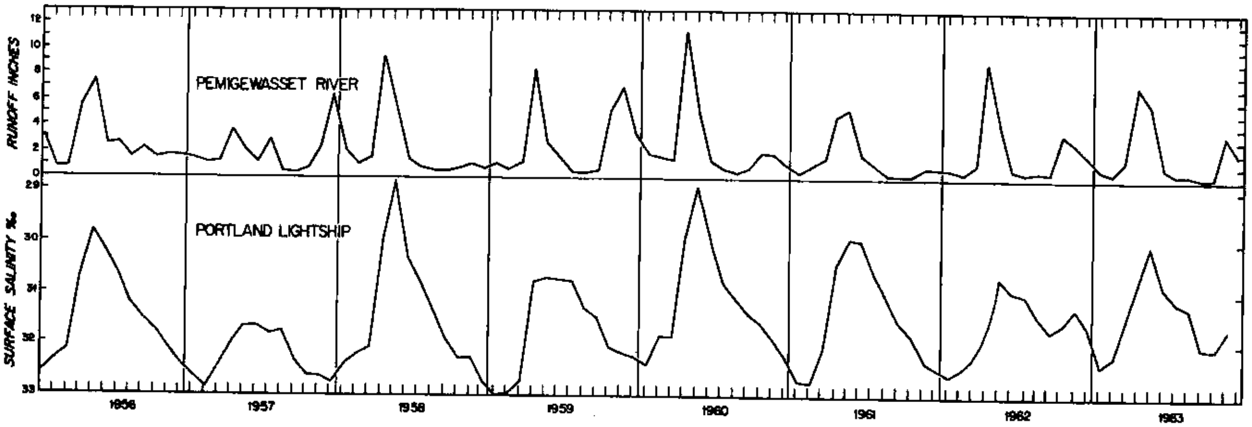

Fig. 5. Runoff of the Pemigewasset River and surface salinity at Portland Lightship.

Reversal off South Atlantic States

One change in the hydrography, which does not properly come under the heading of long-term trends, is a seasonal one but it is mentioned here because we doubt the general awareness of it. That change is the reversal in direction of the non-tidal drift on the continental shelf between North Carolina and Florida.

During the months of December, January and February no drift bottles are recovered from Frying Pan and Savannah Lightships. They presumably drift offshore and get caught up in the Florida Current. During March, April and May the drift is northerly. June appears to be a transition period. During July through October and occasionally November the drift is consistently southerly. Are there other coastal areas where a similar alternation in non-tidal drift has been observed?

SUMMARY

In recent times surface water temperatures at lightships off the United States East Coast have in general followed the trends in air temperature along the coast.

Most of the climatic change in both air and water temperatures has taken place in the winter months rather than in the summer.

Two peaks in winter temperature in about 1931 and 1950 are apparent in all the coastal air temperatures studied and in the water temperatures at the lightships (except Diamond Shoals) within the limits of the available data. A general downward trend is apparent in more recent winter data.

North of Cape Hatteras there was a warming of the air since sometime in the nineteenth century to near the middle of this century. South of Cape Hatteras a minimum occurred near the beginning of this century.

While drift bottles are not very sensitive devices for studying currents, a continuous release of them at discrete locations can reveal some patterns. Anomalous current patterns have been observed in the northwestern part of the Gulf of Maine associated with periods of drought followed by high precipitation and runoff. A periodic reversal in the coastal circulation between South Carolina and Florida have been observed now for three years.

REFERENCES

BIGELOW, H.B. 1927. Physical oceanography of the Gulf of Maine. *Bull. Bureau of Fisheries*, 40 1924 Pt. II: 511-1027.

BJERKNES, J. 1959. The recent warming of the North Atlantic, *The Atmosphere and Sea in Motion*. The Rockefeller Institute Press and Oxford University Press, p. 56-73 (Rossby Memorial Volume).

BUMPUS, D.F. 1957*a*. Surface water temperatures along Atlantic and Gulf coasts of the United States. *Spec. sci. Rep. U.S. Fish. Wildl. Serv.-Fish.,* No. 214, 153 p.

1957*b*. Oceanographic observations, 1956, east coast of the United States. *Spec. sci. Rep. U.S. Fish. Wildl. Serv.-Fish.,* No. 233, 132 p.

1960. Sources of water contributed to the Bay of Fundy by surface circulation. *J. Fish. Res. Bd. Canada,* 17 (2): 181-197.

CHASE, J. 1964. Oceanographic observations, 1961, east coast of the United States. *Spec. sci. Rep. U.S. Fish. Wildl. Serv.-Fish.,* No. 1333 (in press).

DAY, C.G., 1958. Gulf of Maine circulation as deduced from drift bottles. *Fish. Bull., U.S.,* 58: 443-472.

DAY, C. GODFREY. 1959*a*. Oceanographic observations, 1957, east coast of the United States. *Spec. sci. Rep. U.S. Fish. Wildl. Serv.-Fish.,* No. 282, 123 p.

1959*b*. Oceanographic observations, 1958, east coast of the United States. *Spec. sci. Rep. U.S. Fish. Wildl. Serv.-Fish.,* No. 318, 119 p.

1960. Oceanographic observations, 1959, east coast of the United States. *Spec. sci. Rep. U.S. Fish. Wildl. Serv.-Fish.,* No. 359, 114 p.

1963. Oceanographic observations, 1960, east coast of the United States. *Spec. sci. Rep. U.S. Fish. Wildl. Serv.-Fish.,* No. 406, 59 p.

DUCKWORTH, F.S., and J.S. SANDBERG. 1954. The effects of cities upon horizontal and vertical temperature gradients. *Bull. Am. met. Soc.* 35 (5): 198-207.

LAUZIER, L.M., and J.H. HULL. 1961. Temperatures slong the Canadian Atlantic Coast 1950-1959. Fisheries Research Board of Canada. Manuscript report series oceanographic and limnological No. 39.

MITCHELL, J.M., 1963. On the world-wide pattern of secular temperature change. Unesco, Proceedings of the Rome Symposium organized by Unesco and the World Meteorological Organization, p. 161-181.

RODEWALD, M. 1956. Beiträge zur Klimaschwankung im Meere. 5. Beitrag: Die rezente Erwärmung der atlantischen Küstengewässer Nordamerikas. *Dtsch. hydrogr. Z.,* 9 (4): p. 182-186.

1963. Sea-surface temperatures of the North Atlantic Ocean during the decade 1951-60, their anomalies and development in relation to the atmospheric circulation. Unesco, Proceedings of the Rome Symposium organized by Unesco and the World Meteorological Organization, p. 97-107.

SWARTZ, J.R. 1956. A climatological bench-mark network. *Weatherwise* 9 (3): p. 88-89, 106.

TAYLOR, C.C., H.B. BIGELOW and H.W. GRAHAM. 1957. Climatic trends and the distribution of marine animals in New England. *Fish. Bull., U.S.,* 57 (11): 293-345.

VERYARD, R.G. 1963. A review of studies on climatic fluctuations during the period of the meteorological record. Unesco. Changes of climate. Proceedings of the Rome Symposium organized by Unesco and the World Meteorological Organization, p. 3-35.

H-9

INFERENTIAL BIOLOGICAL EFFECTS OF LONG-TERM HYDROGRAPHICAL TRENDS DEDUCED FROM INVESTIGATIONS IN THE FAROE-SHETLAND CHANNEL

By

J.B. Tait[1] and J.H.A. Martin[1]

ABSTRACT

Five different water-masses, only one of which is permanent, occur in the region of the Faroe-Shetland Channel. Three of these are cold, low salinity, water-masses, while two are warm and relatively highly saline.

When they occur, one of the warm and two of the cold masses are intrusive respectively into the two masses which normally characterise the region, namely, the upper, warm and permanent layer, and the lower, cold, semi-permanent layer. The semi-permanence of the latter stems from the fact that, on occasions, one or other or both of the cold water intrusions totally displace it as the bottom water-mass of the Faroe-Shetland Channel.

Of one kind or the other, that is, warm or cold, the intrusions usually occur in groups of from about four to six or seven consecutive years, waxing to maximum intensity in the mid-period of their occurrence and waning to extinction at the end.

A clearly established association has become apparent between the above-mentioned cold water intrusions, which are of Arctic origin, and fish stocks bordering upon the Faroe-Shetland Channel region. As reflected in commercial catches, the annual herring fishery of the Minch area for example, over the 39 years from 1920-59, have been high, medium, or low, according as Arctic water influence in the Faroe-Shetland Channel has been strong, moderate, or non-existent, three years earlier. The summer herring fishery alone (June-September) shows the same relationship with Arctic water influence. When this is eliminated, however, these same catches reveal fluctuations in correspondence with meteorologically cool or warm summers.

Similar trends, apparently more closely linked with sea temperature than with Arctic water influence, are discernible for haddock catches in the Faroe Islands neighbourhood.

It was necessary, first of all, to define the nature of the long-term trends in question.

The Faroe-Shetland Channel region is roughly that enclosed within the relevant coasts and artificial sea boundaries indicated on Fig. 1. This region, particularly the northern part of it between Faroe and Shetland, has been relatively often and to some extent regularly investigated, especially hydrographically but also biologically, during the present century, by successive research ships attached to the Marine Laboratory at Aberdeen. Less frequent investigations of a similar kind in the same region have been made from other countries, notably Norway and Denmark, and more recently, the USSR.

When it came to be realised in the 1920's that an almost necessary counterpart of these mainly hydrographical researches in the northern part of the Channel were similar and, where possible, concurrent investigations at its southern end, in the region between the Butt of Lewis and Faroe Bank, such investigations were thereafter carried out with varying but, after 1946, increasing frequency, and since the observational material for this period had not previously been worked up in detail, a particular study was made of the years from 1927 to 1952, excluding the war period, 1940-46 inclusive (Tait, 1957).

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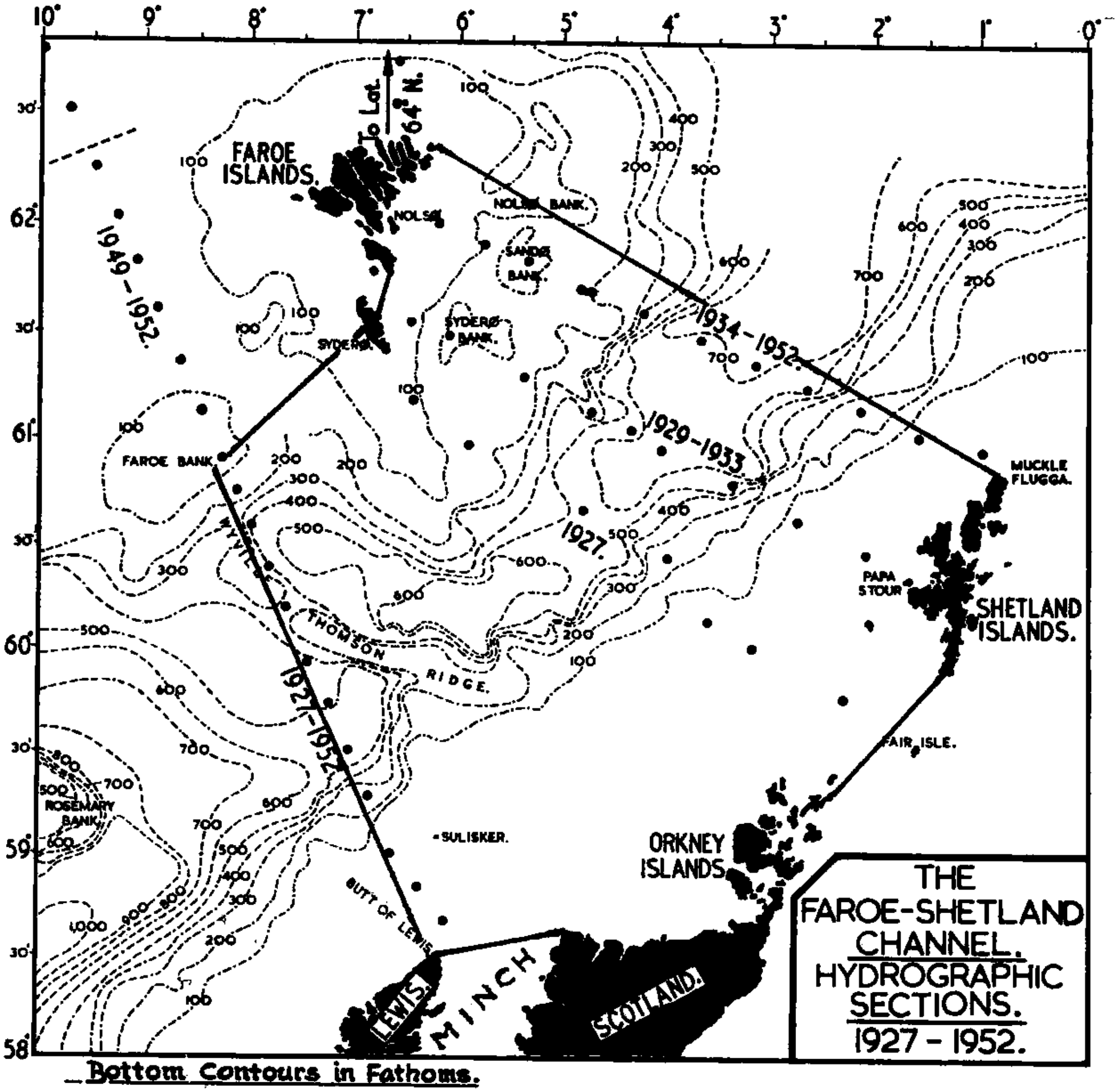

FIG. 1.

This study revealed that, besides the two main water-masses previously recognised as being characteristic of the Faroe-Shetland Channel, at least three more distinctive water types intrude from time to time into the region.

Only the oceanic water-mass, recognised chiefly (in the Channel area) by its salinity of from about 35.25 $^{o}/oo$ to a maximum of 35.44 $^{o}/oo$, is a permanent feature of the region, approximately and normally in its uppermost 300-500 m layer.

Bottom Norwegian Sea water, of salinity between 34.90 $^{o}/oo$ and 34.94 $^{o}/oo$, but relatively steady at 34.92 $^{o}/oo$, while normally characteristic of the deeper Channel to over 1,400 m depth, is not strictly a permanent feature since it can on occasions be more or less totally displaced by one or other, or both, of the intrusive types mentioned below.

In a long series of many hundreds of salinity determinations from within the oceanic water-mass, a distinct hiatus occurs between values of up to 35.45 ^{o}/oo, representing the maximum salinity of the oceanic water-mass proper, and salinities of upwards of 35.50 ^{o}/oo which clearly signify water of a specifically different geographical origin. Its biological content is also distinctive, and from this aspect, Fraser (1955, 1961) has named it Lusitanian water. Its origin would seem to be the vicinity of the deeper Mediterranean Sea outlet into the Atlantic Ocean through the Strait of Gibraltar. Its appearance within the oceanic water-mass of the Faroe-Shetland Channel is usually in disrupted or disintegrated form, an effect apparently of impingement on the southern slope of the Wyville Thomson Ridge, the threshold of the Faroe-Shetland Channel from the North-Eastern Atlantic Ocean. Even so, Lusitanian water seldom if ever occurs in the immediate surface of the Channel, which is probably significant in relation to the depths (800-1,200 m) of the Mediterranean efflux at the Strait of Gibraltar. Sometimes the only evidence of its occurrence in or near the area is in more or less isolated traces. This feature, however, is linked with a further characteristic of this and other intrusions into the main, permanent or semi-permanent, water-masses of the Faroe-Shetland Channel region.

When these intrusions occur in other than mere traces, in obvious isolation from a parent water-mass, they are not as a rule limited to a single year, but pertain to a group of four to six or seven consecutive years. From quantitatively small beginnings in a particular year, they wax to maximum intensity in two to three years, and thereafter wane to extinction, so far as the Faroe-Shetland Channel is concerned, in the next two to three years.

In addition to the above-mentioned Lusitanian (or Gulf of Gibraltar) water intrusion, via the oceanic water-mass, the foregoing characteristics apply also to two Arctic water-mass types which penetrate the Channel region from time to time within the bottom Norwegian Sea water-mass, sometimes displacing the latter from the deeper parts of the Channel at the peak of the phenomenon. These types are (i) intermediate (depth) Arctic water of salinity 34.85 ^{o}/oo to 34.89 ^{o}/oo, and (ii) surface Arctic water with salinity ranging from 34.77 ^{o}/oo to 34.84 ^{o}/oo.

During the period, namely, 1927-52, which has been subjected to closest study so far, although these are discernible in other periods significant evidences of similar circumstances, there were two periods of marked intrusion of (a) Lusitanian water on the one hand, namely, between 1931 and 1938, and (b) Arctic water on the other, between 1946 and 1952. There was evidently, however, a resurgence of the latter influence in 1953-56, and earlier records than those which have been under such close study to date indicate a similar degree of the same influence in 1920-26.

Subsequent investigation by one of us, in collaboration with biological colleagues, has revealed what would appear to be a clearly established association between these intrusive hydrographical phenomena, particularly the Arctic water intrusion, and fish stocks bordering the Faroe-Shetland Channel region. Taking as an example the annual herring fishery of the Minch area just outside the Faroe-Shetland Channel proper, and subdividing the entire period from 1920 to 1959 according to the degree of Arctic water influence as gauged by the mean minimum salinity of the bottom water-mass of the Channel, the following table strikingly indicates the association of this influence, with the Minch herring fishery:

Arctic Influence			Herring Catches	
Period	Degree	Mean Salinity	Period	Average no. crans per landing
1949-56	Strong	34.86 ^{o}/oo	1952-59	22.50
1920-26	Moderate	34.88 ^{o}/oo	1923-29	12.92
1944-48	"	34.90 ^{o}/oo	1947-51	12.36
1956-59	"	34.90 ^{o}/oo	1960-61	17.66
1927-36	None	34.92 ^{o}/oo	1930-39	7.87

The postulate is that Arctic water in the Faroe-Shetland Channel is conducive of increased productivity of the oceanic water-mass by admixture, leading to better fish recruitment in "Arctic" years and this is reflected in commercial catches three years later.

The summer Minch herring fishery (June-September) by itself shows the same sort of trend in relation to Arctic water influence as the annual fishery, but on the other hand, eliminating this trend from the summer fishery by the use of moving averages, it also becomes apparent that meteorologically warm summers are associated with depressed catches per landing. This is true for all the warm summers in that region since 1947, namely, 1947, 1949, 1950, 1953, 1955 and 1959.

These deductions, however, take no account of the differential abundance of spring as distinct from autumn spawning herrings. Since the 1920's, it is evident from biological records that there has been a general replacement in the Minch, and other nearby regions, of spring spawners by autumn spawners, and this replacement appears to reflect both the above environmental factors, namely, Arctic influence in conjunction with increased sea temperature. There would seem on the one hand to be a case for assuming that this sub-Arctic species, *Clupea harengus* has, since the 1920's, retired northward in face of a general temperature increase, and on the other hand, that the partial recovery of spring spawners during Arctic periods is not merely a case of increased productivity but of the promotion of a favourable environment for replenishment of Hiberno-Caledonian herring stocks by extension southwards of the Atlanto-Scandian stock, the influence of Arctic water on the thermal structure of the Norwegian Sea being so very great. In non-Arctic periods, as in the 1930's, there takes place a northwards recession of the Atlanto-Scandian herring stock.

It would appear, therefore, that only a marked reversal of the temperature trend will bring about a recession of southerly (autumn spawning) in favour of northern (spring spawning) stocks, although a decrease in the abundance of the former is likely unless Arctic water influence increases markedly with accompanying increased productivity. By the same token the substantial reappearance of spring spawning herrings in the Minch may not be expected until a further strong intrusion of Arctic water into the Faroe-Shetland Channel takes place.

Similar trends, somewhat more closely linked, however, with sea temperature than with the fact of Arctic water influence, is discernible for haddock catches in the neighbourhood of the Faroe Islands.

REFERENCES

TAIT, J.B. 1957. Hydrography of the Faroe-Shetland Channel, 1927-1952. *Mar. Res. Scot.*, 1957, No. 2.

FRASER, J.H. 1955. The plankton of the waters approaching the British Isles in 1953. *Mar. Res. Scot.*, 1955, No. 1.

1961. The oceanic and bathypelagic plankton of the North-East Atlantic. *Mar. Res. Scot.*, 1961, No. 4.

SECTION

I

I-I

FORESHADOWING OF SURFACE WATER TEMPERATURES AT ST. ANDREWS, N.B.

By

L. M. Lauzier[1]

ABSTRACT

Twice daily surface temperature observations have been recorded at St. Andrews, New Brunswick, Canada since 1921. In the last 42 years, the annual temperature varied between 5.4° and 8.5°C with a long-term average of 7.0°C. The various components of the annual temperature and of its régime, such as the warming and cooling, the annual maxima and minima have been related to each other and to the annual temperatures with varying degree of confidence. Regression equations have been established. These equations are used to foreshadow annual temperatures and the maximum temperatures, mainly to show if above or below average conditions are expected, and if warming or cooling from the previous year is expected. The standard errors of estimate are of the order of 0.4° and 0.6°C for the annual and the maximum temperatures respectively. Similar regression equations were established for other points of the Atlantic seaboard.

INTRODUCTION

The annual mean sea surface temperature along the Canadian Atlantic Coast shows both long and short period variations. The climatic fluctuations of, the waters in the North Atlantic have been discussed at great length (UNESCO-WMO, 1963), but comparatively little has been said about the short term variations as such.

The temperature variations in the Bay of Fundy area, at St. Andrews, N.B., were compared with those at other points along the Atlantic seaboard. Due to strong tidal action in the Bay of Fundy and vigorous mixing, the temperature variations are shown to be a good index of the changes that occur over a large area (Hachey and McLellan, 1948; Lauzier, 1954, and this Symposium). In dealing with warm years and cold years, Hachey and McLellan (1948) have discussed differential warming, the vernal and aestival warming, for the waters of Passamaquoddy Bay. Taylor *et al.* (1957), and Lauzier (1957) have noticed that the increase of winter temperatures during the recent long-term warming trend was greater than the increase of annual mean temperatures in the coastal waters of the Gulf of Maine and for Passamaquoddy Bay. Among others, Mitchell (1961) studied the changes of global air temperatures and discussed the winter and annual changes.

