

**SECTION**

**C**



C-1

## REMARKS ON EFFECT OF FOOD ANIMALS ON COD BEHAVIOUR

By

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## 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 Fischereigebleite 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<sup>1</sup>

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 *Squilla* meal (Karpavitch 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.

Length classes (cm)	1960		1961			1962			
	Otter-trawl	Otter-trawl			Gill nets	Otter-trawl			Gill-nets
		Upper half	Lower half	Total		Upper half	Lower half	Total	
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

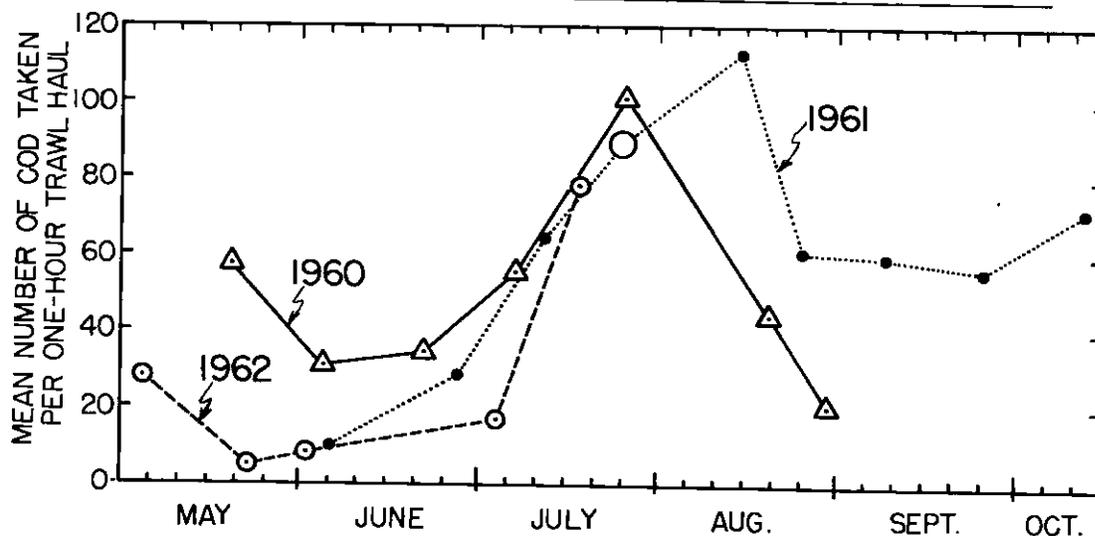


Fig. 1. Seasonal and yearly variations in the cod catch at station D112N in 1960-62. Each symbol represents the average between the mean day catch, based on four (1960) or three (1961-62) tows (one on 1 May 1962, two on 25 September 1961), and the mean night catch, based on two tows (one on 12 October 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.