Year-to-year variations in the annual mean, the minimum, the maximum, the warming and the cooling, as well as the interrelations of these factors were considered in some detail by Lauzier (1957). The deviations from long-term averages in maxima, minima, warming, cooling, and annual means display a definite interrelated pattern that can be used for the purpose of foreshadowing annual temperatures. Here the term foreshadowing instead of forecasting is used because the predicted temperatures are of the nature of an average, for instance, an average of monthly temperatures. It is of interest to fisheries scientists to know whether the temperatures in the forthcoming period will be above or below normal, and also if the temperatures in this period will be above or below that of the preceding period.

DATA

The twice daily observations of surface temperature at St. Andrews since 1921 up to date provide the basis for monthly and annual means. These data have been used by various authors.

Annual means

The annual mean temperature is the average of 12 monthly temperatures from January to December and the average temperature régime can be represented mathematically by a sine curve (Hachey, 1939).

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The absolute value of the change from one year to the next may be as large as 1.8°C; it was less than 0.5°C in 39% of the cases and greater than 0.9°C in 20% of the cases. The annual mean temperature curve for the period 1921-62 is shown in Fig. 1A. The overall average of annual means is 7.0°C; the extremes are 5.4 and 8.5°C, in 1923 and 1951 respectively.

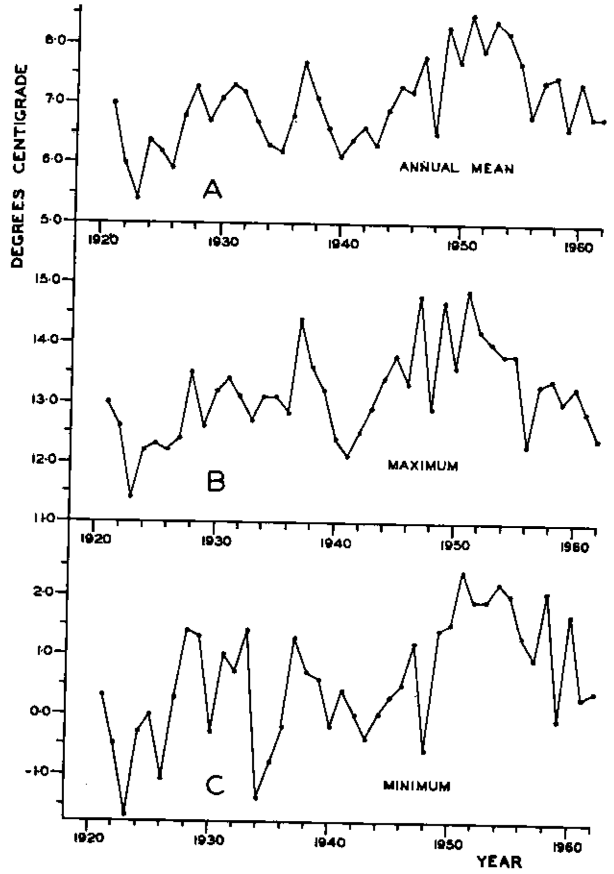

Fig. 1. Surface water temperature variations at St. Andrews, N. B. A. Annual Mean, B. Maximum, C. Minimum.

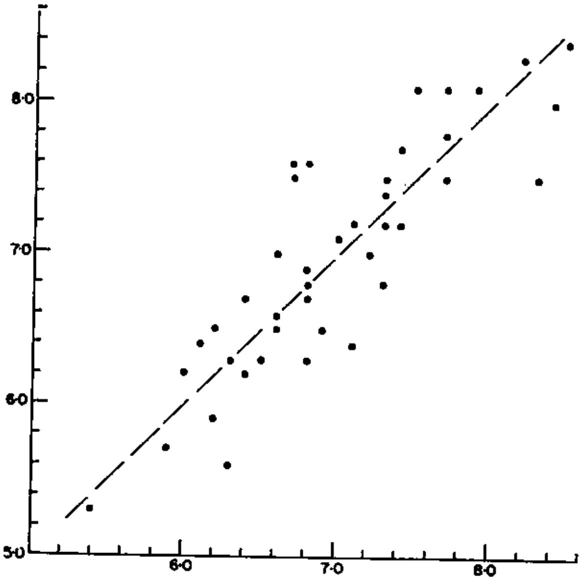

Fig. 2. Comparison of observed (O) and calculated (P) values of annual mean temperatures at St. Andrews, N. B.

Maxima and minima of monthly averages

In Passamaquoddy Bay, the maximum monthly temperature is normally reached in August, but in some years the September average might be equal to or slightly higher than the August one. The minimum monthly temperature occurs usually in February, but in some years, it is delayed until March. The variations in the maxima and the minima during the period 1921-62 are shown in the curves B and C respectively of Fig. 1. The curve of maxima follows fairly closely that of the annual means; except for a short period, 1946-52, the variations for one year to the next were relatively persistent, showing long series of warming and cooling. The curve of minima has different features; the variations seem to be erratic from the beginning of the series to the early forties. After 1942, there was a steady increase up to 1954, with the exceptions of 1948 and 1951 when the minima were somewhat out of line. The overall extremes recorded in maxima were 11.4°C and 14.9°C in 1923 and 1951 respectively. The extreme minima, -1.7°C and 2.4°C were also recorded in 1923 and 1951 respectively.

Computed from maxima and minima, warming and cooling vary from year-to-year over a very wide range; this is more so for the cooling. The same amount of warming in two different years could be related to fairly different maxima, depending on the point of departure, the minima. Similar reasoning applies to the cooling. Values of warming and cooling, adjusted to the general temperature level of the preceding period, are significant in the study of temperature régimes. The aestival warming, from June to August may account for as much as 36%, or as little as 18% of the total. The winter cooling, from December to February may account for as much as 48% or as little as 17% of the total cooling.

STATISTICAL APPROACH

Persistence and variability

Since the purpose of this paper is to establish a method of prediction of temperature values by means of regression equations based on the interrelationships between the variations of different criteria of the temperature régime in the area, it is important to know how persistent and how variable are each one of the criteria.

Observations of surface water temperatures taken at St. Andrews, N.B. since 1921, have been used to evaluate five different criteria of the temperature régime namely, the maximum, the minimum, the warming and the cooling computed from the previous two, and the annual mean. Figure 1 shows that some of the variables are more persistent than others, and also that some vary within wider limits than others. The coefficient of serial correlation (r_a) which is a measure of the persistence, has been calculated for all the variables. It is given in Table 1, together with the standard deviation (σ) of the series of observations as a whole, and the standard deviation (σd) of the difference from one year to the next.

The values given in Table 1 are comparable to a similar Table of a previous publication (Lauzier, 1957). They are generally lower for the present series, 1921-62, than for the previous series 1921-55.

In Table 1, it is shown that the annual mean was most persistent, and the cooling least persistent. The annual mean was however more persistent from 1921 to 1944 than during the decade 1945-55. This is shown in shorter periods of variations from the middle forties up to 1955 (Fig.1A). The same phenomenon was observed in the variation of the maxima (Fig. 1B). Table 1 also shows that the minimum has a relatively high standard deviation but still it has a fair degree of persistence.

TABLE 1.—COEFFICIENTS OF SERIAL CORRELATION AND STANDARD DEVIATIONS

criterion	period	r_a	σ	σd
Annual mean	1921-62	0.58	0.70°C	0.65°C
	1921-44	0.69	0.67	0.53
	1945-55	0.59	0.92	0.83
Maximum	1921-62	0.43	0.76	0.81
Minimum	1921-62	0.42	1.00	1.07
Warming	1921-62	0.22	0.77	0.96
Cooling	1921-62	-0.14	0.97	1.46

Correlation coefficients

After considering the variations of the different criteria like the minimum, the maximum, the annual mean, etc., and their order of occurrence, the joint variations of two or more criteria or their interdependence, are studied by evaluating correlation coefficients.

The reader should be aware that the criteria considered here are not absolutely independent since we are dealing with different stages of a "régime".

The correlation coefficients "r" have been based on at least 42 pairs of observations for the period 1921-62; then coefficients with values of "r" greater than 0.40 and 0.31 are significant at the 99% and 95% probability levels respectively. The coefficients calculated in the previous paper (Lauzier, 1957) for the period 1921-55 were useful to indicate which combinations of criteria did not show any correlation and also the combinations that exhibit a significant degree of correlation.

Among the latter ones, there were some spurious correlations, those relating the minimum or the maximum temperature of one year with the annual temperature of the same year.

It is of interest to consider the relationship between parameters which represent a time lag large enough to be of some value from the point of view of foreshadowing, such as between:
annual temperature of one year (T_N) and annual temperature of preceding year (T_{N-1});
annual temperature of one year and minimum temperature of same year (Min_N);
annual temperature of one year and cooling during previous autumn and winter (C_N);
maximum during one year (Max_N) and maximum during preceding year (Max_{N-1});
maximum during one year and minimum during same year (Min_N);
minimum during one year (Min_N) and minimum during preceding year (Min_{N-1});
minimum during one year and maximum during preceding year (Max_{N-1}).

The time lag varies between 10 and 12 months for the annual temperature, between 6 and 12 months for the maximum and minimum.

The correlation coefficients are listed in Table 2. These values are higher than 0.40 which is that of the 99% probability level.

TABLE 2.—CORRELATION COEFFICIENTS BETWEEN DIFFERENT CRITERIA OF THE SURFACE TEMPERATURE REGIME AT ST. ANDREWS, N.B.

	T_N	Min_N	Max_N
T_{N-1}	0.582 (1)		
Min_N	0.823 (2)		
Min_{N+1}	0.617	0.423 (1)	
Max_N	0.875 (2)	0.648	
Max_{N-1}		0.434	0.434 (1)

(1) these are the same as those listed in Table 1 as coefficients of serial correlation.

(2) the correlation between the annual temperature and the minimum and maximum respectively of the same year are spurious.

Even if the values of "r" considered are statistically significant at the 99% probability level, it is important to use, wherever possible, elements which are correlated by a coefficient of a value of 0.71 or better. Such coefficient means that at least 50% of the variance of the changes of one element can be attributed statistically to the variance of the changes of the other element.

Figure 1 shows long-term variations in annual temperatures, minima and maxima. It is suspected that the minima and the annual temperatures have a "long-term" relationship superimposed to an "annual" relationship. It is possible to "eliminate most of the long-term variations by making two new series of observations each consisting of the change from one time interval to the next" (Brooks and Carruthers, 1953). This is called the "variate-difference" correlation. The correlation coefficient for T_N Min_N is 0.82 and the coefficient for the variate-difference correlation is 0.72. It is concluded that 0.15, $(1-0.72^2) - (1-0.82^2)$, or 15% of the variance of the changes of the annual temperature could be attributed statistically to the variance of the long-term changes and 52%, $r^2 = (0.72)^2 = 0.52$, to the variance of the changes of the minimum.

FORESHADOWING FROM REGRESSION EQUATIONS

The study of correlations between the different components of the temperature régime has the ultimate purpose of foreshadowing the temperatures at least 9 or 10 months in advance. Such a requirement forcibly eliminates use of correlation between the warming during a year or of the maximum during a year and the annual temperature of the same year, because it would give predictions only 4 months beforehand; however they could be very useful in making shorter predictions. The cooling and the minimum could be used for making predictions. As mentioned before, our aim in foreshadowing temperatures is to predict the changes from one year to the next. Will the temperature level stay the same (on the average) during the next 10 months as it has been during the previous 12 months?

Will it be above or below normal, and by how much? One should realize that it is statistically easier to predict an annual temperature which is an average of twelve monthly temperatures, than a maximum or a minimum which is one monthly temperature.

For prognostication, there are two aspects to consider: 1. Are these correlations of any value to the "forecaster", and are the correlation coefficients sufficiently high to be of significant value statistically? 2. What are the physical processes involved to explain the cause and effect relationship? Question 1 was answered in the previous section. Question 2 will be considered in the discussion.

On all regression equations, the standard error of estimate $\sigma\ y, xz$ has been calculated (Snedecor, Brooks and Carruthers) as well as the standard deviation of the difference between predicted and observed values σ_{PO}. For each equation, a verification factor, V_{PO}, has been calculated; it is the percentage of cases in which observed and predicted values agree as to sign of deviation from one year to the next, (those equal to zero either predicted or observed are computed as one half). The correlation coefficients r and R for simple and multiple correlation respectively will be given for each equation.

Annual temperatures

A regression equation relating the change in annual temperatures and the cooling C_N during the previous winter has been established. The equation is based partly on the persistence of the annual temperature, and also on the cooling adjusted to the level of the previous year's annual temperature:

$$T_N = T_{N-1}\ (1.00 - 0.040\ C_N) + 3.6 \qquad (1)$$
$$r = 0.70;\ \sigma_{y,x} = 0.46°C;\ \sigma_{PO} = 0.45°C;\ V_{PO} = 78\%$$

The computed values from equation (1) seem to be restricted to a much narrower range than the observed values.

A second regression equation based on a more persistent variable than the cooling has been established using the minimum temperature:

$$T_N = 0.58\ \mathrm{Min}_N + 6.7 \qquad (2)$$
$$r = 0.82;\ \sigma_{y,x} = 0.41°C;\ \sigma_{PO} = 0.38°C;\ V_{PO} = 83\%$$

The computed values from equation (2) have the same disadvantage as those of equation (1).

Based on the multiple correlation between the annual temperature of year N., the annual temperature of the previous year (N-1) and the minimum temperature of year N, an equation has been established:

$$T_N = 0.69\ \mathrm{Min}_N + 0.14\ T_{N-1} + 5.6 \qquad (3)$$
$$R = 0.83;\ \sigma_{y,xz} = 0.40°C;\ \sigma_{PO} = 0.38°C;\ V_{PO} = 88\%$$

where T_N is the annual temperature of year N, M_N is the minimum temperature which occurs normally in February, T_{N-1} is the annual temperature of the previous year (N-1).

The relationship between observed and computed values of annual temperatures from equation (3) is given in Fig. 2. As pointed out previously, we are interested in the changes from one year to another. In 88% of the cases, the predicted change, an increase or a decrease, agreed with the observed change. The absolute value of the difference between the observed and predicted value was equal to or less than 0.4°C, ($\sigma\ y,xz$), in 78% of the cases, and greater than 0.7°C in less than 10% of the cases. The standard deviations σ and $\sigma\ d$ (Table 1) are respectively 0.70 and 0.65, a much higher value than that of $\sigma\ y,xz$ which means that the 50-50 chance to get a correct prediction from equation (3) is very remote.

Maximum and minimum temperatures

Regression equations relating maximum and minimum temperatures to each other, as well as to the preceding values in the time series, have been established in an attempt to foreshadow these temperature levels at least 6 months in advance. They are:

$$\mathrm{Max}_N = 0.42\ \mathrm{Min}_N + 0.20\ \mathrm{Max}_{N-1} + 10.3 \qquad (4)$$
$$R = 0.67;\ \sigma_{y,xz} = 0.59°C;\ \sigma_{PO} = 0.57°C;\ V_{PO} = 81\%$$

$$\mathrm{Min}_N = 0.27\ \mathrm{Min}_{N-1} + 0.34\ \mathrm{Max}_{N-1} - 4.5 \qquad (5)$$
$$R = 0.67;\ \sigma_{y,xz} = 0.77°C;\ \sigma_{PO} = 0.97°C;\ V_{PO} = 64\%$$

where

Max_N is the maximum temperature of year N
Min_N is the minimum temperature of year N
Max_{N-1} is the maximum temperature of the previous year (N-1)
Min_{N-1} is the minimum temperature of the previous year (N-1)

From equation (4), the absolute value of the difference between the observed and the predicted value was equal to or less than 0.6°C in 73% of the cases. From equation (5), the equivalent difference was equal to or less than 0.8°C in 54% of the cases.

It should be noted that while the standard error of estimate is approximately 60% of the standard deviations for the annual temperature, it becomes approximately 75% for both the maximum and minimum.

It is concluded that, for prediction purposes, the value of equation (4) is dubious and that equation (5) should be used very cautiously, while equation (3) could be used advantageously.

DISCUSSION

This study of the variations of sea water temperatures at St. Andrews, N.B. was made to relate the various components of the annual temperatures or the various phases of the temperature régime, between themselves and also with the annual temperatures. It was possible to evaluate, statistically, the interrelationship of cooling, the level of the annual mean, maximum and minimum temperatures. From the relationship between the different criteria, considering their persistence, it was possible to establish regression equations, and from these make an attempt to foreshadow annual temperatures, maximum and minimum temperatures.

The equations chosen are not the only ones that can be fitted to the data. In all cases it was assumed that there is a linear relationship between each pair of variables. Consequently the sum of the squares of the deviations between the predicted and observed values is at or near a minimum. The highest percentage of agreement between the observed and predicted change (either an increase or a decrease) from one year to the next is also considered. Under these assumptions the equations are considered to be valuable to the "forecaster".

The average temperature régime of such coastal waters as those of St. Andrews, where ice is not generally formed, can be represented mathematically by one sine curve (Hachey, 1939). Therefore, the average temperature over one cycle could be estimated by the general equation:

$$T_N = K\ (\mathrm{Max}+\mathrm{Min}) + \text{constant}$$
K being approximately 0.5

Such equations have been calculated as well as others by the method of multiple regression. It should be pointed out that all the correlations are spurious, and that the foreshadowing value of these equations is somewhat limited covering only a four-month period. However they could be used for predicting, in August and in February, twelve month averages for periods ending in December and in June respectively from equations:

$$T_{J_A - D} = 0.54\ \mathrm{Max}_N + 0.31\ \mathrm{Min}_N - 0.3 \qquad (6)$$

for the period January - December with $V_{PO} = 87\%$, and

$$T_{J_Y - J_u} = 0.34\ \mathrm{Max}_{N-1}\ 0.51\ \mathrm{Min}_N + 2.3 \qquad (7)$$

for the period July to June with $V_{PO} = 88\%$

The standard deviations between predicted and observed values, σ_{PO}, are 0.25 and 0.23 for equations (6) and (7) respectively. Even if the four-month predictions have been previously discarded as such, those based on equations (6) and (7) would be useful in connection with an "extrapolated" curve for twelve-month moving averages.

This numerical "forecasting" seems to be solely statistical. A priori, it does not seem to consider the variations of the factors controlling the temperature variations, such as heat transfer across the air-sea boundary, the heat content of the whole body of water under consideration, or advection and mixing. The processes involved have been considered using to a large extent the temperature and salinity data from monthly observations made at a deep station in the Bay of Fundy. The effect of these processes on the different components of the temperature régime have been estimated. Hachey's theory of the replacement of Bay of Fundy waters (1934), used later by Bailey (1957) has been applied, with some modification, to a much longer period of observations, including 1924-62 data. The results indicate a good agreement with theoretical considerations. The scope of this paper does not permit expanding on the details of such considerations.

In general we might say that changes in the minimum and maximum temperatures from one year to another are attributed mainly to changes in the circulation and in the heat transfer at the air-sea boundary as well as between layers. These three are a complex function of the meteorological conditions - wind, air temperature, evaporation, precipitation - eventually of the run-off from rivers and of oceanographic conditions. The variability in wind mileage, air temperature and run-off are greater in the autumn and winter seasons, during the cooling period, than in the spring and summer seasons during the warming period. So is the variability of minimum and cooling as compared to that of maximum and warming (of Table 1). The coefficients of partial correlation from equations (6) and (7) show that the major part of the changes in 12-month averages are related to changes in the minimum which is the end point of the cooling period as compared to the maximum which ends the warming period. It seems then that a general temperature "level", a temporary régime, is likely to be established during the cooling period of the annual cycle and that its effect seems to persist for the following 8-10 months. Variations from "normal" in the factors responsible for the circulation, the heat transfer, etc. during the warming period of the annual cycle do affect the temperature régime but do not seem to counterbalance the established temperature level. It seems then that a high annual temperature is better related to a lack of cooling during the preceding autumn and winter than an intense warming during the year. Finally, let us keep in mind that successive oceanographic phenomena, as weather phenomena, do not occur at random. Oceanographic conditions of this month have a bearing on the conditions of next month, the conditions of this year on those of next year.

The foreshadowing of annual temperatures by this method seems to be modestly satisfactory on statistical bases. The changes in the "independent variables", the different components of the temperature régime, are indicative of changes in the processes involved in controlling the annual temperature of the water and its variations.

Regression equations relating the annual temperature to its persistence and the minimum temperature, (equation 3) have been calculated for other areas along the Atlantic seaboard. The areas were picked because of availability of published data and also because the factors responsible for the temperature régime such as circulation, heat transfer at the air-sea boundary, stratification, tidal mixing, etc. are somewhat different than those experienced in the Bay of Fundy. The equations are given in an appendix for Boothbay Harbour, Maine, Atlantic City, N.J., Halifax, N.S. and Sambro Lightship, off Halifax, N.S. It was most unfortunate that the data at Halifax and Sambro were so discontinuous, yielding only 24 and 16 years of annual temperature data respectively. Considering the high multiple correlation coefficient for all areas and the high percentage of agreement between the observed and predicted sign of variation, except for Halifax Harbour, it is felt that this type of foreshadowing could be of considerable value to the "forecaster" of the marine environment.

SUMMARY

1. Year-to-year variations of water temperatures at St. Andrews, N.B., are presented.

2. The various components of the temperature régime, the annual means, the maxima and the minima vary in a similar fashion but the range of variations over the 42-year period is the smallest for the annual means and the greatest for the minima. The warming and cooling vary erratically.

3. The variables such as the annual means, the maxima and the minima are shown to be persistent, as compared to the warming and cooling. Of the five variables, the minima have the highest standard deviation.

4. The correlation coefficients have been calculated between several variables. The maxima and minima show respectively significant correlations with the annual temperatures. However it seems that a high annual temperature is better related to a lack of cooling, during the preceding autumn and winter, than an intense warming during the year.