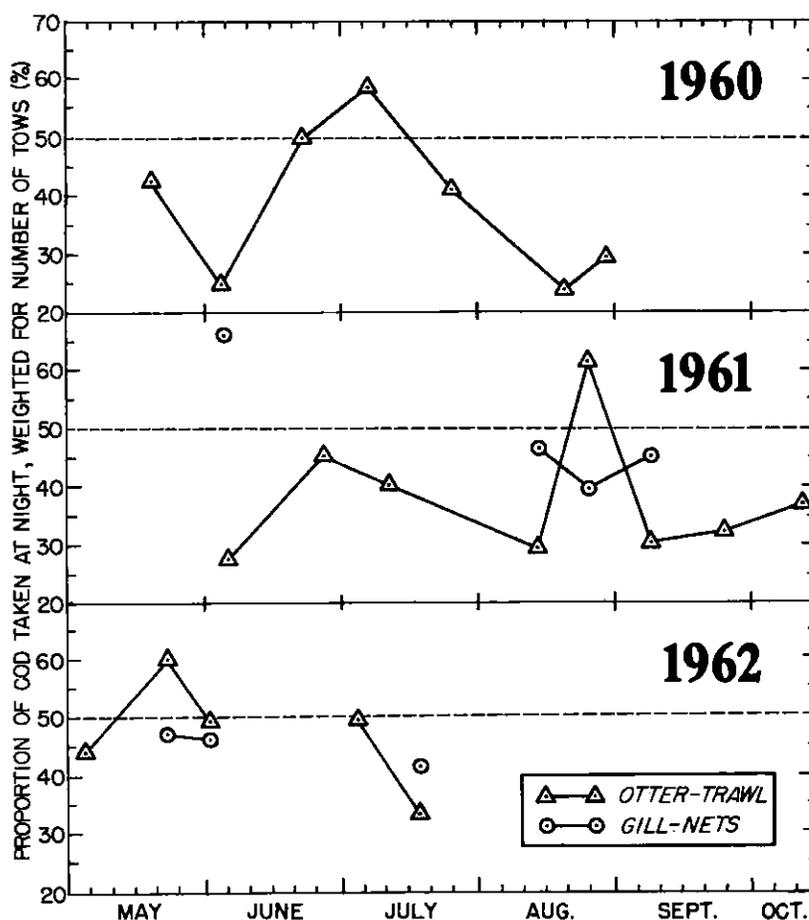


Fig. 2. Seasonal fluctuations in 1960-62 of the extent of the nocturnal vertical migrations of cod in midwater, as indicated by the difference between the mean day catch and the mean night catch at a single locality.

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

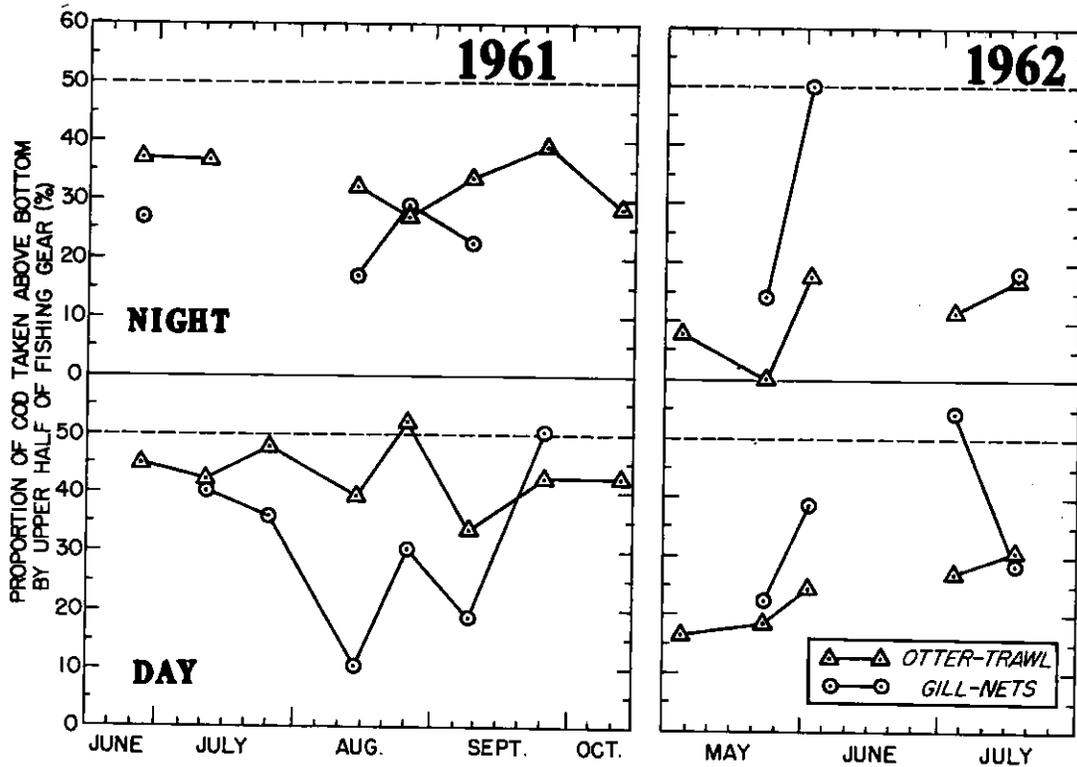


Fig. 3. Seasonal fluctuations in 1961-62 of the extent of the vertical migrations of cod in the vicinity of the bottom (up to 9 m from the bottom), at night and in the day, as indicated by simultaneous fishing at a single locality with a horizontally bipartitioned otter-trawl and with a pair of gill-nets set on and above the bottom.