5. Multiple correlation coefficients have been calculated and regression equations established in an attempt to forecast annual temperatures, maxima and minima. The standard errors of estimate are 0.40°C for the annual temperatures, 0.59°C for the maxima, and 0.77°C for the minima.

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REFERENCES

BAILEY, W.B., D.G. MACGREGOR and H.B. HACHEY. 1954. Annual variations of temperature and salinity in the Bay of Fundy. *J. Fish. Res. Bd. Canada*, 11(1): 32-47.

BAILEY, W.B. 1957. Oceanographic observations in the Bay of Fundy since 1952. *Fish. Res. Bd. Canada, MS Rept. Biol. Sta.*, No. 633, 37 p., mimeographed.

BROOKS, C.E.P., and N. CARRUTHERS. 1953. Handbook of statistical methods in meteorology. M. O. 538, Air Ministry, H. M. S. O. London. 412 p.

HACHEY, H.B. 1934. The replacement of Bay of Fundy waters. *J. Biol. Bd. Canada*, 1(2): 121-131.

1939. Surface water temperatures of the Canadian Atlantic Coast. *J. Fish. Res. Bd. Canada*, 4(5): 378-391.

HACHEY, H.B., and H.J. MCLELLAN. 1948. Trends and cycles in surface temperatures of the Canadian Atlantic. *J. Fish. Res. Bd. Canada*, 7(6): 355-362.

LAUZIER, L. 1954. Recent surface water temperatures along the Canadian Atlantic Coast. Cold years - warm years. *Fish. Res. Bd. Canada, Atlantic Prog. Rept.*, No. 58: 6-11.

LAUZIER, L.M. 1957. Variation of surface water temperatures at St. Andrews, N.B. Numerical forecasting of temperatures. *Fish. Res. Bd. Canada, MS Rept. (Oceanogr. and Limnol.)* No. 1: 16 p., mimeographed.

1964. Long-term temperature variations in the Scotian Shelf area. *This symposium Contribution No. H-3.*

MITCHELL, J.M.J. 1961. Recent secular changes of global temperatures. *In* Fairbridge, R.W. *et al.* Solar variations, climatic changes, and related geophysical problems. *Ann. N.Y. Acad. Sci.*, 95(1): 235-250.

SNEDECOR, G.W. 1946. Statistical methods applied to experiments in agriculture and biology. Ames. The Iowa State College Press. 485 p.

TAYLOR, C.C., H.B. BIGELOW and H.W. GRAHAM. 1957. Climatic trends and the distribution of Marine Animals in New England. *Fish. Bull., U.S.* 57: 293-345. (*Fish. Bull. No.115*)

UNESCO-WMO. 1963. Changes of climate. Proc. of the Rome Symposium organized by Unesco and the World Meteorological Organization. Aird zone Research.

APPENDIX

1. Regression equations for annual temperatures at:

Boothbay Harbour, Maine. $T_N = 0.41\ Min_N + 0.14\ T_{N-1} + 6.7$

Atlantic City, N.J. $T_N = 0.39\ Min_N + 0.21\ T_{N-1} + 8.9$

Halifax Harbour, N.S. $T_N = 0.41\ Min_N + 0.33\ T_{N-1} + 4.8$

Sambro Lightship off Halifax $T_N = 0.41\ Min_N + 0.25\ T_{N-1} + 5.7$

2. Pertinent information

		Boothbay Hr.	Atlantic City	Halifax Hr.	Sambro LS
Number of years		42 (1906-1948)	47 (1913-1920) (1924-1962)	24 (1927-1962)	16 (1937-1960)
Annual Temp.	average	7.8°C	12.2°C	7.7°C	8.4°C
	max.	9.2	13.7	9.4	10.0
	min.	6.3	10.9	5.9	7.2
Min. Temp.	average	0.1	2.0	0.9	1.4
	max.	3.3	5.4	2.6	3.8
	min.	-1.7	-1.2	-0.5	-0.2
σ annual temp.		0.75°C	0.65°C	0.69°C	0.79°C
Coefficient of multiple correlation		0.709	0.798	0.613	0.731
Standard error of estimate		0.54°C	0.41°C	0.57°C	0.58°C
V_{PO}		82%	83%	67%	87%

I-2

FACTORS AFFECTING WATER TEMPERATURE IN THE SEAS NORTH OF NORWAY

By

John Harvey[1]

ABSTRACT

The correlation between the rise of the Barents Sea cod fishery and the increase in the mean water temperature along the Kola section is noted. The factors leading to an increase in water temperature in this region are then considered. They are divided primarily into advective and non-advective factors. Using temperature and salinity data from two stations, S and W, in deep water west of Bear Island, correlation coefficients are established between water temperature in each 100 m layer between 0 and 600 m at station S and

a) meteorological parameters during the preceding ten days at Bear Island,

b) transport of water northwards between the two stations,

during the whole year and during different parts of the year. The relative importance of the advective and the non-advective factors in determining water temperature at various depths, and in different seasons, are then discussed.

INTRODUCTION

The climatic improvement which has been taking place in northern Europe and the adjacent part of the Arctic during the present century (Hesselberg and Johannessen, 1958) has been considered by many writers to have brought about the rise of the great cod fisheries in the seas north of Norway since 1925. The great increase in catch by trawlers in this region has been due partially to the use of larger ships and to the improvements in fishing methods, but it seems certain that there has also been a considerable increase in the size of the cod stocks. Hill and Lee (1957) suggested that this could have been brought about by an increase in the strength of the West Spitsbergen current, carrying eggs and larvae more quickly from the Lofoten spawning grounds to the nursery grounds on the Spitsbergen Bank during the spring and summer months. The environmental conditions on the banks, notably the water temperature, may be expected to have affected the survival of the young cod and the distribution of the adult cod. Blacker (1957) has examined the distribution of various species of benthos in this region, both between 1878 and 1931, and between 1948 and 1955, and found that the "Atlantic" species which require water temperatures exceeding 2°C extended considerably further north in the latter period than they did in the earlier one. He suggested that the change had been brought about both by changes in the mechanical transport of larvae by water movement and by changes in the physical environment, in particular the water temperature. Woodhead and Woodhead (1959) have found that cod in the Barents Sea are apparently limited in their distribution by low water temperatures. The limiting temperature was found to vary during the course of the year in relation to endocrinally controlled changes in physiology, but during the greater part of the year it was found to be 2°C. Cod avoid water of a lower temperature, and if trapped in cold water are likely to die. Thus if the water temperatures, either on the nursery grounds to which the larvae are carried by the West Spitsbergen current, or on passage to these nursery grounds, are below this limit, the survival of the larvae, and hence the recruitment to the stock, will be poor. It is therefore pertinent to examine the changes in water temperature in this region and the factors which have brought them about.

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THE CHANGES IN WATER TEMPERATURE ON THE KOLA SECTION

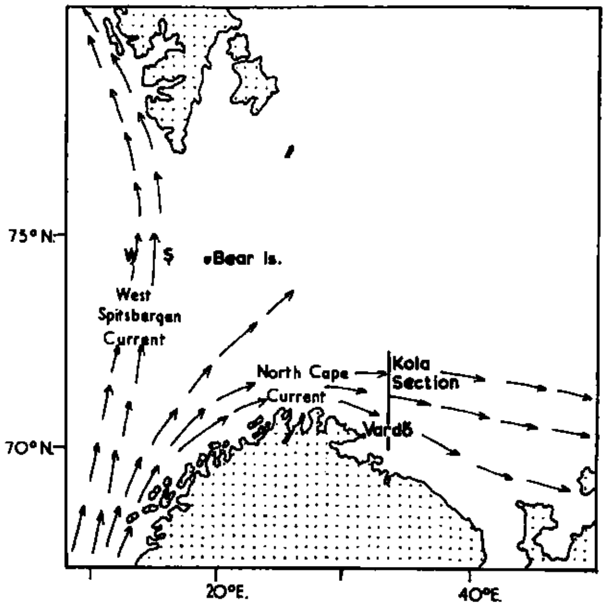

Fig. 1. Positions of places referred to in the text.

Few long period records of water temperature are available for this region. Jensen (1939) assembled the records available to him up to 1936, but although they indicated a general increase in water temperatures they were too scattered to permit any firm conclusions as to the actual changes which had taken place. Observations have been made of water temperature along the Kola Meridian between 70°30'N and 72°30'N since 1900 from which mean, mid-monthly temperatures for the 0-200 m layer and the 0-50 m layer have been obtained. The section is shown in Fig. 1. I am extremely grateful to the Polar Research Institute of Marine Fisheries and Oceanography, Murmansk, who supplied the Fisheries Laboratory, Lowestoft with this data. In Fig. 2 the mean values for the 0-200 m layer between 1921 and 1960, excluding those for the years 1940-45, are shown plotted against time, in the form of 5 yearly running means. The increase between the mid-1920's and the late 1930's, when the great rise in the fisheries took place, is very marked. Since 1945 the 5 yearly running mean temperatures have been mainly above the overall mean value, but lower

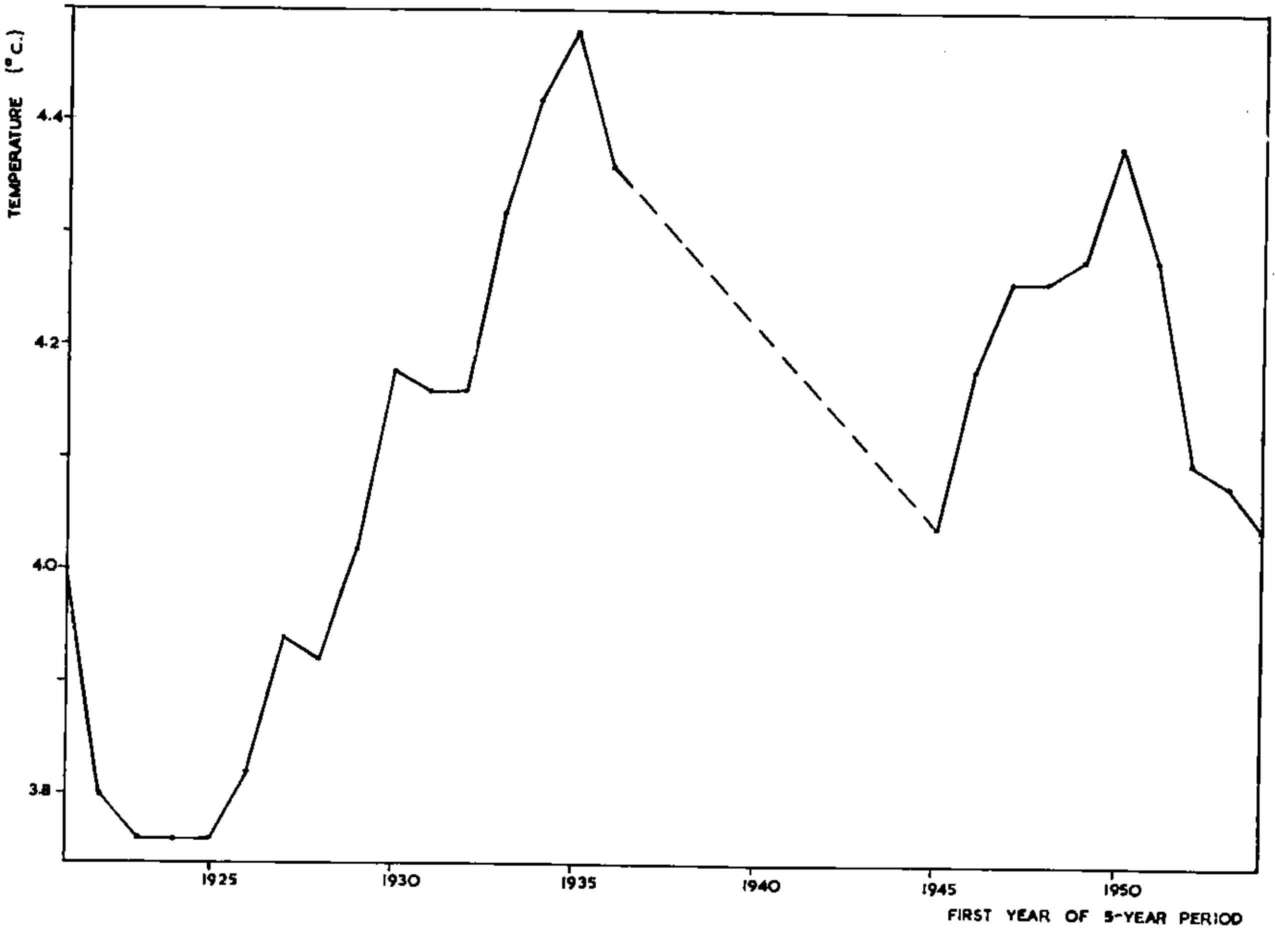

Fig. 2. Water temperature of the 0-200 m layer on the Kola Section (5 yearly running means).

than the maximum reached in the 1930's. Inspection of the annual mean values shows a somewhat different pattern to have existed before 1940 from that which has existed since 1945. The root mean square of the differences between annual mean temperatures of successive years was 0.39°C for the period 1921 - 39, 0.55°C for the period 1946 - 58. In the earlier period a general trend towards warming is evident, whereas in the latter period the year to year variations completely obscure any general trend.

The temperature trends may be considered during particular parts of the year only. The pattern is very similar in all cases, as is the range, showing that the changes in mean annual temperatures were brought about by changes in temperature during all parts of the year. If, however, the mean temperatures of the 0-50 m layer only are considered, for which mean values are available for every month from 1929 - 40 and 1945 - 58, it is found that there were greater changes in temperature in the summer and autumn months than in the winter and spring, *e.g.* the lowest February mean temperature was 3.0°C, the highest 4.5°C; the lowest August mean temperature was 6.5°C, the highest 9.2°C. From this it may be concluded that the greater part of the warming between 0 and 50 m took place in late summer and autumn. Figure 3 shows 12 monthly running means of temperature in the 0-200 m layer. From it 18 well defined stationary points, where there is a change in the trend of the graph, may be identified. More than 75% of these occur at points representing the temperatures of 12 monthly periods beginning with one of the 5 months October to February inclusive. Hence it may be concluded that the majority of trends are established during these months and that they then persist for at least the following 12 months. This is in agreement with Drogaitsev (1959) who found that the water temperature in the 0-200 m layer during each month from January to October inclusive was closely related to an indice of meridional heat transport in the preceding late autumn.

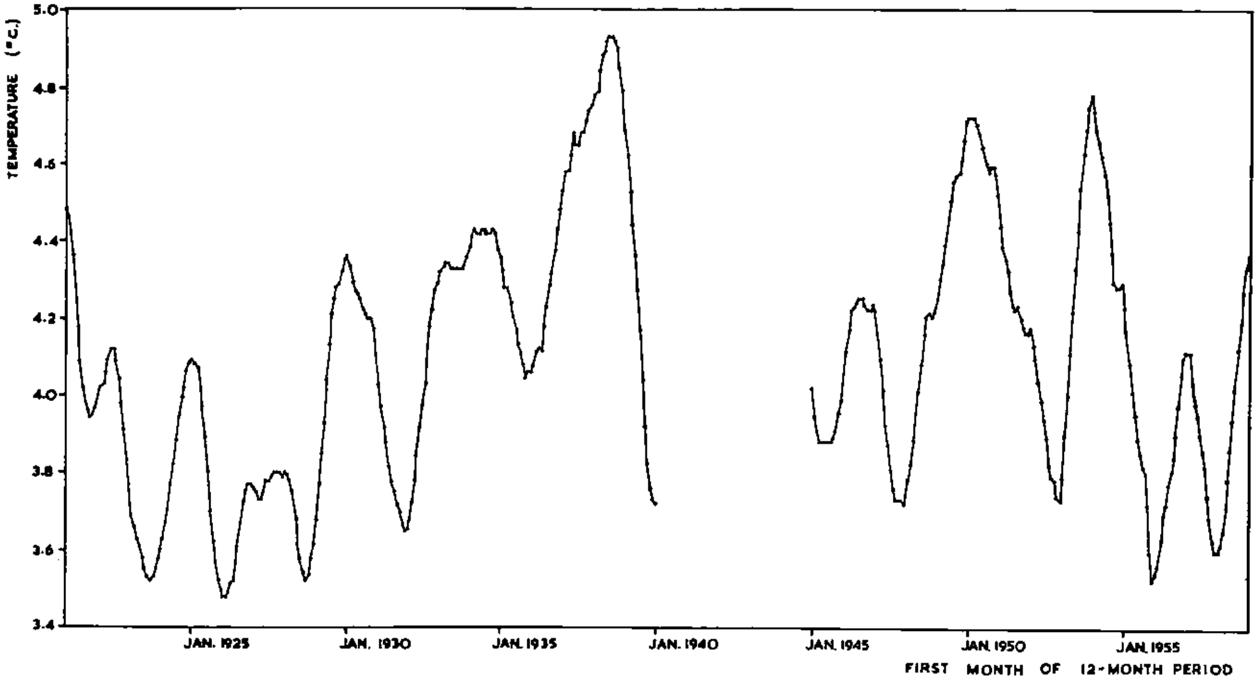

Fig. 3. Water temperature of the 0-200 m layer on the Kola Section (12 monthly running means).

Other Russian workers, analysing the factors which control the temperature of the water along the Kola Section, have come to differing conclusions. Their results, which have been summarised by Lee (1963), disagree mainly regarding the relative importance of the advection of heat in this region; *e.g.* Denisov (1958) considers local meteorological factors to be of prime importance, advective factors accounting for only 17% of the observed variation, whereas Seryakov (1960) finds that advection accounts for 56% of the total amount of heat received in the southern half of the Barents Sea during each year.

In order to ascertain that a relationship exists between the changes in the water temperatures in the Kola Section and the meteorological changes which took place, correlation coefficients have been established between water temperature in the 0-200 m layer on the Kola Section and (a) air temperature at Vardö, (b) southerly and westerly components of the wind at Bear Island. In all cases the correlation coefficients have been determined with various time lags between the two sets of data in order to find that at which each was greatest. The mean water temperatures for each period December-November were used as this appeared to be most suitable from the analysis of the 12 monthly running means described above. Table 1 shows the correlation coefficients obtained, and also the probability that the coefficient will reach each value between two sets of the same number of figures, selected at random. Where this probability exceeds 0.1 the correlation must be considered to be insignificant. The significance increases as the probability decreases, and when the probability is less than 0.001 the correlation is highly significant. The highest correlation coefficients exist between the water temperature and the air temperature at Vardö when the 12 monthly mean values of air temperature were taken for periods preceding those for water temperature by between 2 and 8 months. The correlation coefficients between water temperature and the southerly and westerly wind components at Bear Island show a similar pattern but are generally smaller. The southerly wind shows the highest correlation with water temperature when it precedes it by 11 months whereas the westerly wind, which almost invariably shows lower correlation coefficients than the southerly wind, is most closely related to the water temperature when it precedes it by 3 months.

TABLE 1. CORRELATION COEFFICIENTS, AND THE PROBABILITY OF THEIR EXISTING IN TWO RANDOM SETS OF FIGURES, BETWEEN 12 MONTHLY (DECEMBER - NOVEMBER) MEANS OF WATER TEMPERATURE OF THE 0-200 M LAYER ON THE KOLA SECTION AND (A) 12 MONTHLY MEANS OF AIR TEMPERATURE AT VARDO, (B) 12 MONTHLY MEANS OF SOUTHERLY WIND COMPONENT AT BEAR ISLAND, (C) 12 MONTHLY MEANS OF WESTERLY WIND COMPONENT AT BEAR ISLAND (1921-40 AND 1945-58). (MO. = MONTH).

(a)	12 monthly air temperature preceding 12 monthly water temperature by:								
	17 mo.	14 mo.	11 mo.	8 mo.	5 mo.	2 mo.	-1 mo.	-4 mo.	-7 mo.
Correlation Coefficient	+0.19	+0.21	+0.45	+0.74	+0.72	+0.78	+0.53	+0.21	+0.08
Probability	>0.1	>0.1	0.009	<0.001	<0.001	<0.001	0.002	>0.1	>0.1

(b)	12 monthly wind component preceding 12 monthly water temperature by:							
	13 mo.	11 mo.	9 mo.	7 mo.	5 mo.	3 mo.	1 mo.	-1 mo.
Correlation Coefficient	+0.38	+0.54	+0.43	+0.45	+0.30	+0.37	+0.30	+0.10
Probability	0.03	0.001	0.01	0.009	0.1	0.04	0.1	>0.1

(c)	12 monthly wind component preceding 12 monthly water temperature by:							
	13 mo.	11 mo.	9 mo.	7 mo.	5 mo.	3 mo.	1 mo.	-1 mo.
Correlation Coefficient	+0.24	+0.29	+0.33	+0.31	+0.25	+0.37	+0.26	-0.02
Probability	>0.1	>0.1	0.08	0.1	>0.1	0.04	>0.1	>0.1

These correlation coefficients suggest that there is either an external factor, bringing about the changes in the meteorological conditions and in the water temperature, which affects the former more rapidly, or that the changes in the meteorological factors considered are themselves responsible for the changes in water temperature. The changes in air temperature are obviously not brought about directly by the changes in water temperature.

WATER TEMPERATURES AT STATION S

Observations of temperature and salinity have been made at two stations, S and W, along a section extending westwards from Bear Island across the West Spitsbergen Current in latitude 74° 25'N on 36 occasions between 1949 and 1958 from the Ministry of Agriculture Fisheries and Food Research Vessel *Ernest Holt*. Station S is sited at 16° 08'E and is just off the continental shelf in a depth exceeding 900 m; station W sited at 13° 00'E is in a depth exceeding 2,000 m (Fig. 1).

Station S is in a similar position to the Kola Section, each being located in a branch of the Norwegian Current, and, being close to the atmospheric Arctic Front, each subject to similar meteorological conditions at the surface. The variations of water temperature at Station S may therefore be expected to result from similar factors to those which bring about the variations along the Kola Section. At Station S, however, temperature variations, and the factors which bring them about, can be examined to a considerably greater depth.

Method

The temperature observations at station S have been used to determine the mean temperature of each 100 m layer between the surface and 600 m on each of the 36 occasions when observations were made. These values were then compared with the factors comprising the heat budget which were thought most likely to have varied from year to year and thus to have brought about changes in the water temperature.

The terms involved in the heat budget of the sea can be divided primarily into the advective and the non-advective terms. Assuming that variations in the vertical advection of heat are small compared with those in the horizontal advection, and that the West Spitsbergen Current dominates the horizontal advection of heat in this region, the advective term may be considered to depend on the temperature and strength of the West Spitsbergen Current. Hill and Lee (1957) have used the temperature and salinity data from stations S and W to calculate the transport of water northwards between these two positions and between the surface and 400 m, using the hydrodynamical method, and these values may be used as a measure of the strength of the West Spitsbergen Current. Its temperature will depend on its strength, as the more quickly the water moves northwards the less it will be cooled. Hence the volume transport of the water northwards between stations S and W has been taken as a measure of the advective term in the heat budget at station S.

The most important non-advective terms are the radiation, the evaporation and the convection terms. If the radiation received on a horizontal surface outside the earth's atmosphere is considered to remain constant from year to year, variations in the radiation received by the water surface from year to year result from variations in cloudiness. Similarly the effective back radiation from the sea surface at a particular temperature is dependent upon cloudiness and relative humidity. The convection term is dependent on the wind velocity and the difference between the surface water temperature and the air temperature. Changes in water temperature can, therefore, be brought about by changes in wind velocity or in air temperature. Similarly the evaporation term is dependent on wind velocity and on the difference between the surface water temperature and the air temperature, and also on the relative humidity of the air. Thus the atmospheric factors which enter into the heat budget of the sea, and which could bring about year to year changes in sea temperatures, are cloudiness, relative humidity, air temperature and wind velocity. Seasonal changes, however, may be partly brought about by the annual cycle of radiation received from the sun.

In order to determine the importance of each item in the heat budget of the different water layers, correlation coefficients have been determined between each of these items and the mean temperatures of the various water layers at station S on each of the 36 occasions when observations were made.

The most suitable meteorological data available are those from Bear Island, approximately 83 km to the east of station S. As the cause of the variations in water temperature are being sought, the meteorological data have been averaged over the 10 days before observations were made at station S, on each occasion, and these 10 day mean values correlated with the water temperatures. The only volume transport values available, however, are those calculated for the actual occasions when the temperature observations were made, and simultaneous values for volume transport and temperature have therefore had to be used. It is, however, thought that oceanographical conditions change much more gradually than atmospheric conditions, and the volume transport values should

TABLE 2. CORRELATION COEFFICIENTS, AND THE PROBABILITY OF THEIR EXISTING IN TWO RANDOM SETS OF FIGURES, BETWEEN WATER TEMPERATURE AT STATION S AND FACTORS FROM THE HEAT BUDGET:

(A) ACTUAL VALUES, ALL YEAR;
(B) DEVIATIONS FROM MONTHLY MEAN VALUES, ALL YEAR;
(C) DEVIATIONS FROM MONTHLY MEAN VALUES, 28TH MAY - 27TH SEPTEMBER ONLY;
(D) DEVIATIONS FROM MONTHLY MEAN VALUES, 30TH NOVEMBER - 1ST MAY ONLY.

(a)	Volume Transport		Air Temperature		Cloud Cover		Relative Humidity		Wind Velocity	
	Coeff-icient	Proba-bility	Coeff-icient	Proba-bility	Coeff-icient	Proba-bility	Coeff-icient	Proba-bility	Coeff-icient	Proba-bility
Temp. of water layer between 0-100m	0.10	>0.1	0.70	<0.001	0.24	>0.1	0.37	0.03	-0.89	<0.001
100-200m	0.42	0.01	0.41	0.01	0.09	>0.1	0.16	>0.1	-0.25	>0.1
200-300m	0.59	<0.001	0.24	>0.1	-0.01	>0.1	-0.01	>0.1	-0.06	>0.1
300-400m	0.70	<0.001	0.08	>0.1	-0.07	>0.1	-0.10	>0.1	0.32	0.05
400-500m	0.81	<0.001	0.04	>0.1	-0.01	>0.1	-0.07	>0.1	0.56	<0.001
500-600m	0.78	<0.001	0.10	>0.1	0.08	>0.1	0.01	>0.1	0.51	0.001
0-600m	0.65	<0.001	0.34	0.04	0.07	>0.1	0.09	>0.1	-0.06	0.1

(b)	Volume Transport		Air Temperature		Cloud Cover		Relative Humidity		Wind Velocity	
	Coeff-icient	Proba-bility	Coeff-icient	Proba-bility	Coeff-icient	Proba-bility	Coeff-icient	Proba-bility	Coeff-icient	Proba-bility
Temp. of water layer between 0-100m	0.31	0.1	0.52	0.003	0.29	>0.1	0.12	>0.1	-0.40	0.03
100-200m	0.52	0.004	0.46	0.01	0.57	0.001	0.21	>0.1	-0.04	>0.1
200-300m	0.56	0.002	0.45	0.01	0.50	0.005	0.14	>0.1	-0.01	>0.1
300-400m	0.58	0.001	0.46	0.01	0.44	0.02	0.20	>0.1	0.12	>0.1
400-500m	0.69	<0.001	0.51	0.004	0.48	0.008	0.23	>0.1	0.22	>0.1
500-600m	0.69	<0.001	0.54	0.002	0.43	0.2	0.20	>0.1	0.11	>0.1
0-600m	0.68	<0.001	0.57	0.001	0.51	0.004	0.20	>0.1	-0.01	>0.1

TABLE 2 - CONTINUED.

	(c)	Volume Transport		Air Temperature		Cloud Cover		Relative Humidity		Wind Velocity	
		Coeff-icient	Proba-bility	Coeff-icient	Proba-bility	Coeff-icient	Proba-bility	Coeff-icient	Proba-bility	Coeff-icient	Proba-bility
Temp. of water layer between	0-100m	0.01	>0.1	0.35	>0.1	-0.62	0.003	-0.37	>0.1	-0.65	0.02
	100-200m	0.74	0.006	-0.14	>0.1	0.38	>0.1	0.11	>0.1	0.12	>0.1
	200-300m	0.72	0.008	0.06	>0.1	0.54	0.07	0.22	>0.1	0.07	>0.1
	300-400m	0.58	0.05	0.24	>0.1	0.52	0.08	0.38	>0.1	0.08	>0.1
	400-500m	0.71	0.01	0.27	>0.1	0.50	0.1	0.34	>0.1	0.05	>0.1
	500-600m	0.67	0.02	0.36	>0.1	0.22	>0.1	0.12	>0.1	-0.21	>0.1
	0-600m	0.76	0.004	0.26	>0.1	0.29	>0.1	0.10	>0.1	-0.18	>0.1

	(d)	Volume Transport		Air Temperature		Cloud Cover		Relative Humidity		Wind Velocity	
		Coeff-icient	Proba-bility	Coeff-icient	Proba-bility	Coeff-icient	Proba-bility	Coeff-icient	Proba-bility	Coeff-icient	Proba-bility
Temp. of water layer between	0-100m	0.44	>0.1	0.61	0.04	0.66	0.02	0.34	>0.1	-0.22	>0.1
	100-200m	0.42	>0.1	0.64	0.02	0.64	0.02	0.34	>0.1	-0.19	>0.1
	200-300m	0.48	>0.1	0.63	0.03	0.49	>0.1	0.19	>0.1	-0.11	>0.1
	300-400m	0.56	0.06	0.67	0.02	0.46	>0.1	0.26	>0.1	0.07	>0.1
	400-500m	0.73	0.007	0.73	0.007	0.58	0.05	0.35	>0.1	0.28	>0.1
	500-600m	0.77	0.003	0.65	0.02	0.61	0.04	0.36	>0.1	0.29	>0.1
	0-600m	0.63	0.03	0.70	0.01	0.62	0.03	0.33	>0.1	0.03	>0.1

therefore be fairly representative of the periods over which the meteorological data have been averaged. Table 2(a) shows these correlation coefficients, (each of which have been determined from 36 pairs of variables), together with the probability of their reaching each value by chance.

The existence of a significant correlation coefficient between two sets of variables does not necessarily mean that there is any cause and effect relationship between them. In particular, meteorological and oceanographical data such as that used to obtain the correlation coefficients in Table 2(a) will almost certainly have seasonal trends, and similar seasonal trends in two sets of variables may lead to a significant correlation coefficient existing between them even though there is no interdependence of the two. In order to eliminate the effects of these seasonal variations, deviations have been determined from mean monthly values based only on the data used in calculating the correlation coefficients. This was done because these were the only data available for water temperature and water transport, and the use of meteorological data from other occasions might have biased some meteorological monthly mean values in favour of years for which no oceanographical data is available. In order to smooth the data all oceanographical observations made within the 5 week period centred on each calendar month were taken into account in calculating the mean value for that month.

Although the meteorological observations extended over the period of 10 days immediately preceding each set of oceanographical observations, they were taken in each case to relate to the same month or months as the oceanographical observations which they preceded. The mean monthly values obtained are based on 4 or more values in 8 months, but on less than 4 in the remaining 4 months. The average monthly temperatures of each water layer thus determined are shown in Table 3.

TABLE 3. AVERAGE MONTHLY TEMPERATURES (°C) OF VARIOUS WATER LAYERS AT STATION S (1949-58)

	Month	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
	No. of occasions from which mean calculated	1	2	5	4	7	5	5	2	4	2	4	5
Water Layers	0-100m	5.9	6.2	4.8	4.8	5.2	5.7	6.5	6.8	6.9	7.2	6.0	6.1
	100-200m	5.7	6.2	4.7	4.7	4.9	5.1	5.6	6.1	5.6	6.1	5.9	6.1
	200-300m	5.2	6.0	4.5	4.4	4.7	4.7	5.0	5.6	4.9	5.1	5.4	5.6
	300-400m	4.8	5.6	4.1	3.9	4.2	4.0	4.2	4.6	4.2	4.4	4.7	4.9
	400-500m	4.3	4.7	3.5	3.0	3.6	3.4	3.5	3.4	3.4	3.6	3.7	4.1
	500-600m	3.8	3.9	2.8	1.9	2.7	2.5	2.7	2.4	2.6	3.1	2.5	3.2
	0-600m	5.0	5.4	4.0	3.8	4.2	4.2	4.6	4.8	4.6	4.9	4.7	5.0

It was considered that deviations from monthly means based on less than 4 values were unsatisfactory and therefore the observations for these 4 months - January, February, August and October - were omitted from this part of the study. Deviations from the monthly mean were determined for each of the remaining 29 values, the deviation from the average of the two mean values being used where an observation had been included in two 5 week periods. These deviations from the monthly means were then correlated in the same way as the actual values described above. The correlation coefficients obtained are shown in Table 2(b).

It is possible that particular items in the heat budget will be of greater importance in bringing about changes in water temperature during some parts of the year, than during others. The relative importance of atmospheric factors, which operate at the surface, and advection, which operates throughout the water column, in bringing about changes in water temperature in different layers will vary according to the amount of vertical mixing which takes place. As one of the main causes of this mixing is the extent of warming or cooling at the surface by the evaporation and convection terms, two seasons have been defined according to the differences between surface water temperature and air temperature, each of between 4 and 5 months duration. During the first period (28 May to 27 September) the surface water temperatures generally exceeded the air temperatures by lesser amounts than they did during the second period (30 November to 1 May).

In determining correlation coefficients between water temperature and the various factors in the heat budget during each of these seasons, the same deviations from monthly normals were used as above, again omitting those for the months where the mean values were based on less than 4 observations. Twelve sets of observations remain during each period, and the correlation coefficients obtained are shown in Tables 2 (c) and 2 (d).

DISCUSSION

The tables show that highly significant correlation coefficients exist between certain factors in the heat budget and the water temperatures in various layers at station S, and between deviations from monthly normals of factors in the heat budget and similar deviations from monthly normals of the water temperatures in the various layers. The volume transport of water between 0 and 400m between stations S and W shows the most consistently significant correlation with water temperature in all of the tables, demonstrating the considerable importance of the advection of heat by the West Spitsbergen current on water temperatures in this region. The correlation coefficients between volume transport and water temperature in Table 2(a) are slightly more significant than those in Table 2(b) for the water temperatures of the layers below 200m but the converse is true above 200m, suggesting that volume transport and water temperature above this depth have opposing seasonal trends, whereas below this depth they have common seasonal trends. Both sets of coefficients show a general increase with depth. From Tables 2 (c) and 2 (d) it can be seen that higher correlation coefficients generally exist during the summer period than during the winter period, although this is certainly not so between volume transport and water temperature in the uppermost 100m layer.

Air temperature and water temperature have a common seasonal trend in the upper layers (above 100m), as might be expected from the direct effect of the sun's radiation as well as from any interaction between the two. Below 100m, however, water temperatures appear to follow seasonal trends opposed to those of air temperature, and hence although significant correlation coefficients exist between air temperature and water temperature at all depths in Table 2 (b) no such significant correlation coefficients are found below 200 m in Table 2 (a). Perhaps surprisingly, Table 2 (b) shows that there is little variation in the correlation coefficients between the deviations of air temperatures from monthly normals and those of water temperature in successive 100 m layers to 600 m. This is indicative of the fairly strong vertical mixing which generally occurs throughout the year in this region. Tables 2 (c) and 2 (d) show a considerable contrast, however, between the relationship between air temperature and water temperature in summer and that in winter. In summer, when the difference between surface water temperature and air temperature is generally least, the correlation coefficients between the air temperature and water temperature deviations from monthly normals are insignificant for water temperatures in each 100 m layer, whereas in winter they are highly significant at all depths. This is because the major term in the heat budget in which the air temperature appears, is the net convection term, which is generally considered to be proportional to the difference between surface water temperature and air temperature, and which will therefore be of greatest importance in the heat budget when this difference is greatest.

Correlation coefficients between water temperature and cloud show similar trends to those between water temperature and relative humidity in all of the tables, as is to be expected by the close relationship between cloud and relative humidity— a higher relative humidity will give rise to an increase in cloud and a lower relative humidity to a decrease. In Table 2 (a) a significant correlation exists between relative humidity and the water temperature of the upper 100 m whilst in Table 2 (b) highly significant correlations exist between cloud and water temperature in all layers below 100 m. The absence of a significant correlation in the upper 100 m, however, where any changes brought about by variations in the cloud cover would be expected to be most marked, suggests that the relationship is an indirect one. An external factor which would bring about similar changes in the cloud cover and in the volume transport, which also shows higher correlation coefficients with water temperature below 100 m than above it, seems the most likely reason for this relationship. The external factor is very probably the southerly wind component which Hill and Lee (1957) have shown to be related to the volume transport, and which would be expected to be closely related to the cloud cover also.

Whereas relative humidity does not show any significant correlation with water temperature in Tables 2 (c) and 2 (d) cloud cover shows a number of highly significant correlations, positive in all cases but one. This contrast between a highly significant negative correlation between cloud cover and the water temperature in the upper 100 m in summer, and a highly significant positive correlation between the same factors in winter is, however, to be expected from the way in which cloud cover appears in the heat budget. Its main effect is to reduce radiation, whether incoming or outgoing. During the summer, incoming radiation exceeds outgoing radiation and hence an increase in cloud cover will reduce the heat gained by the surface water. In winter, however, there is little incoming radiation and it is exceeded, in this region, by the outgoing radiation. An increase in cloud cover in winter, therefore, leads to a reduction in the heat lost by the surface water. Again the positive significant relationships between cloud cover and water temperature in the deeper layers in both tables suggest the indirect relationship referred to above.

The correlation coefficients between wind velocity and water temperature in Table 2 (a) show a significant negative correlation existing with the upper 100 m of water, and significant positive correlations existing with the water layers below 300 m. Comparison with Table 2 (b), however, shows the positive correlations with the deep water to result primarily from common seasonal trends. The negative correlation between wind velocity and the temperature of the upper 100 m of water is highly significant during the summer period, as shown in Table 2 (c) but insignificant during the winter period, as shown in Table 2 (d). This is because the wind velocity affects water temperature by promoting vertical mixing, and thus increasing the loss of heat by evaporation and net convection. During the winter the rapid loss of heat from the surface water gives rise to strong vertical mixing which thus continues in the absence of any wind. In summer, however, when the net loss of heat from the surface water is greatly reduced, or even reversed, the wind velocity becomes very much more important in promoting vertical mixing.

CONCLUSIONS

The changes in water temperature in the seas north of Norway which have been inferred by many authors, both from changes in climate and from the changes in marine fauna which have been observed, are confirmed by the data from the Kola Section. The short term variations of water temperature between 0 and 600 m at station S between 1949 and 1958 have been related to the most probable causal factors in the heat budget. The dominant causal factor appears to be the horizontal advection of heat, but other factors become of greater importance with regard to water at particular depths, and at particular times of year. Atmospheric factors are most important in the upper layers, as would be expected. Cloud and wind velocity show particularly high negative correlations with the temperature of the upper 100 m of water in the summer period, whilst air temperature and cloud show similarly high positive correlations with the temperatures of each 100 m layer of water to 600 m in the winter.

I wish to express my gratitude to Mr Arthur Lee for his advice and encouragement during this investigation.

REFERENCES

BLACKER, R.W. 1957. Benthic animals as indicators of hydrographic conditions and climatic change in Svalbard waters. *Fish. Invest., Lond. (2)* 20 (10).

DENISOV, A.S. 1958. Prichiny izmeneniia temperatury vody Nordkapskogo techeniia (Causes of variation in the water temperature of the North Cape current). *Probl. Arkt., Leningr.*, 5 19-26. In Russian.

DROGAITSEV, D.A. 1959. Long-term variations of meridional heat transport in the atmosphere, as basis for the forecasting of water temperature in the ocean. Paper No. 5 Conference on the problem: Interaction between the atmosphere and the hydrosphere in the North Atlantic, 2 *Hydromet. Institute. Leningrad.* In Russian.

HESSELBERG, T. and T.W. JOHANNESSEN. 1958. The recent variations of the climate at the Norwegian Arctic Stations. *In* Sutcliffe, R.C. (editor) *Polar Atmosphere Symposium, Oslo, 1956*. Pergamon Press, Part 1: 18-29.

HILL, H.W. and A.J. LEE. 1959. The effect of wind on water transport in the region of the Bear Island fishery. *Proc. roy. Soc. Edinb.* (B) 148 104-116.

JENSEN, AD. S. 1939. Concerning a change of climate during recent decades in the Arctic and Sub-arctic regions. *Biol. Medd. Kbh.* 14 (8) 1-75.

LEE, A.J. 1963. The hydrography of the European Arctic and Sub-arctic Seas. *Oceanogr. Mar. Biol. Ann. Rev.* 1 69-71.

SERYAKOV, E.I. 1960. Ob advektsii tepla techeniyami v Barentseuom More (The advection of heat by means of currents in the Barents Sea). Sovetskie Rybokhozyaistvennye Issledovaniya v Moryakh Evropeiskogo Severa. *In* Soviet Fisheries Investigations in North European Seas, Moscow: 81-88. In Russian.

WOODHEAD, P.M.J. and A.D. WOODHEAD. 1959. The effects of low temperatures on the physiology and distribution of the cod, *Gadus Morhua L.*, in the Barents Sea. *Proc. zool. Soc.* Lond. 133 (2) 181-199.

I-3

IS OCEANOGRAPHIC FORECASTING (HYDROSIS) FEASIBLE FOR FISHERIES?

By

T. Laevastu[1]

ABSTRACT

This paper presents a brief review of present practices of weather and oceanographic forecasts and examines future needs and the feasibility of improvements.

SHOULD FISHERIES ESTABLISH FORECASTING SERVICES?

Fisheries trade is one of man's occupations which is most exposed to the weather and the sea. In order to plan successful fishing trips or to determine where to fish, there is a need for both weather and oceanographic forecasts. The following brief summary will examine the needs in fisheries for improved and extended weather and oceanographic forecasts and the best possibilities for issuing such forecasts for fisheries purposes.

It is quite obvious that the time has come when the fisheries research should be divided into two parts: One, for basic research and the other for fisheries services, mainly in the form of forecasts. As the fisheries trade does not possess a strong organization for processing such forecasts, collaboration should be sought with the existing weather services, which, in most cases, are more than willing to provide such collaboration. Benefits of such services are obvious in terms of economic returns as well as through support to further research to fill existing gaps in the knowledge, necessary for forecasting both the behaviour of fish and of its environment.

TYPES OF FORECASTS CURRENTLY GIVEN AND THEIR ADEQUACY

Weather forecasts

The North Atlantic is at present well served by a number of countries with 24-hr forecasts given in coded form as well as in plain language (both in local and in the English languages). Those forecasts are mainly meant for merchant shipping and, only in a few special areas, for high seas and coastal fisheries.

Medium range weather forecasts are especially useful for planning high seas fisheries. They are prepared only by a few countries a few times a week and their availability to fisheries varies. Difficulties exist in transmitting those forecasts to the vessels at sea.

The seasonal weather forecasts, although issued by several countries, are still very general and inaccurate, and are not too useful for fisheries. However, fisheries would be interested in the analyses of the past season's weather, especially with respect to wind anomalies and the resulting anomaly of wind currents and the accompanying changes of water temperature.

Oceanographic forecasts

Wave forecasts are at present prepared for the North Atlantic by the USA. Other countries prepare such forecasts on an experimental basis and for routing a number of ocean-crossing ships.

Wave forecasts are only available in exceptional cases to large fishing vessels. In certain instances there is, however, a need and economic gain in routing fishing vessels to and from distant fishing grounds, based on extended weather and sea (wave) forecasts.

No current forecasts are issued at present. However, there is a need for such forecasts, both

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for bottom trawling and for pelagic fisheries. As the knowledge on the behaviour of fish in respect to currents accumulates, there is a need for long-range hindcasts for the currents and current anomalies on fishing grounds.

The U.S. Naval Oceanographic Office issues, at present, 10-day temperature charts for the North Atlantic. A general sea surface temperature chart for Northern Hemisphere is also prepared by the U.S. Fleet Numerical Weather Facility in Monterey, California. Thermocline depth predictions are also made for limited areas in the North Atlantic. However, before oceanographic forecasts have any real, direct value and demand by fisheries skippers, some educational work must be made among fishermen and skippers by distributing and popularizing the knowledge on fish behaviour in relation to temperature structure and of other environmental factors.

Fisheries (biological) forecasts

No general biological forecasts in general terms have been issued to fisheries, but limited forecasts of various kinds have been attempted in the past, such as forecasts of the year-class strengths; forecasts of the arrival of winter spawning herring in Norwegian coastal waters, etc. The ICES working group on the telecommunication of oceanographic observation in the Norwegian Sea is working on a comprehensive, but specific, fisheries forecasting scheme. There are possibilities of issuing a variety of biological forecasts which would be useful, especially for fishing industries for planning purposes and could be issued regularly for different major fishing grounds.

SPECIAL REQUIREMENTS AND FUTURE PROSPECTS OF FORECASTING SERVICES FOR FISHERIES

Weather forecasts

The present 24-hr forecasts fill most of the requirements for frequented shipping lines. However, in many areas, there is a need for special coastal forecasts, as the coastal weather differs considerably, at times, from that on the land and that farther offshore. Further improvements of medium range weather forecasts could be achieved by careful analysis of the existing peculiarities in these areas, and by establishing special and local forecasting models. Obviously, all improvements can be made only on the basis of good and complete weather reports from those fishing areas and therefore, effort should be made to recruit a number of fishing vessels as voluntary observing and reporting vessels. This recruitment could be connected with short courses in meteorology to skippers which can be done during the off-season of the given fisheries.

Many fishermen might not be familiar with the present available weather services and here, short courses and pamphlets could also help. Furthermore, different countries could make further effort through port meteorological officers meeting all fishing vessels and providing them with the necessary materials, especially with the charts of forecast areas and the times of forecasts. (There is a slight discrepancy in the names and boundaries of forecast areas from different countries.)

Oceanographic forecasts

It is highly desirable for fisheries that future wave forecasting should include the sea and weather routing of trawlers from distant fishing grounds. The medium range prognosis of weather should be given to the trawler, including expected wave conditions on the fishing ground and on the way from the ground to the port, in order to enable the skipper to make proper decisions on when to start returning home.

The separation of swell and sea could be made in the wave forecasts and the reporting of wave parameters should be adapted to the prevailing boat sizes on given fishing grounds. Forecasting the average length and height is not always sufficient for fisheries. Wave forecasts should also be given in plain language, in more descriptive form than present ones, and some special features such as the cross seas should be included in the forecasts.

Current forecasts are not issued at present mainly because of lack of knowledge. Currents in a given location are not strictly correlated with the prevailing weather (winds) in this given locality, but are determined by the wind fields over large areas. The wind currents could be estimated from the prevailing wind systems as well as from the changes of atmospheric pressure and occasionally as caused by inertia currents. Current forecasts could be included in the weather forecasts and should also include data on the tidal currents. Special tidal current charts (ebb and flood) should be provided to the fishermen and the forecasts should give the slack waters (or specific direction in relation to tidal ellipse in case of rotary currents) in any given area so that the fishermen can interpolate the currents from the charts provided. The current prediction should include information on movement and sharpness of current boundaries.

The depth of the thermocline can be predicted at present with some degree of accuracy, especially when this is supported by field observations. Therefore, a number of bathythermographs should be provided to fishing vessels for observing and reporting the temperature structure. In certain cases, it is sufficient to predict only the sea surface temperature, temperature at the current boundaries, and the depth in which the thermocline is expected to intercept the bottom.

Detailed forecasts on thermocline depth could be issued to certain fisheries, *i.e.*, herring fishery, tuna fishery, etc. The average depth of the thermocline could be given and its possible magnitude of fluctuations indicated. It should also include indications on the sharpness of the thermocline and the sea surface temperatures.

Fisheries forecasts

A variety of direct fisheries forecasts could be issued, such as the estimation of the arrival of fish to spawning grounds, the availability of fish in different areas as reported by a number of fishing vessels, depth of the occurrence of schools, etc.

In biological forecasting, two different ways could be followed: One way would be to explain to the fishermen the existing knowledge on the behaviour of fish in different hydrographic conditions and to leave the conclusions up to the fishermen. Another way would be to make analyses and issue an exact fisheries forecast for the fishermen which would include the optimum depth of the fish schools (*e.g.*, often related to sharp thermoclines), the aggregation of these schools in different areas, the possible arrival of spawners in a given spawning ground, the dispersal of fish in different wave and current conditions, etc. Furthermore, the actual occurrence of fish could be reported as observed in the actual fishery. However, the latter one is a questionable proposition because fishermen usually do not like to report their position, the fishing, and their actual catches in order to avoid crowding of given small fishing grounds.

THE AVAILABILITY AND REQUIREMENTS OF BASIC OBSERVATIONAL DATA FOR FORECASTING PURPOSES

The present observations on fishing grounds are sparse, indeed, and in order to establish accurate forecasts, a much denser net of observations is required. The accuracy of the weather reports from fishing vessels should be greatly improved. There is a possibility that a number of fishing vessels and/or companies could establish special scouting vessels which would not only make observations of the weather and aquatic environment, but also would analyze the data, make different forecasts, and report the occurrence of fish. The existing fisheries protection vessels could be used for this service. The codes devised by the ICES working group may be most appropriate for such observational and forecasting services.

EXPECTED ACCURACY OF SPECIFIC FORECASTS FOR FISHERIES

As in any forecast, in the beginning the fisheries forecasting would be more an art than a science and great errors might be made. However, fishermen should be informed about the possible errors so that the future confidence in such forecasts would not suffer. The accuracy of the present weather forecasts leave much to be desired in the "sparse areas." The wave forecasts are closely connected with the forecasts of winds and are reasonable in accuracy. However, new ways must be found to describe the actual sea for fisheries purposes. The thermocline forecasts have just been started for naval purposes. They are reasonably accurate in certain areas, but in others, there are considerable difficulties caused by large internal waves, which at present, are unpredictable; and by more permanent depressions of thermocline, which seem to move around. These depressions seem at times to be connected to wind convergences and might be predictable with reasonable accuracy in the future. There should be no difficulties in predicting offshore tidal currents in the future; however, prediction of wind currents and permanent flow need considerable research work.

It is quite obvious that considerable emphasis should be devoted, in the beginning, to the verification of the forecasts through which additional experiences will be gained.

ORGANIZATIONAL ASPECTS OF FORECAST SERVICES FOR FISHERIES

Analysis messages could be broadcast to fishing vessels where the skippers would make the necessary plottings and analyses. This possibility, however, is limited because the skippers are extremely busy while fishing and have no time to make good analyses on board. Hence, there remains the possibility that several companies might get together to establish a scouting vessel which would take care of the observations and analyses and direct the fishing fleet of several companies accordingly. The same can be made on the basis of governmental service as at present done to some extent by Germany on the "distant fishing grounds."

There are areas where several nations are interested in the same fishery, and inter-governmental cooperation might be useful. An experiment is being carried out in the Norwegian Sea at present through ICES.

The success of the forecasts and services depends primarily on several factors outside the reach of the forecaster. The first is a requirement of educational work among fishermen and fishing industries, explaining the present knowledge on fish behaviour in relation to environment and to the westher. Second, the availability of different forecasts should be made known to fisheries and the use and accuracy should be explained. The success of all forecasts depends on the reporting of actual data and this can only be improved if the fishermen cooperate and see the value of such forecasts.

I-4

DAILY HEAT EXCHANGE IN THE NORTH PACIFIC; ITS EFFECTS ON THE OCEAN AND ITS RELATIONS TO WEATHER

By

T. Laevastu[1]

ABSTRACT

The oceanographic and meteorological significance of heat exchange between the sea and the atmosphere is briefly summarized. The components of heat exchange between the sea and the air over the North Pacific have been computed by five degree squares for a number of days. The computation procedure is described. The accuracy of these computations has been investigated and found to depend mainly on the meteorological data and their manipulation. Most of the heat exchange features are of large scale and relatively long-lived. Sample distributions of different components are illustrated.

A preliminary analysis of heat exchange has been made in respect to oceanographic and meteorological factors. The following conditions suggest themselves as a result of this preliminary analysis:

1. A remarkably high loss of heat from the sea occurs during the winter along about 22°N from the Asian coast to about 155° E and along the Asian coast itself. The depth of the thermocline in these heat-loss areas is determined by convective stirring. This high heat loss suggests furthermore the formation of intermediate waters at relatively low latitudes and along the western coasts of the oceans in general.

2. The comparison of the charts of Q_a (the sum of latent heat and sensible heat transfer) with the weather charts shows that the patterns of these heat exchange components are closely related with wind patterns; cyclonic circulations prevailing over positive Q_a "centers" and anticyclonic circulation over negative Q_a centers in the western parts of the oceans.

3. The dissipation of North Pacific cyclones seems to occur over areas where Q_a is low and/or negative, and no sharp Q_a gradients exist in the vicinity. This seems to be predictable a few days ahead.

4. The birth of cyclones seems to occur at certain defined places at the fronts where Q_a gradients and "centers" are created. These births might also be predictable about one to two days ahead, before they can be recognized on surface synoptic charts.

SIGNIFICANCE OF HEAT EXCHANGE

More than 40 years ago, Helland-Hansen and Nansen (1920) published a pioneering work about the temperature variations in the North Atlantic Ocean, and indicated some possible ways to predict the year-to-year variations, with the condition that more thorough investigations be conducted to clarify some open questions raised by them, especially in respect to the regulating action of thermal conditions on the circulation of the atmosphere. Relatively few follow-up works have appeared during this past 40-year period and one of the main reasons might be that synoptic oceanography has not yet been established. Namais (1962) emphasized the importance of the feed-back systems between the ocean and the atmosphere and stated: "Such studies suggest that the time has arrived for synoptic oceanography to take its place alongside synoptic meteorology." He also suggested that the history of meteorology indicates that imaginative hypotheses are initially required in such complex fields as the study of climatic anomalies and of sea-air interactions.

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Considerable knowledge has been accumulated on the influence of temperature on the behaviour of fish. Most of this knowledge has been summarized by Hela and Laevastu (1962). Considering this knowledge and other pertinent factors, it seems that we are now approaching the prediction stage in fisheries where the fisheries authorities might be devoting part of their energy to servicing the fisheries through a variety of fisheries forecasts. It seems natural that one of the first services would be the prediction of sea surface temperature and thermal structure within depth. Obviously, these predictions must be connected with actual surveys and measurements, at least in the beginning.

The forces which cause changes in the sea are of atmospheric origin, therefore, the present study deals with the energy (mainly heat) exchange between the sea and the atmosphere. It was initiated for evaluating the possibility of forecasting the temperature structure of the sea over large oceanic areas, and for forecasting the depth of the thermocline.

Besides oceanographic objectives, the present study might also have some meteorological significance. As pointed out by Petterssen (1956), the energy necessary for setting the atmosphere in motion and for maintenance of winds is of solar origin. He indicated that for maintenance of frontal zones, it is necessary to have over-all temperature contrasts. These temperature contrasts are achieved by the unequal exchange of heat between the surface of the earth and the atmosphere. Petterssen (*op. cit.*) also emphasized that the configuration of the temperature contrasts might determine, to a large extent, the movement of the cyclone centers at sea level.

Namias (1962) stated that it is possible that interactions between abnormal surfaces may be largely responsible for climatic fluctuations on all time scales. These abnormal surfaces affect the feed-backs and these feed-backs may play major roles in weather patterns as increasing synoptic statistical evidence indicate. In order to discover those abnormal surfaces, heat exchange computations are required.

A number of seasonal investigations of heat exchange have been carried out in the past by, *e.g.*, Jacobs (1951), Albrecht (1960), Mosby (1962), and Seckel (1962). However, the daily heat exchange computations are scarce. One of the best treatise on this subject is by Petterssen, *et al.* (1962) which deals with two components of heat exchange (sensible heat and latent heat) in relation to Norwegian cyclone models.

COMPUTATION OF HEAT EXCHANGE COMPONENTS

The heat budget and formulas for computation of different heat exchange components are given in the appendix to this paper. For a detailed discussion on the origin and accuracy of these formulas, reference is made to previous works of the present author (Laevastu, 1960, 1963). For computation of the local changes, heat advection is of primary importance. This advection is not considered in the present paper. It requires detailed knowledge of the surface currents. The present possibilities for prediction of those currents are also summarized by the present author (Laevastu, 1962).

The "hand" computation of heat exchange over large sea areas is time consuming. Use can be made of a number of nomographs which are found in Laevastu (1963). The heat exchange formulas are being programmed through a large computer in Monterey (Wolff, pers. comm.) and it is hoped to make use of those programs in the future.

Data

The meteorological data reported by voluntary observing and reporting merchant vessels form the basis for any heat exchange computation and oceanographic forecast. The data coverage is, in general, sufficient on frequented merchant ship routes, but is very scarce from areas away from these routes. No possibilities are in sight for improving these coverages, but it may be possible to improve the coverage from fishing grounds by recruiting more fishing vessels as observing and reporting vessels. The accuracy of the data leaves much to be desired. This situation could be improved by intensive instruction of the observers on board and by more careful and frequent checking of the ships' instruments.

The daily reported sea surface temperatures are too few for the construction of a detailed picture of daily surface temperature distribution. In some areas, the ten-day running averages could form a reasonably accurate basis as the sea surface temperature is much more conservative than the air temperature. Perlroth and Simpson (1962) concluded that the synoptic sea surface temperature chart for a period of a month can be constructed with a high degree of reliability. Such monthly charts can be used for present purposes by interpolating surface temperature by, *e.g.*, 5-day groups from one month to another.

The monthly average sea surface temperature charts for 1956 and 1957 (United States Bureau of Commercial Fisheries, Biological Laboratory at Stanford, 1962) have been used in the present work. Meteorological data for the present computations were taken from daily series of synoptic weather maps (United States Department of Commerce, Weather Bureau).

The air temperatures are unfortunately reported to a full Fahrenheit degree (or 0.5°C). As the sea-air temperature difference is used in most computations, it would be desirable to have both sea and air temperatures reported with ± 0.1°C. Great inaccuracies in the reporting of the dew point have been noted, and in many ship reports the dew point is entirely missing. These shortcomings are rectified to some extent by contouring the distribution of a given property before computing the averages by five degree squares.

The actual reported winds can deviate considerably, at times, from the isobaric gradient winds. Therefore, in the present work, the main emphasis has been put on the actual reported winds. An accurate estimation and plotting of the cloudiness data is difficult. In the present work, both the actual reported cloudiness and the frontal models of Bergeron have been taken into consideration in determining the cloudiness patterns. In case of scarcity of data, climatological data were used to fill the gaps.

Computation procedure

Each weather element necessary for heat exchange computations was plotted on different base maps and contoured and the average values for five degrees were computed from this distribution. After obtaining the averaged values of the elements by five degree squares, it would be possible to make punch cards and to perform heat exchange computations by computer; however, in most cases, only three parameters are used for individual computations and these are already written down on charts. Therefore, it was found simpler and more economical to "hand" compute the heat exchange components, using the nomographs.

Obviously, in computing the five degree square averages some involuntary smoothing of the values would occur, and the computed values might not exactly present the actual heat exchange in a given location and time. However, in most cases, we are not concerned with the actual values, but rather with the gradients and heat exchange patterns and the existing procedure is hence sufficiently accurate for this purpose.

Accuracy and errors

If exact values of the heat exchange components over the sea are desired, the computations should be made for 12-hr periods, utilizing the noon and midnight values of meteorological parameters. However, this work would be very time consuming and would offer little in improved accuracy because the inter-diurnal changes of properties are much bigger than the diurnal ones. These inter-diurnal changes along the western sides of the oceans are very much bigger than over the eastern sides. In most cases, it seems to be sufficient to make computation with synoptic data for a 24-hr period, using noon data. For several research purposes, more accurate computation would be desired and will be attempted when the formulas have been programmed for the computer.

The errors caused by inaccuracies in empirical and semi-empirical formulas are much smaller than the inaccuracies caused by the averaging procedure of meteorological elements and the errors in the meteorological reports themselves.

Estimation of the possible magnitude of errors caused by subjective analyzing of meteorological data was obtained by having the same computations done independently by two workers, using data with different origin (historic weather maps for the northern hemisphere and synoptic weather maps from the Weather Bureau, Honolulu Office). Considerable differences in individual values of heat exchange components were observed in some locations, however, the patterns remained approximately the same and the differences were relatively small at large gradients. The positions of the isopleths were, on occasion, considerably different in the areas where the distribution of given properties was flat.

Another set of computations was made by different workers, using the same data, but one set used two and a half degree squares, the other, five degree squares. Again, differences were noted but the patterns remained approximately the same. Obviously, the two and a half degree square computations revealed many more details.

The statistical treatment of the errors and accuracies of these computations is complex and too lengthy for this paper. References on this subject are made in an interim report (Laevastu, 1963) and in an extensive report in preparation. The general conclusion of this accuracy study may be briefly stated:

1. The accuracy depends largely on the accuracy, density and manipulation of meteorological data.

2. Considerable differences in subjective analyses between different workers can occur especially in Q_e and Q_h where the gradients are relatively flat.

3. However, most of the heat exchange features are of a large scale and relatively pronounced and persistent from day to day (Fig. 6 and 7) and the heat exchange computations are consistent and significant in respect to these large-scale features and in respect to sharper gradients.

EXAMPLES OF DISTRIBUTION OF DIFFERENT HEAT EXCHANGE COMPONENTS OVER THE NORTH PACIFIC

A few examples of the heat exchange components are presented in Fig. 1 to 11. The radiation received on 15 February, 1957 is shown in Fig. 1. This is given as insulation by given cloudiness

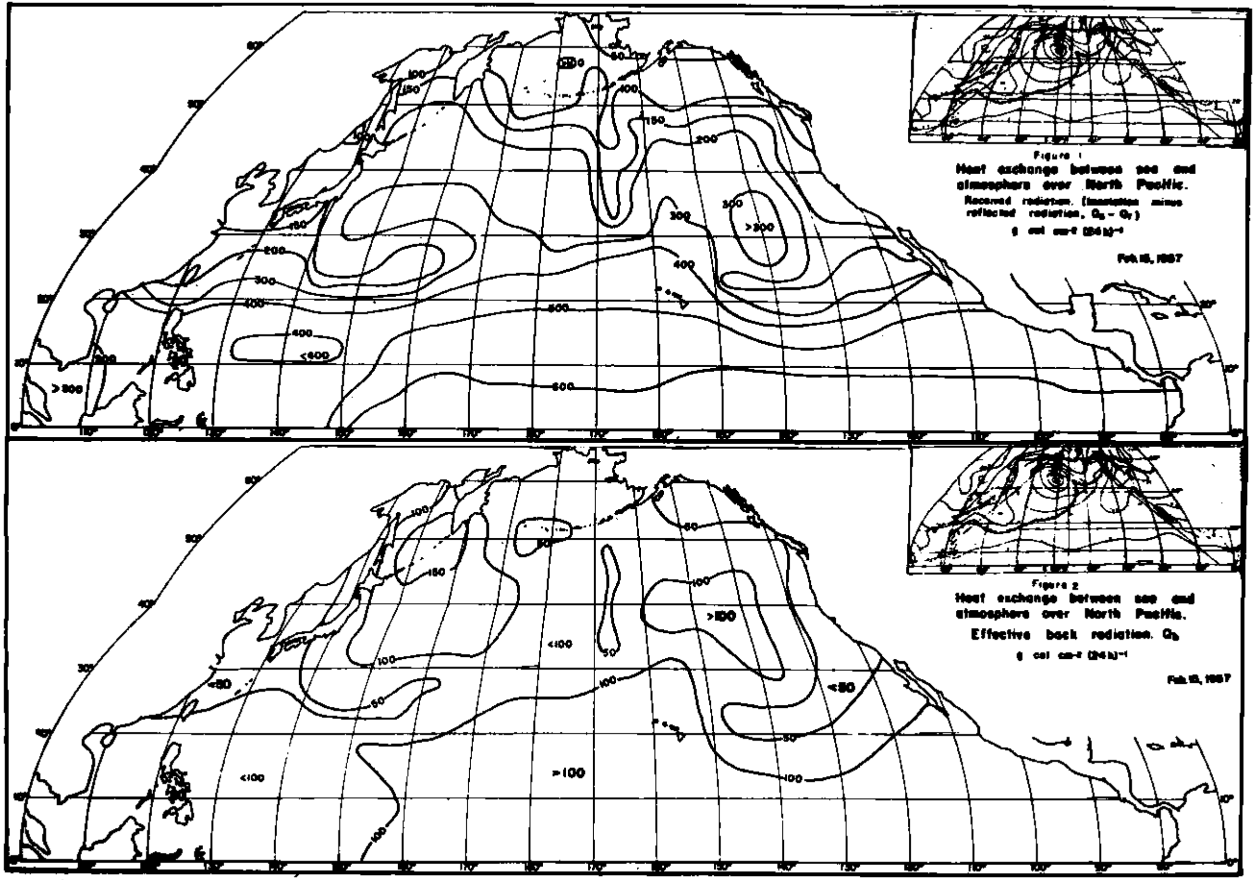

Fig. 1 and 2.

minus reflected radiation ($Q_s - Q_r$). In general, it has been noted that the sharper gradients of $Q_s - Q_r$ coincide with sharper gradients of sea surface temperature (oceanic fronts) and with higher cloudiness at atmospheric fronts.

The effective back radiation on the same date is given in Fig. 2. This heat exchange component is a function of cloudiness and of relative humidity and sea surface temperature. The transfer of sensible heat on the same day is given in Fig. 3. This component shows higher values and greater variability along the western side of the oceans. High positive values are found where relatively cold air dominates and low and/or negative values are found in warm sectors and in or near the center of anticyclonic circulations.

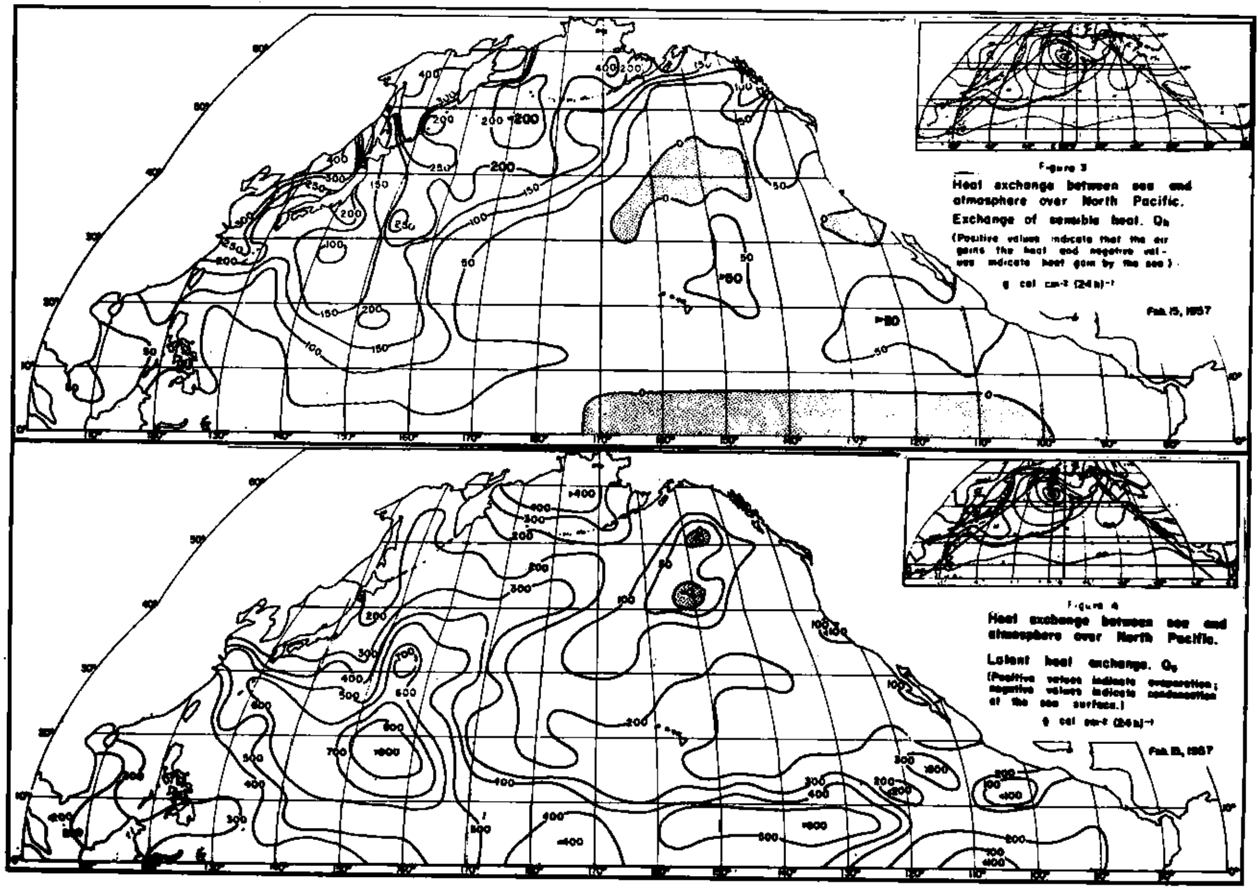

Fig. 3 and 4.

The latent heat of vaporization is the largest component of the transfer of heat from the sea surface to the atmosphere. The Q_e is shown on Fig. 4. Its patterns roughly coincide with the patterns of the transfer of sensible heat. The transfer of sensible heat and latent heat of vaporization/condensation are summed together and mapped as sea-air exchange (Q_a) in Fig. 5 to 7. The first of these figures show the Q_a in February, whereas the two following figures illustrate two consecutive days in May. Further discussions on those charts are found in Chapter 5. The total heat exchange (Q_I) is given in Fig. 8 to 11, illustrating the differences in various seasons. The total heat exchange is most pertinent to the oceanographic problems and is discussed in the next chapter.

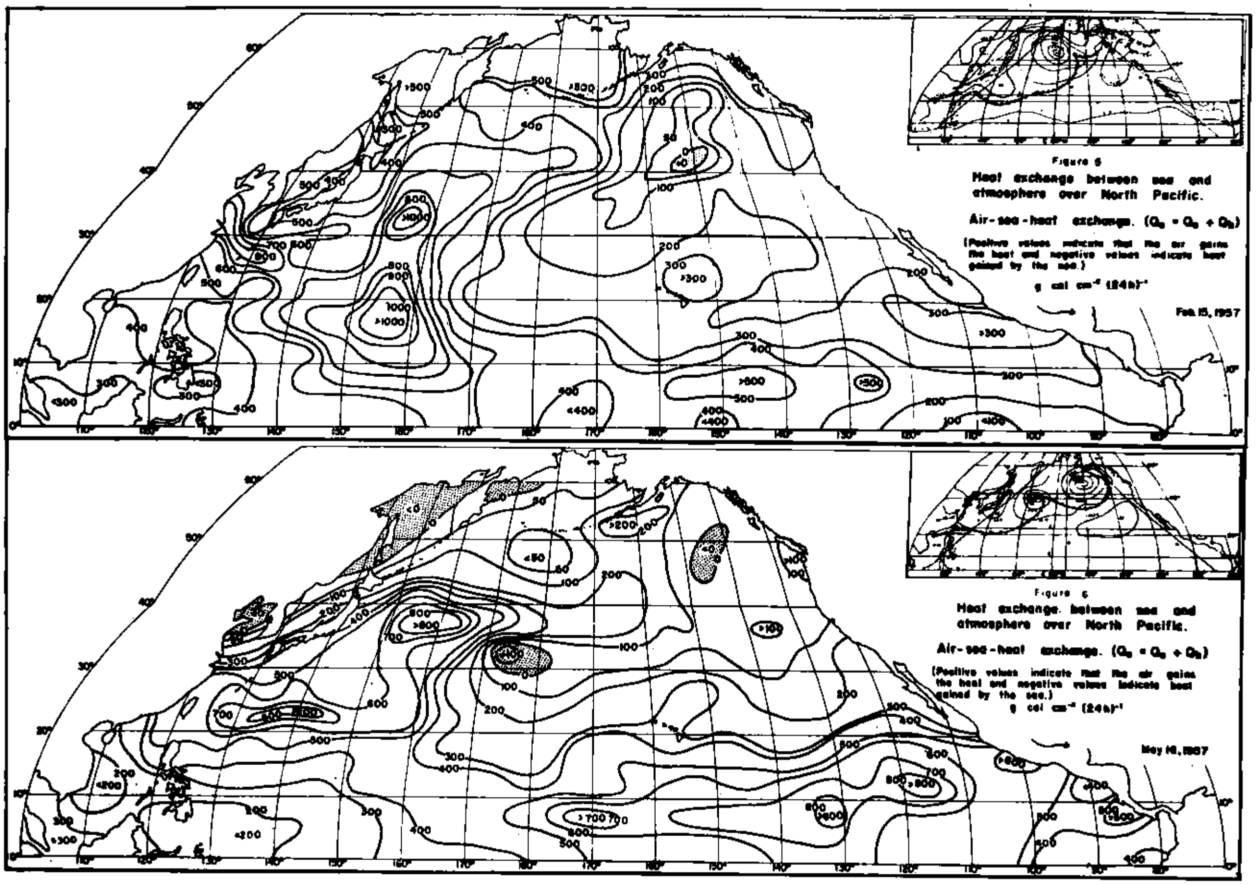

Fig. 5 and 6.

TOTAL HEAT EXCHANGE AND ITS EFFECTS ON THE OCEAN

The boundaries of the change of heat exchange from positive to negative values have several oceanographic consequences. In the positive heat exchange areas, the depth of the thermocline is determined mainly by forced mixing, *i.e.*, mixing by wave action. In the areas of negative heat exchange, the thermocline depth is determined by convective stirring, but only if this stirring reaches deeper than the forced mixing. A further consequence is the formation of deep and intermediate waters in highly negative areas of total heat exchange.

Sharper total heat exchange gradients are usually found in the vicinity of atmospheric fronts, in general between 30-40°N and along about 22°N lat, from the Asian coast to about 155°E, especially during the winter. These energy exchange gradients coincide roughly with the oceanic fronts and raise the question of whether the oceanic fronts are caused by the heat exchange differences or whether the heat exchange differences are caused by the fronts. This cause-effect principle is being investigated. Local cooling is also apparent at some places along the coast of Central America and off the Central and South Asian coast. Locally, this cooling might lower the temperature so that these locations may give the impression (by surface temperature distribution) of areas of coastal upwelling.

Of significance in many oceanographic problems, especially in respect to seasonal cooling and heating and in fluctuations of thermocline depth are the highly negative heat exchanges along the western sides of the oceans and the seasonal movement of the southern boundary of these negative areas. The charts of Q_e (*e.g.*, Fig. 4) indicate condensation of water at sea surface. Some further computations are necessary to determine whether this condensation might have any noticeable influence on the sea surface salinity.

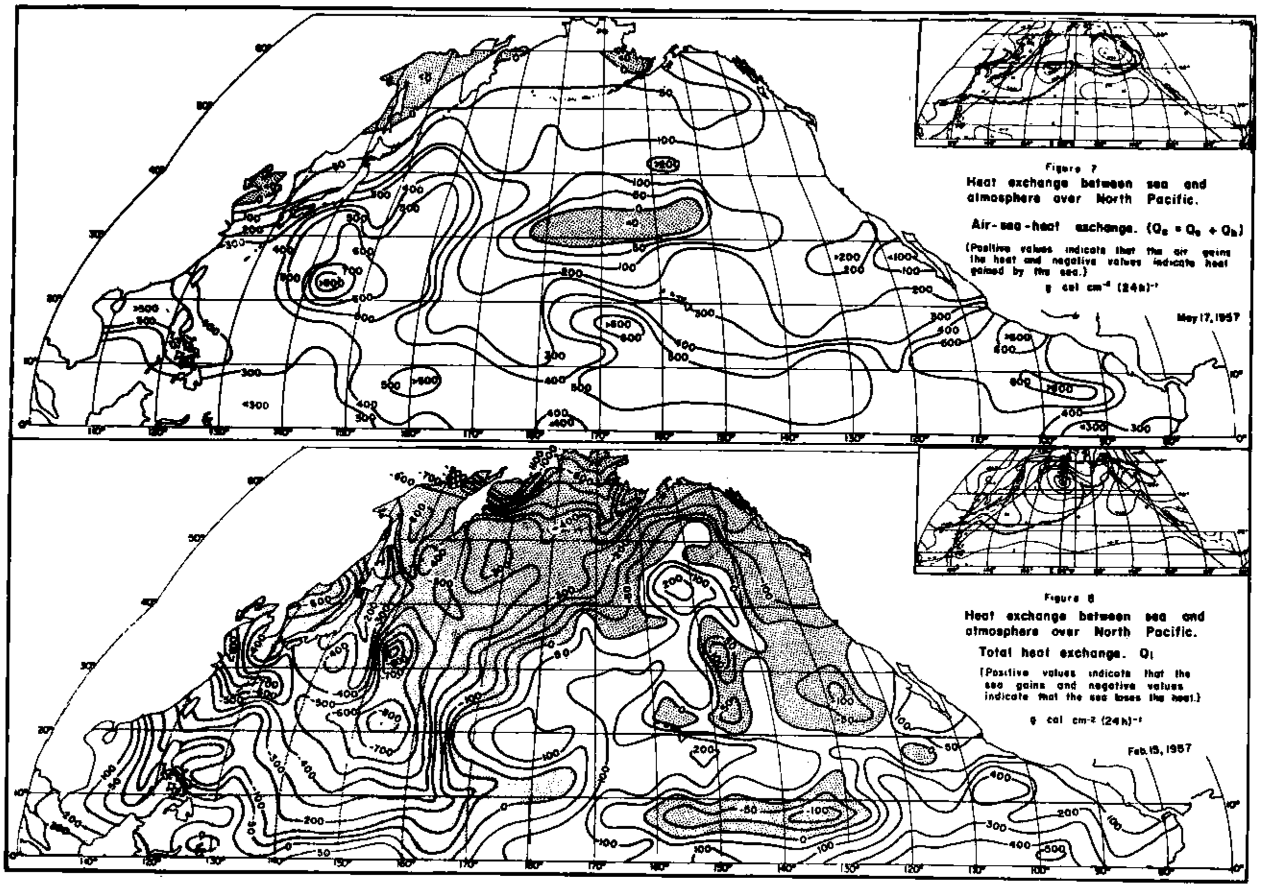

Figure 7

Heat exchange between sea and atmosphere over North Pacific.

Air-sea-heat exchange. $(Q_e = Q_e + Q_h)$

(Positive values indicate that the air gains the heat and negative values indicate heat gained by the sea.)

g cal cm^{-2} (24h)$^{-1}$

May 17, 1957

Figure 8

Heat exchange between sea and atmosphere over North Pacific.

Total heat exchange. Q_t

(Positive values indicate that the sea gains and negative values indicate that the sea loses the heat.)

g cal cm^{-2} (24h)$^{-1}$

Feb. 15, 1957

Fig. 7 and 8.

The results of the total heat exchange computations (Fig. 8 to 11) seem to point out some necessity for revision of presently accepted views on the formation of intermediate and deep waters in the North Pacific. This revision, based on total heat exchange, must of course be checked with oceanographic data.

The peculiar high loss of heat at low latitudes centered about 22°N, 155°E, and at 27°N, 162°E, on 15 February 1957 might indicate the general area of formation of intermediate water masses at such low latitudes. This area might also be the area of origin of the waters for countercurrents under the equatorial current system. It is, of course, necessary to investigate the persistency of negative Q_1 in this area. The areas of high losses of heat along the Asian coast during the winter (Fig. 8 to 11) might be the areas of formation of bottom waters. Whether these bottom waters reach the ocean basins or are mixed while passing over the shallow areas (*e.g.*, the China Sea) is an open question. This high loss of heat along the western coast is expected to cause local changes of bottom water temperature, changes in current patterns and variations of local convergences, which are important factors for fisheries. A more detailed investigation of these mechanisms in relation to heat exchange is contemplated. It seems possible that heat exchange computations, together with computation of advection might be specially useful for estimating the changes of water temperature along the western sides of oceans.

THE PATTERNS OF SEA-AIR EXCHANGE IN RELATION TO WEATHER

Though the description of the meteorological results of this work is not the prime purpose of this paper, some preliminary results are worth pointing out. Comparing the present data with the data obtained by Petterssen, *et al.* (1962), one can find considerable similarity in the patterns of

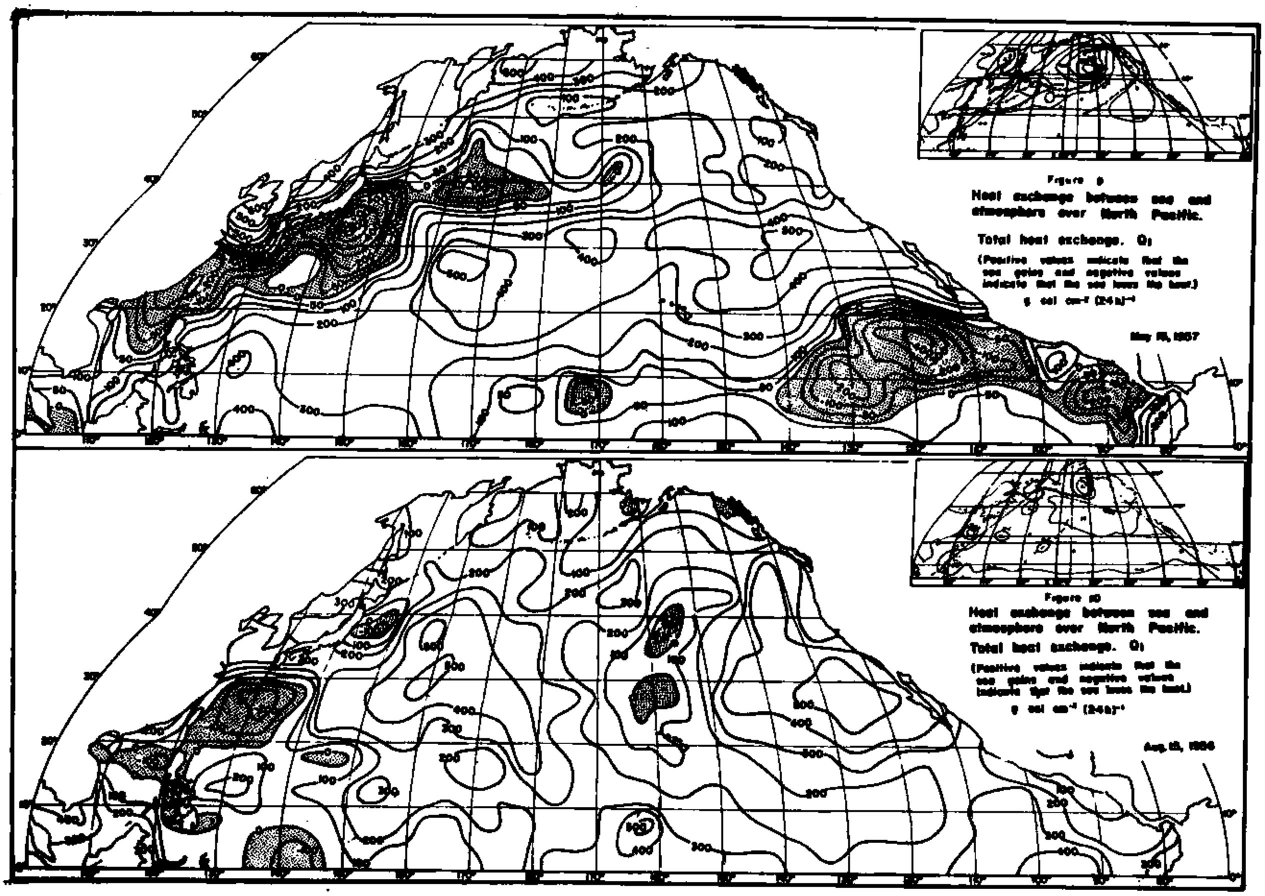

Fig. 9 and 10.

Q_a in the Northwest Atlantic and in the Northwest Pacific, despite the differences in grids and in formulas used. However, the warm sectors of Petterssen, Bradbury and Pedersen do not show the negative values of Q_a as our computations do. The forementioned authors conclude that their results indicate that the heat and cold sources, associated with eddy transfers of sensible heat from the ocean surface with the liberation of latent heat in the cloud systems, contribute significantly to the cyclone development.

Our data (not reproduced here) show some possible ways of how blocking anticyclones are formed, especially during the month of August. Some generalization of the data indicates that the formation of cyclones and anticyclones is directly related to the heat exchange. On the cause and effect principle, one could assume that cyclonic circulation should prevail over positive areas of Q_a and anticyclonic circulation on negative areas. This seems to be confirmed by our study (Fig. 12).

Petterssen (1956) stated that the major components of motion are along the gradients of the thermal advection and are such that cyclones move in a direction from cold to warm advection while anticyclones move in the opposite direction. This seems to be partly confirmed by our study. Strong winds are found to be predictable from Q_a distribution even in cases where they cannot be predicted from the rather flat distribution of pressure. The heat exchange patterns seem to be determined largely by the direction of the movement of the air in relation to the direction of the sea surface isotherms and it seems that the formation of cyclones and anticyclones is largely determined by the heat and cold sources at the surface. A further detailed investigation and possible proof of this should come from future studies.

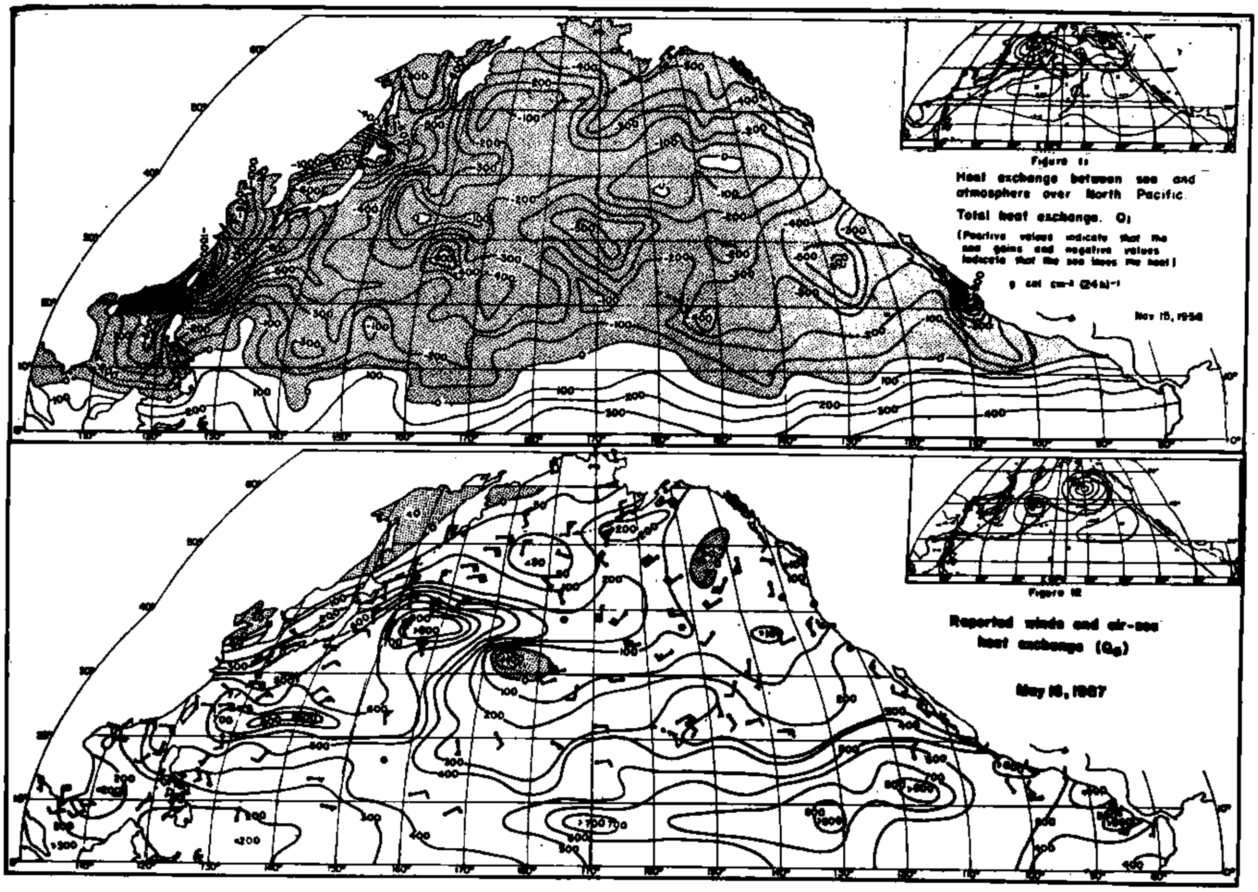

Fig. 11 and 12.

No comparison has as yet been made between the total heat exchange and the depth of the thermocline and/or change of sea surface temperature, because considerably more data are required for such a comparison. It seems to be certain, however, that the heat exchange computations will form a basis for future detailed oceanographic forecasts. These computations will also make it possible to forecast or prognosticate the surface current field. This attempt will be made within this project, but, unfortunately, the verification of these current prognoses will be only partial because no actual current data are available for open areas. However, the heat advection computed as a difference between measured and computed local change might prove to be a means, though very indirect, for confirmation of the current field.

ACKNOWLEDGEMENT

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REFERENCES

ALBERCHT, F. 1960. Jahreskarten des Wärme — und Wasserhaushaltes der Ozeane. *Ber. dtsch. Wetterdienstes* 9 (66): 1-19.

HELA, I. and T. LAEVASTU, 1962. Fisheries hydrography. Fishing News (Books) Ltd., London, 138 p.

HELLAND-HANSEN, B. and F. NANSEN. 1920. Temperature variations in the North Atlantic Ocean and in the atmosphere. Introductory studies on the causes of climatological variations. *Smithson misc. Coll.*, 70 (4): 1-408.

JACOBS, W.C. 1951. The energy exchange between sea and atmosphere and some of its consequences. *Bull. Scripps, Instn. Oceanogr.* 6 (2): 27-122.

LAEVASTU, T. 1960. Factors affecting the temperature of the surface layer of the sea. *Soc. Scient. Fennica, Comment. Physico-Mathem.* 25 (1): 1-136.

1962. The causes and predictions of surface currents in sea and lake. *Hawaii Inst. Geophysics* Rpts. 21: 55 p.

1963. Energy exchange in the North Pacific; its relation to weather and its oceanographic consequences. Parts I to III. *Hawaii Inst. Geophysics* Rpts. 29 to 31.

MOSBY, H. 1962. Water, Salt and heat balance of the North Polar Sea and of the Norwegian Sea. *Geofys. Publ. (Geophys. Norv.)* 24 (11): 289-313.

NAMIAS, J. 1962. Research on long range forecasting. *WMO Bull.* 11 (3): 128-131.

PERLROTH, J., and L. SIMPSON, 1962. Persistence of sea surface temperature patterns. *Mariners Weather Log,* 6 (6): 201-216.

PETTERSSEN, S. 1956. Weather analyses and forecasting. I Motion and motion systems. McGraw-Hill, N.Y., 428 p.

PETTERSSEN, S., D.L. BRADBURY and K. PEDERSEN. 1962. The Norwegian cyclone models in relation to heat and cold sources. *Geofys. Publ. (Geophys. Norv.)* 24 (9): 243-280.

SECKEL, G.R. 1962. Atlas of the oceanographic climate of the Hawaiian Islands region. *Fish. Bull., U.S.* 63 (193): 367-427.

U.S. BUREAU OF COMMERCIAL FISHERIES, BIOLOGICAL LABORATORY, STANFORD, CALIFORNIA. 1962. Monthly mean charts, sea surface temperature, North Pacific. *U.S. Fish Wildl. Serv. Circular* 134.

U.S. DEPARTMENT OF COMMERCE, WEATHER BUREAU. 1956, 1957. Daily series synoptic weather maps, Part I, Northern Hemisphere sea level and 500 millibar charts.

APPENDIX

FORMULAS FOR COMPUTING HEAT EXCHANGE BETWEEN THE SEA AND THE ATMOSPHERE

The following is a condensed summary of formulas for computing of heat exchange between the sea and the atmosphere. Detailed description and discussion of the formulas and procedures as well as the nomographs are given by the present author in other publications (Laevastu, 1960 and 1963).

The amount of heat used in the change of temperature in a given locality and time can be represented by Formula (1) (for notations and units used, see end of this summary):

$$(1)\quad Q_s + Q_B + Q_{wt} + Q_k + Q_f + Q_c - Q_b - Q_r - Q_h - Q_e + Q_p + Q_v = Q_1$$

The amounts of Q_B, Q_{wt} and Q_k are found in the major part of the oceans to be <1% of Q_s or even very much smaller and can therefore be ignored for practical purposes. The formula can be reduced to:

$$(2)\quad Q_s + Q_f + Q_c + Q_p - Q_b - Q_r - Q_h - Q_e + Q_v = Q_1$$

Q_f can be ignored in offshore areas and Q_p needs to be taken into account if there is a considerable amount of precipitation, if the temperature of the precipitation differs considerably from the temperature of the sea surface, and especially if the precipitation comes down as snow or hail. Q_c and

Q_e are computed with the same formula where the negative values give Q_c.

The following empirical formula was used for estimating insolation from the noon altitude of the sun, the length of the day and the cloudiness:

(3) $$Q_s = 0.014\, A_n t_d\, (1 - 0.0006\, C^3) \qquad [\text{g cal cm}^{-2}(24\ \text{h})^{-1}]$$

This formula is valid to $A_n = 75°$; above this value Q_{os} remains constant.

For short periods, the following formula can be used.

(4) $$Q_{os} = 1.9 \sin \bar{a} \qquad [\text{g cal cm}^{-2}\ \text{min}^{-1}]$$

For estimating radiation reflected from the sea surface, the following empirical formula, which is valid only for daily computations, was derived:

(5) $$Q_r = 0.15\, Q_s - (0.01\, Q_s)^2 \qquad [\text{g cal cm}^{-2}\ (24\ \text{h})^{-1}]$$

For the computation of short term (hourly or three hourly) albedo, a simplified formula can be used:

(6) $$Q_r = Q_s \frac{300}{\bar{a}} \qquad [\text{g cal cm}^{-2}\ \text{min}^{-1}]$$

For the computing effective back radiation, the linear formula of Lönnquist was adopted and a graph was constructed for the estimation of effective back radiation. The effective back radiation was corrected for the effect of cloudiness with Möller's formula:

(7) $$Q_b = Q_{ob}\, (1 - 0.0765\, C) \qquad [\text{g cal cm}^{-2}\ \text{min}^{-1}]$$

The modified formula of Rohwer was found to be the most accurate for estimating evaporation:

(8) $$E = (0.26 + 0.077\, V) \quad (0.98\, e_w - e_a) \qquad [\text{mm}\ (24\ \text{h})^{-1}]$$

Convective transfer of sensible heat was computed with the formula:

(9) $$Q_h = 39(0.26 + 0.077\, V) \quad (T_w - T_a) \qquad [\text{g cal cm}^{-2}\ (24\ \text{h})^{-1}]$$

When the differences $(T_w - T_a)$ or $(0.98\, e_w - e_a)$ are negative, sensible heat is transferred to the sea or condensation of vapor takes place on the sea surface. In these conditions, high stability of the air close to the sea surface is expected, and therefore, the following modified formulas were proposed:

(10) $$Q_c = 0.077\, V\, (0.98\, e_w - e_a)\, L_t \qquad [\text{g cal cm}^{-2}\ (24\ \text{h})^{-1}]$$

(11) $$Q_h = 3\, V\, (T_w - T_a) \qquad [\text{g cal cm}^{-2}\ (24\ \text{h})^{-1}]$$

Notations and units used

A_n - Noon altitude of the sun (degrees)
E - Evaporation [mm $(24\ \text{h})^{-1}$]
e_a - Water vapor pressure of air (mb)
e_w - Saturated water vapor pressure at the temperature of the water surface (mb)
L_t - Latent heat of evaporation (g cal)
Q_c - Heat transfer by condensation of water vapor
Q_b - Effective back radiation from the sea surface (long wave radiation)
Q_B - Heat from the bottom of the sea
Q_e - Transfer of latent heat of vaporization
Q_f - Heat transferred by fresh water run-off

Q_h - Convection of sensible heat to and from the atmosphere
Q_k - Heat released by chemical processes
Q_l - Total heat exchange
Q_{ob} - Back radiation by clear sky
Q_p - Heat transferred by precipitation
Q_r - Reflection back from the sea surface (albedo of the sea surface)
Q_s - Total incoming radiation (solar and sky)
Q_{os} - Total incoming radiation by clear sky
Q_v - Heat transfer by advection
Q_{wt} - Heat from the dissipation of wind and tidal energy
T_a - Temperature of the air (°C)
T_w - Temperature of sea surface (°C)
t_d - Length of the day from sunrise to sunset (minutes)
t_h - Time in hours
V - Wind speed (m sec^{-1})
$\bar{a}$ - Average solar altitude (degrees)

I-5

NOTES ON THE PROBLEM OF PREDICTING NEAR SURFACE TEMPERATURE GRADIENTS IN THE OPEN OCEAN

By

C.O'D. Iselin[1]

ABSTRACT

Some of the factors are discussed which will have to be taken into account if useful predictions are to be made of the near surface temperature structure in the open ocean. A preliminary test has been carried out in the trade wind latitudes of the Atlantic with encouraging results.

Until recently it seemed rather hopeless to display near surface temperature conditions in the open ocean, except on a climatological basis. However, the availability of large computers and electronic contouring machines has very much changed the situation. In fact, the U.S. Navy is already preparing frequent synoptic northern hemisphere maps of a number of oceanographic parameters on an experimental basis.

In the case of the North Atlantic a most useful series of charts of average temperature at 200m has recently been published by Schroeder (1963). By combining this with monthly or shorter period surface temperature maps one can immediately know the difference in temperature between the surface and 200m on a seasonal and geographical basis.

If one also has available seasonal layer depth charts, then one has three points for the construction of a temperature-depth curve of the near surface waters. Since temperature at 200m varies seasonally only slightly, except in the vicinity of the permanent surface currents, and since the horizontal shifts of these can be deduced from say 10 day averages of surface temperature, the problem, to take an optimistic view, reduces itself to how best to deal with the seasonal and shorter period changes in layer depth, that is to say, in the thickness of the nearly isothermal surface layer.

Unfortunately, the file of temperature data from the North Atlantic available to Woods Hole is not yet sufficiently complete on a seasonal and geographical basis to permit monthly average layer depth charts to show adequate detail. While about 500,000 observations have accumulated and are incorporated in the Schroeder charts, and for each of these points of observation layer depth has been recorded, studies now in progress at Woods Hole make it clear that two months and possibly more will have to be combined to produce a useful set of charts showing average seasonal changes in layer depth.

This is a more variable quantity than either surface temperature or 200m temperature. The variability of layer depth is not only due to internal waves, but it also changes more gradually as a result of the present and previous winds. Especially the strength and direction of winds stronger than about 12 knots are important. In short, in the case of layer depth the ocean to as yet an unknown degree has memory for the past weather. A computer starting off with average layer depth values will have to be told how to change these in view of the recent and expected weather. It is hoped that a start on the quantitative aspects of this part of the problem can soon be made on the basis of continuous data from moored temperature sensing buoys. However, from the biological point of view it might be sufficient to know layer depth on a week by week basis to within 10%. Over very large areas, especially in the tropics, such accuracy is now achievable on

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[1] Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA. Contribution No. 1466 from the Woods Hole Oceanographic Institution.

an empirical basis.

To summarize, it does not seem too difficult a task to learn how to instruct a computer with knowledge of existing and recent winds, and cloud cover to correct the climatological temperature information in the near surface waters of the open ocean so as to produce more nearly synoptic maps.

This is certainly true under more or less average weather conditions. It will be easier to do well when the sea is losing heat to the atmosphere than during nearly calm weather in spring and summer. A modest data gathering network for the water half of the system will certainly be useful and the abilities of ships to report both meteorological and oceanographic data on a daily or shorter basis should certainly be improved, but the writer after considering these problems for some time remains optimistic about the successes that might be achieved in the near future.

Obviously the ship observation and the radio telemetering buoy program will require the same sort of international cooperation that has prevailed in meteorology for many years. As each nation develops oceanographic predicting techniques for the waters having special importance to its fisheries, and as methods and communications are standardized, it will become easier to feed' the whole ocean wide task to a few major forecasting centers equipped with suitable electronic facilities.

The payoff will come when a proper marriage between meteorology and oceanography has come about. For too long each subject has been pursued more or less separately. One bottleneck in long range weather forecasting has been the sparcity of information from over the oceans. As Namias (1963) has so clearly shown, the ocean often acts as a flywheel that causes weather patterns to persist over very large areas. If the reliability of oceanographic forecasts could be improved so as to make longer range weather forecasts a possibility, then radical increases in the useful lengths of both types of forecasts becomes a probability.

So as to make these general remarks a little more specific and to perhaps throw additional light on the problem as seen by a physical oceanographer, a brief summary of the author's preliminary conclusions after returning recently on a passage from Cape Town to Woods Hole on *Atlantis II* may be of interest. The southeasterly trades were picked up two days out of Cape Town and the wind remained nearly aft for roughly 7000 miles until the ship was approaching Bermuda. On this long northwesterly slant across the whole of the Atlantic trade wind system the wind velocity varied only from about 10 knots to about 14 knots. Since our speed through the water averaged 12 knots, sometimes we were going a little slower and sometimes a little faster than the wind.

Each morning at breakfast time a prediction was made of the temperature-depth curve that would be observed during the afternoon. As far as the equator there was no advance, closely spaced information on temperature at 200m or on layer depth. The prediction simply assumed that both values would be somewhat less than in the corresponding parts of the North Atlantic during early spring. Since the ship left Cape Town on November 22, as far as the equator the surface layer was gaining heat quite rapidly. Thus a critical question each morning was whether or not a diurnal thermocline would develop within the wind stirred surface layer formed during the previous night. This depended on whether or not the early afternoon winds exceeded 12 knots and on cloud cover. While at sea the author was careful not to inspect the previous hourly bathythermograph lowerings. In other words, all that went into the forecast was the date, the latitude, and the wind and cloud cover in the early morning. Since the wind direction and velocity hardly varied at all during daylight hours, cloud cover was the critical factor in determining whether or not a diurnal thermocline would develop during the afternoon on the majority of days having 12 knot winds. Having had only a few days since returning to Woods Hole, the writer cannot now say just how successful his predictions were. This will be the subject of a later paper, but enough bathythermograms have been looked at to state that he did better in the North Atlantic where the surface layer was on the average being cooled than in the latitudes where the opposite conditions prevailed.

It is clear that the near surface thermal structure on the direct course from Cape Town to Barbados is simpler and more uniform south of the equator than on a corresponding course in the North Atlantic. The currents are weaker in the South Atlantic and there are fewer minor temperature fronts. In the North Atlantic we probably have the most difficult ocean for predictions, but this is also the ocean that we know the most about.

REFERENCES

NAMIAS, JEROME. 1963. Large-scale air-sea interactions over the North Pacific from summer 1962 through the subsequent winter. *J. geoghys. Res.* 68 (22): 6171-6186.

SCHROEDER, ELIZABETH H. 1963. Serial Atlas of the Marine Environment, Folio 2. North Atlantic Temperatures at a Depth of 200 Meters. *Amer. Geographical Society*, 11 p.

I-6

FORECASTING ENVIRONMENTAL CONDITIONS IN THE FAROE-SHETLAND CHANNEL REGION

By

J.B. Tait[1]

It can be said at once that until hydrographical, or hydrological, parametric observations can be taken on some such pattern as that represented by the daily intake of meteorological data, effective forecasting of the marine environmental conditions of fish-life on which there is reason to believe that life to be closely dependent for its existence, maintenance, and general well-being, is scarcely a practicable proposition. That it is a desirable and practical objective, however, particularly in regions of fisheries significance, follows from certain considerations.

There can be no gainsaying, for instance, the significance of the temperature of the sea in almost all aspects and at all stages of fish life. A fundamental question, however, is whether it is always temperature *per se* which is the determining factor, in the spawning process for example, or environmental heat, of which temperature is an index. An investigation by Tait (1951) has suggested perhaps the greater relevance of the latter.

These and related studies, however, in respect of other parameters in the marine environment, such as, salinity, transparency, nutrient salt content, etc., indicate that all such factors are in fact and in their effects, fundamentally and collectively linked in the common factor of water-masses of differing physical and biological characteristics.

Still the most fundamentally reliable index of water-mass differentiation is salinity, which, although not strictly a physical property of the sea, in the terms in which it is rendered, is sufficiently close to such to justify its acceptance empirically as an index of water-mass types.

On this basis, long term researches in the Faroe-Shetland Channel region have revealed at least five distinct water-mass types to be found there, and it is the manner of their occurrence that suggests the distinct possibility of forecasting them, under the primary condition of systematic observation.

The oceanic water-mass is the only permanent water-mass of the Faroe-Shetland Channel region, occurring at all times as the uppermost 300-500 m layer. Borne by the North-Atlantic Drift Current, it is normally characterised by a core of relatively high salinity, and the boundary salinity of this core may be taken as an index of the quality of the oceanic water-mass. This, over a period of time of the order of 25 years, may vary between salinities of 35.25 °/oo and 35.45 °/oo. The variation is gradual, which lends to this particular phenomenon the aspect of climatic change in the sea, and the fact that it is gradual anticipates the possibility of forecasting it, provided observations in the region are sufficiently regular and systematic.

Occasionally, but again spread over a period of from 4-6 or 7 years, the oceanic water-mass of the Channel region includes water which, by its salinity (also by its biological content), of upwards of 35.50 °/oo to nearly 36.00 °/oo, as happened in 1933-34, derives ultimately from the Mediterranean Sea. The intrusion is relatively gradual, waxing to maximum intensity in about mid-period, and waning to extinction at the end of the period. In this circumstance again obviously lies the possibility of forecasting the phenomenon by systematic observation.

The bottom water-mass of the Faroe-Shetland Channel region is normally bottom Norwegian Sea water of salinity 34.90 °/oo to 34.94 °/oo, but usually fairly constant at 34.92 °/oo. This mass, however, can on occasions be totally replaced, at the peak of the 4-6 yearly phenomenon, by the intrusion, at first gradual, of one, but sometimes two, types of Arctic water-mass, the first,

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intermediate Arctic water, designated by salinities of 34.85 °/oo to 34.89 °/oo, and the second, surface Arctic water (possibly originally at least sub-Polar water) of salinity 34.77 °/oo to 34.84 °/oo. These are distinctive types; their advent and departure are characteristically gradual as that of the Mediterranean type in the oceanic water-mass, and the phenomenon of their substantial occurrence - they can appear intermittently as mere traces - lasts usually for a period of again from 4-6 or 7 consecutive years. This particular phenomenon has been shown apparently to relate to certain fisheries phenomena (Tait and Martin, this symposium).

As said in the beginning, however, the possibility of effectively forecasting these phenomena, is conditional upon observations being taken systematically and regularly, comparable with those of meteorology. The prospect of introducing such intensity and system into oceanographical observations is only now apparently coming within reach, as it were, through the development of the automatically recording, and probably telemetering, oceanographic buoy, a development which seems unquestionably to hold enormous promise for the future.

REFERENCES

TAIT, J.B. 1951. On the application to marine research of the meteorological concept of accumulated temperature. *J. Cons.*, 17 (2): 111-120.

TAIT, J.B., and J.H.A. MARTIN. 1965. Inferential biological effects of long-term hydrographical trends deduced from investigations in the Faroe-Shetland Channel. *This symposium, Contribution No. H-9.*

I-7

THE POSSIBILITY OF FORECASTING OCEANOGRAPHIC CONDITIONS IN NORTHWEST EUROPEAN WATERS AND THEIR SIGNIFICANCE FOR FISHERIES

By

Jens Eggvin[1]

ABSTRACT

Oceanographical material from research ships, fixed oceanographical stations, coasting vessels, liners and weather ships has been used together with meteorological material in order to follow the flow of individual water masses. An attempt has been made to forecast hydrographic situations which, according to experience, influence fisheries in various ways.

In physical oceanography systematic and yearly observations are only available for a relatively short number of years and for those areas of the ocean that have been most thoroughly examined.

Complete and repeated observations at relatively short intervals in suitable positions are of great importance when the aim is to secure clues to certain causal connections that can supply the solution to oceanographic problems of general, as well as of special, character. This is the case, particularly in the solution of many important problems within oceanographic fishery research.

With regard to fishery research, it has been our aim, among other things, to be able to foretell something with reference to the fishing. In order to contribute hereto on an oceanographic basis, it is essential that the work be carried out on two fronts.

First, observations must be made on the oceanographic conditions during the actual fishing and on the course of the fishing. These facts, together with previous knowledge must then form the basis for the theories that fishing is dependent on certain oceanographic conditions.

Second, it is necessary to be able to foretell the hydrographic conditions during the coming fishing season.

If we are, however, to be in a position to foretell how conditions in the sea will develop some time in advance, then it is of primary importance to have equipment that allows us to follow the developments in the sea from month to month and week to week. For economic reasons, research vessels cannot operate year round in the different areas, but can, at best, only visit certain places a few times during a year. It would be of great assistance if we could supplement this with observations made at shorter intervals. We would then be in a better position to know when any comparatively great changes in the distribution of the several types of water have taken place, and what changes in different oceanographical parameters are supposed to take place. Fixed oceanographic stations of different kinds would here be of great help.

Sometimes nature herself can speak to us more clearly than usual, and if we are at the time able to make suitable observations, interesting causal connections may be discovered. For example, the southeasterly storms, prevailing in the latter half of January and February 1937, transported great masses of cold water of low salinity towards the southern Norwegian Coast from the Kattegat and the Baltic. This gave rise to a strong current which, in February, caused serious difficulties for the spring herring fishery. On account of its low salinity, the water was considerably lighter than the underlying, warmer but more saline bankwater. Even if this surface water was further cooled off the Norwegian Coast, it could not become heavy enough to sink down and be substituted by warmer water from beneath. Consequently, this surface water had to give up so much of its heat to the air that

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the freezing point was reached. This resulted in ice obstruction and the killing of fish (on one day 50,000 kg) in well boats bound for Oslo, despite the fact that the mean air temperature in February 1937 remained normal along the Skagerack Coast.

The detailed movement of the water masses in question both in extent and depth, from the time it was observed at Ferder on 30 January to when it reached the Møre Coast on 19 March, 48 days later, was successfully followed with help from various investigations, cruises with research ships, the recording of sea surface temperature and collection of samples for salinity from coasting vessels and from fixed oceanographical stations (Eggvin, 1940).

By an unavoidable freak of nature, this frigid cold water front of low salinity, made its way along the south and west coasts displacing the salter and warmer water that had been present from 0-40 m earlier. On 7 February at about 0300 hr, the front passed off Lillesand. It reached Ogna at Jaeren at 1200 hr on 18 February and passed Jaerens Reef 42 hr later. At 2145 hr on 26 February the front was 5.5 nautical miles north of the south end of Karmøy, and at 0330 hrs on 9 March it reached Askvoll in Sogn.

The average speed of the current along the various stretches of the coast was from 13 to 25 cm/sec (6.5 to 12 nautical miles a day). The average speed for the whole distance was 19.4 cm/sec or 9.75 nautical miles in the 24 hr.

As the cold water moved westwards and northwards along the coast displacing the bottom waters on the banks, the herring fishery that was being carried on at that time, suddenly ceased. It appeared that the herring left the banks and sought the deeper, warmer water.

Petterson and Ekman (1891) have shown that herring avoid this cold Baltic water along the west coast of Sweden. Hjort (1896) and Runnstrøm (1933) proved the same for the Norwegian west coast. Runnstrøm points out that, when the effects of the Baltic cold water are especially great, the quantity of herring in the spring herring fishing areas can, in some years, be reduced to a half of which, from the biological point of view should have been present. The oceanographic conditions during the spring herring fishery are, therefore, undoubtedly of great economic importance.

It has also been possible to follow such Baltic water fronts in summer, but in that season the water coming from the south was warmer than that displaced. It flowed into the fjords of the west coast bringing with it shoals of sprats, according to information from Mr Bjerkan.

The above example shows how oceanographical and meteorological conditions prevailing in the Baltic and the Skagerack at one time can indirectly influence the herring fishery on the Norwegian west coast later on. We have used the knowledge gained here in different ways concerning icedrift, front-passages at different places and influence on fisheries.

Since we have succeeded through a combination of several research methods in following, in detail, the movement of an individual mass of water over a stretch of several hundred kilometers, it must be presumed that this can also be carried out at other places, even if the oceanographical conditions should not be as favourable as they were in the area in question.

If we follow the water masses from the south coast of Norway to the Murman Bank, we will see how the boundary line separating the Atlantic water from the coastal water is found deeper and deeper as the water masses move northward and become mixed with each other. Along most of the Norwegian Coast, there is a transition layer, but off the coast of East Finnmark and farther east, the water has become almost homogenous from surface to bottom. This fact is of great practical importance for both fisheries and climate. Because of the great instability of the water masses from surface to bottom during winter along the Finnmark Coast, no ice can form there, whereas, along the south coast where there is a light water layer on the top of a heavier one, ice can form in spite of the air temperature there being so much higher than in Finnmark during winter.

It is known that there are considerable variations from year to year in the influence of the Atlantic current off the northern coast of Norway. Off the coast of East-Finnmark there is a border-area where the water from the Atlantic is strongly mixed with the colder eastern water. The position of this area shifts from year to year and it appears that the fishing at Finnmark is greatly influenced by its position. With a strong inflow of Atlantic water, certain temperature limits *e.g.* 3° or 4°C will be forced eastward and northward. On the other hand, with a slighter inflow the same temperature limits will be found to the westward and nearer the land.

At the same time, the fluctuations in the appearance of the fish varies with the oceanographic conditions. With much water from the Atlantic (warm water) present, the spring cod fishery (immature cod) takes place far from the land at East Finnmark, and to the east on the banks off Fishermans Peninsula and farther eastward. Then the distance to the fishing grounds is too great for the small vessels and open boats. If, on the other hand, little Atlantic water is present, then the above mentioned temperature limits will be found farther west and nearer the land. The fishing then takes place nearer land and over a great area of the Finnmark coast which is more favourable especially for the smaller vessels.

The theory that the spring cod fishery along East Finnmark is dependent on certain temperatures in the border area between Atlantic and eastern colder waters was published in the Lofoten report of 1936 (Lofotfisket, 1936). Observations have supported the theory.

Observations made before the spring cod fishery at Finnmark begins, should help to forecast whether the position of the above mentioned border area will be situated far to the east or to the west. The following is an example of this.

Observations from a cruise and from the fixed oceanographical stations showed us that the deep water along the Norwegian Coast in late autumn 1938, and early 1939, was very warm. This was the case, especially off Lofoten, Vesterålen and West Finnmark. Since some of this water flows on eastward to the coast of East Finnmark, the temperature should remain comparatively high there, especially while the salinity was lower than normal in the upper 50-75 m. Here, the water was light compared with the underlying layer. The vertical circulation brought about by the winter cooling would, therefore, be hindered to a certain extent. Such a state would hasten the cooling of the surface water but retard the cooling of the underlying layers.

The following forecast was printed in the Lofoten report in January 1939:

> "As conditions in the sea off the north of Norway, and to the south are, at present, it must be expected that the temperature of the deep water will remain relatively high during the spring cod fishery 1939 at East Finnmark which takes place from April to June. Consequently, it will be necessary to go far offshore (northwards) and far to the east in order to arrive at the above mentioned favourable temperature limits. From previous experience there is every reason to believe that there will be little chance for the small vessels to make reasonable catches during the coming spring cod fishery (loddetorsk) off East Finnmark".

A cruise to Finnmark by the research ship *Johan Hjort* during the actual fishing season together with observations made at the fixed stations at Ingøy and Vardø in Finnmark satisfactorily answered the question as to the correctness of the prediction.

The Lofoten cod-fisheries (February-April) takes place, as is known, in an intermediate layer between the relatively cold and slightly saline coast-water and the underlying saline and warmer Atlantic water.

The depth at which this layer is situated during the fishing varies from year to year while the fluctuations during the same year are considerably less. A strong continuous wind can, of course, cause changes in the depth of this layer but after the cessation of the wind it reoccupies its approximate depth.

The depth at which this layer will be situated during the fishing season is of the greatest importance. If it should be situated comparatively deep, then the fishing takes place in deep water and far offshore. If, on the other hand, the intermediate layer is found at more shallow depths, then the fishing takes place in shallow water, and near land.

Since a very great percentage of the Lofoten fishing is carried on from small vessels and open boats, it depends, during this rough period of the year (February-April) much on the distance to the fishing grounds. Further, if the intermediate layer should be shallow, then the fishing is best at East Lofoten, otherwise the chances are best at those fishing grounds situated far out in the fjord, West Lofoten.

Winter cooling causes the formation of this layer. The depth at which it will be situated depends on stability conditions. The intermediate layer remains shallow if the salinity of the upper layer is comparatively low and the winter cooling during the autumn and not before the winter is slight (high air temperature). Further it depends on the relative quantity of coastal water and Atlantic water.

In 1935, 1940 and 1956 the salinity in the surface water during the late autumn was comparatively high and the upper 50-75 m was almost homogenous, and the winter cooling could press the transition layer deep down in the sea. Forecasts of the depth of the transition layer in the Vestfjord (Lofoten) have been satisfactory.

During the winter of 1963, with great negative anomalies in the air temperatures and relatively low cloudiness, the cooling of the sea by radiation, conduction and also partly by evaporation has resulted in very low sea temperatures in wide areas and heavy formations of ice in the Baltic, the Kattegat and the Skagerack (Eggvin, 1963).

The density of the water in the south-eastern part of the North Sea was greater than in the other areas including the Norwegian Channel. Taking the direction of the current into consideration, it was anticipated that the deep- and bottom-water of the Norwegian Channel would be renewed by that heavy and much colder water. Further, it was expected that it would take a relatively long time (months) before normal temperature conditions could be established again in the deepest parts of the Norwegian Channel. This came true. Even in January 1964 there still remained relatively cold water which had flowed into the Channel during the previous spring.

The very cold water in the southeastern part of the North Sea and off the west and south coast of Norway hampered fishing in those areas. This situation was expected on the basis of previous experience.

SUMMARY

With the help of different research methods, it has been possible to follow individual water masses penetrating as fronts along the Norwegian Coast. Since these water masses can influence fisheries (herring and sprats), knowledge of their origin and character and of the influence meteorological agencies have on their transport and stability, has been of practical value.

Off the coast of Northern Norway (Finnmark) there is a border-area where the Atlantic water is strongly mixed with the colder eastern water. The position of this area shifts from year to year and it appears that the spring cod fishery is greatly influenced by its position. Forecasts of this position have been made.

As the Lofoten cod fishery (February-April) takes place in the transition layer between the relatively cold and slightly saline coastal water and the underlying saline and warmer Atlantic water, forecasts of the depth and, in part, the thickness of this layer have been of interest to the fishing fleet and the fishing industry.

The heavy cooling of the sea during the winter 1963 resulted in abnormal oceanographical conditions, partly of long lasting character as expected and also influenced some of the fisheries.

REFERENCES

EGGVIN, JENS. 1940. The movements of a Cold Water Front. *Fiskeridir. Skr. Havundersøk.* Vol. VI, No. 5, 1940.

1963. Tilstanden i havet under den unormale vinter 1963. *Fisk. og Hav.*, No. 1, 1963.

HJORT, JOHAN. 1896. Hydrographic-Biological Studies of the Norwegian Fisheries. *Videnskabsselskapets Skr.* I math.-naturv. klasse. No. 9, Oslo 1896.

LOFOTFISKET. 1936. Årsberetning vedk. *Norg. Fisk.* 1936, No. 2.

PETTERSON, O., and G. EKMAN. 1891. Outlines of the Hydrographic of the Skagerack and Cattegat. K. *Svenska Vetensk. Akad. Handl.* Vol. XXIV, No. 11, Stockholm 1891.

RUNNSTRØM, S. 1933. Sildeundersøkelsene 1931-32. Årsberetn. vedk. *Norg. Fisk.*, 1932, No. 1, Bergen 1933.

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SOME ASPECTS OF OCEANOGRAPHIC PREDICTION

By

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The purpose of this paper is to discuss several problems which arise in connection with the general problem of the development of oceanographic forecasting techniques. Of course, possible solutions to these problems will to a large extent be guided by the particular use to which the environmental information is to be put, and there is a broad possible spectrum of such applications. There are two requirements, however, that appear to be common to almost every attempt to extrapolate oceanographic conditions into the future: the nature of the sea surface, and the three dimensional structure of the ocean's physical variables, with special emphasis on temperature and salinity. Since the first of these has been thoroughly discussed on many occasions, this paper will confine itself to the latter.

Although there are doubtless many areas in the ocean of sufficient stability in time to permit the preparation of useful predictions by recourse to analysis of historical data alone, in those areas where significant time variability exists it seems clear that accurate predictions will only be developed if continuing surveillance of oceanographic conditions is maintained in order to provide data to use as initial conditions. I therefore believe that we can divide the process of providing environmental predictions on a synoptic basis into four separate phases:

1. The collection and transmission of the basic data.

2. The analysis of the data to define the present situation.

3. The prediction of the present situation in time.

4. The application of both the analysis and prediction to the particular practical problem being considered.

With regard to the first of these, the collection and transmission of data, it appears that the first problem is to define the work "synoptic" where oceanographic conditions are concerned. Clearly we are not dealing with a medium where time scale phenomena are comparable to those in the atmosphere, for instance. It is important to know over what period of time significant time changes do not occur, so that the data may be lumped together and considered as occurring at approximately the same time. This period will not be the same for all oceans, nor even the same for areas within an ocean. Several studies have been or are being made of this problem; one such study, conducted by the Travelers Research Center, was made for the western North Atlantic. Considering the accuracy and time and space frequency of data now available, it was found that a period of about 1 1/2 days is appropriate for very active areas such as the Gulf Stream, a period of three days for reasonably active areas such as the North Atlantic drift, and a period of 15 days or more for inactive areas well away from major current systems.

The second consideration in the collection of data is the spatial variations in the medium, which will affect the spacing of platforms from which the data is to be collected. Here again, great variability in observational requirements in the space domain is to be expected. Since so far attempts at synoptic oceanography have been dependent mainly on data collected from ships of opportunity in one form or another, there has been little control over this factor. One obvious answer is to develop platforms over which we do have control, such as aircraft and buoys; both of these approaches are being pursued. From those areas which prove to be more homogenous horizontally than expected, it will no doubt be possible in the future to require fewer observations than we either receive now or will receive in the future. At the present time, however, observational data are so

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scarce that we should collect them wherever and whenever possible, so that criteria for spatial distribution may be determined.

A third problem in data collection is that of what to collect and how accurately, and here the problem is inextricably linked with available and projected instrumentation capability. One of the things we really would like to assess and predict is the three dimension thermohaline structure. Since our instrumentation capability does not permit this measurement on a routine scale at the present time, we shall have to be content with three dimensional temperature measurements, backed up with infrequent salinity observations from specialized platforms. For those areas where horizontal variations are important, which unfortunately include a large portion of the oceans, current information is desperately needed. These at present cannot even be inferred on a synoptic basis with too much accuracy. This brings up a point which might possibly apply to variables other than currents - is data of questionable accuracy better than none at all?

I might add that all the factors that affect the obtaining of synoptic oceanographic information are linked up in various inter-relationships. For instance, decision on the period of time over which the ocean may be considered synoptic is not only a function of the oceans behaviour but also the number and accuracy of our observations as well as our ability to analyze them correctly. Should our capability increase in either of these latter fields, the synoptic period could be shortened and the data would still be meaningful. But this would then have to be balanced against the expense involved and the practical requirements of the user of the prediction.

Turning to the second phase of the problem, that of data analysis, the basic approach most employed has been to infer the horizontal field of various parameters most descriptive of the oceanic structure, such as sea surface temperature, layer depth, and vertical gradients, in a manner similar to the preparation of synoptic meteorological charts. Our ability to specify these fields without error is severely limited by the scarcity and inaccuracy of data now available routinely, it is fair to state that it is not possible now to construct a very accurate analysis of the data obtained during one rather short synoptic period, such as one day, when these data are considered independently. As mentioned above, however, the fact that the oceans exhibit more conservatism in many areas than the atmosphere does permit the grouping of data over a specified period for synoptic analysis, thus increasing the density of observations considerably. Most of the experiments carried out in this area have employed a period of three to five days as an acceptable compromise. Another factor favourable to the analysis procedure is that one does not consider each set of data independently, but rather uses continuity considerations in which each set of data is considered in light of the data that has gone before. In this way the development and the movement of analysis features may be studied from day to day, true features identified and spurious features eliminated.

A regular program of employing such techniques to provide synoptic analysis of surface and subsurface variables in the ocean has been carried on at the U.S. Naval Oceanographic Office during the past two years. Methods employed have been subjective in nature, and the charts were prepared manually. Most of the emphasis has been placed to date on analysis of the sea surface temperature, the mixed layer depth, and the vertical gradient of temperature immediately below the mixed layer. Because of the relative abundance of sea surface temperature observations and the fact that the sea surface temperature serves as an anchor for the vertical temperature trace, initial emphasis has been placed on the analysis of this variable. The picture emerging from this analysis program is one that is very complicated near the Gulf Stream with a considerable amount of fine detail, mainly consisting of alternate warm and cold tongues of surface water. In general these features are observed to be quite conservative with time, being identifiable on the charts for many days. Although some of these features have been tracked from one area of the chart to another, many of them are observed to move little, if at all. Away from major current systems such as the Gulf Stream, gradients are still observed; although not nearly so strong as those observed in the neighbourhood of the Gulf Stream, these gradients still tend to be larger than originally expected. The major problem, therefore, appears to be the amount of detail that should be included in the analysis, in light of either the actual oceanic structure or the requirements of the application.

Achieving adequate analyses of sub-surface variables is a more difficult problem, owing to the relative scarcity of data. While we have been able to collect about 100 bathythermograph observations from the western North Atlantic daily, until this number is increased the data density will scarcely be enough to permit analyses in the same detail as the sea surface temperature. For some time therefore it will be necessary to supplement direct contouring of sub-surface data with indirect assessment of the sub-surface conditions. One helpful factor has been that, in certain areas and at certain times of the year, it has been possible to use the pattern of sea surface temperature as a rough guide to the pattern of mixed layer depth. While such an analyses aid is strictly qualitative rather than quantitative, it has given rise to the idea that an organized program of statistical analysis might be able to develop relationships which would be of direct assistance in the assessment of current sub-surface conditions.

Although the initial experiments in synoptic oceanographic analyses have been carried out using manual techniques, the concept of computer analysis of these data is extremely attractive, both from the standpoint of objectivity and ease of handling the prediction problem, which almost certainly will involve mathematical computations concerned with the heat budget, vertical mixing, and horizontal advection. Experiments in this area carried out by organizations in the United States have resulted in charts which are much less detailed than the manual product; in many areas the contours are considered too smooth to represent the nature of the ocean structure adequately. The achieving of a more detailed picture by objective means will involve a much closer grid spacing in the computations; this will require a greater data density than we have at present. Although attempts are underway to increase the detail in present objectively prepared charts, for some time one of the decisions that will have to be made is the extent to which we can sacrifice detail for the sake of objectivity. The aim should be to retain as much real detail as the user of the prediction needs.

With regard to the problem of oceanographic prediction, there are many approaches that have been and are being employed to develop forecasting techniques for the variable temperature field. In general, they can be summarized by outlining four different types of approach to the problem.

The first would emphasise the factors of continuity and persistence exhibited by the ocean, as discussed above in connection with synoptic analysis. Here one assumes that day to day changes in intensity and motion of oceanographic features are relatively small, and these changes occur in a continuous manner and may therefore be projected into the future. Such a technique naturally depends on the quality and detail of the synoptic analysis available. The importance of this approach to oceanographic prediction, elementary as it is, should not be underestimated. Prior to the development of objective methods, this was the approach used by meteorologists for many years with considerable success; the slower time scale of events exhibited by the ocean should make it an even more valuable tool. It may even very well be that for forecasts of very short duration, such as a day or so, it will not be possible to surpass this method by the development of specific objective equations.

The second approach might be termed a point prediction in that it involves operating on a single vertical temperature trace. Once an initial condition, such as a bathythermograph reading, is obtained, the changes in the vertical trace are calculated in terms of predictable variables such as wind, air temperature, cloudiness, and others. Changes calculated by this means will be limited to those resulting from energy exchange at the sea surface at the point of observation. These changes will include addition or subtraction of heat at the surface, convection due to heat loss, and vertical mixing due to wind and other factors. The prediction itself consists of modifying the vertical temperature trace in accordance with the calculated changes; a considerable body of information exists to make these calculations, mostly in the form of empirical formulae developed over the years.

By far the greatest number of experiments made in oceanographic prediction have been of this type, and work of this nature has been carried on in several countries. Such prediction techniques when adequately developed could be expected to provide useful forecasts in those stable areas away from major current systems where the major effects on the ocean structure or those taken into account in this type of calculation. It could not be expected however, that this type of prediction will be completely successful in those areas where it is necessary to take into account effects of horizontal variations, such as those due to advection or internal waves. However, even in these areas such daily computations are important to indicate the magnitude of energy exchange factors.

The third approach may be termed the dynamic approach in that it involves development of mathematical models of the ocean using the hydrodynamic equations as a basis. Given such a model and at initial distribution of variables such as can be gathered by a synoptic network, numerical integrations can be carried out by high speed computers, and the conditions in the future calculated. This process is usually repeated for small intervals of time over the entire forecast period. Development of such a system will be a lengthy process; although some precedence exists for this type of forecast in meteorological procedures, there are enough important differences between the structure of the ocean and the atmosphere to warrant considerable effort in the model development. A few projects have been established in this area, and testing of various models is now underway. It will be some time, however, before such models can be used on a routine basis; the input requirements for such equations are much more stringent than those of other approaches to the prediction problem, and routine use of such models will have to await further development of synoptic data collection techniques.

The fourth approach is statistical, and such an approach assumes special significance for several reasons:

1. A certain amount of statistical analysis is required to use any other prediction technique, in that the objective analysis that serves as an input to the prediction model usually has, at least in part, a statistical basis.

2. No matter what approach is taken to prediction, it is necessary to know the statistical population within which the prediction is to be made - what might be called a first order prediction.

3. Statistical considerations are the only logical means now available of making long range predictions, for instance seasonally, in addition to possible statistical applications to short range prediction.

In the field of short range prediction by statistical means, the objective is to develop some type of regression equation which may be used to predict a specific oceanic variable for a specified period of time. A large body of historical data is of course required to employ such an approach; the analysis is so designed as to yield knowledge of those factors which had the most effect on time changes in the variable being predicted. These factors are given the most weight in the regression equation.

While we are a long way from having oceanographic prediction systems capable of meeting all the requirements that exist for them, there has been a great increase in activity in this field in recent years. Several countries have synoptic oceanographic programs, and from research on these data will come increased knowledge of the time changes in oceanic behaviour. Although these projects are not yet completed, work is actively underway in almost all the areas discussed above; the foreseeable future should see a significant increase in our capability to provide advance oceanographic information to those who operate at sea.

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