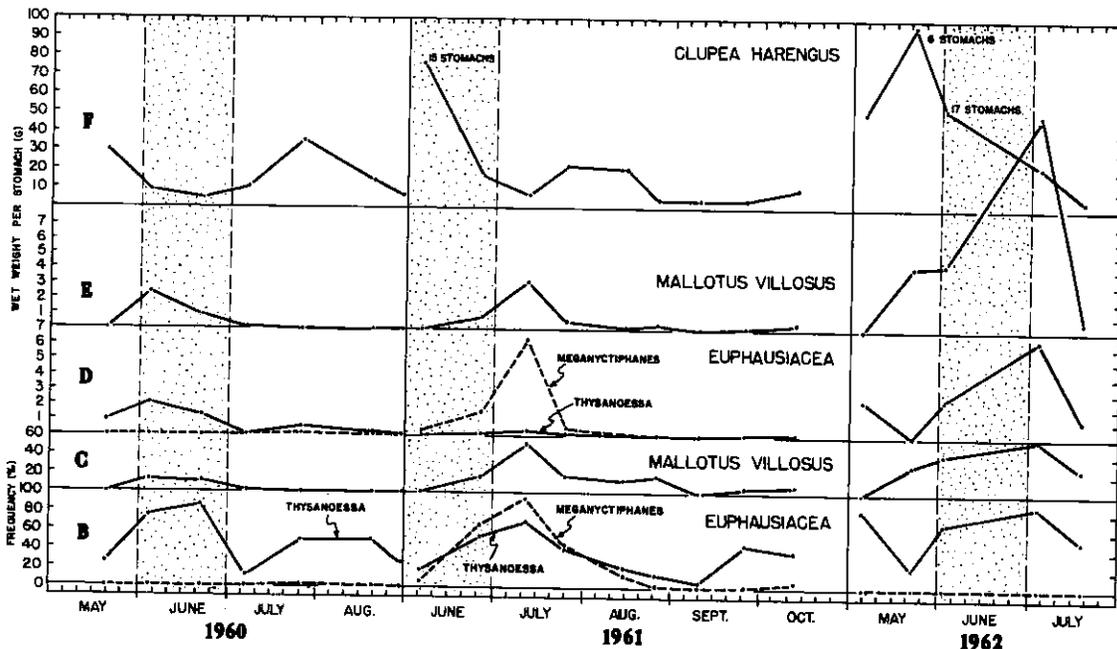


Fig. 4. Seasonal and yearly variations, from 1960 to 1962, of the frequency and wet weight of the three main categories of pelagic prey in the stomachs, euphausiids (B,D), capelin (C,E) and herring (F). Each dot is typically based on 5-6 one-hour trawl hauls, made within 24 hours, and, except as noted, 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 *Thysanessa* 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.

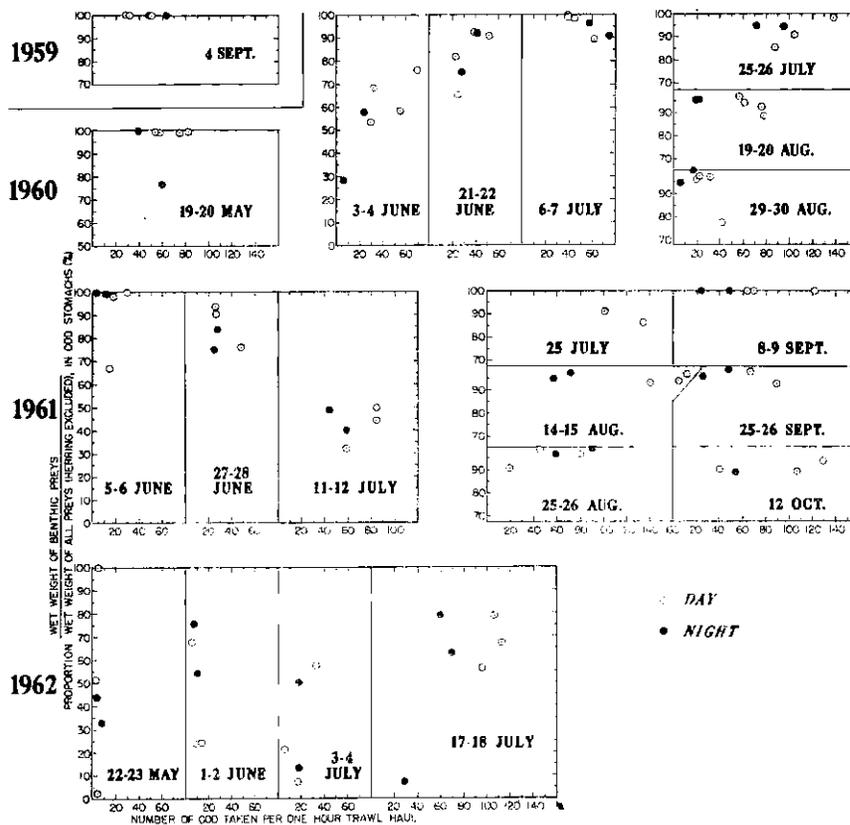


Fig. 5. Relation between the abundance of cod in the vicinity of the bottom and the proportion of benthic prey in their stomachs. The same locality, 10 miles southeast of Grande-Rivière, at a depth of 60 fathoms, was used throughout, except in 1959.

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 and horizontal 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.

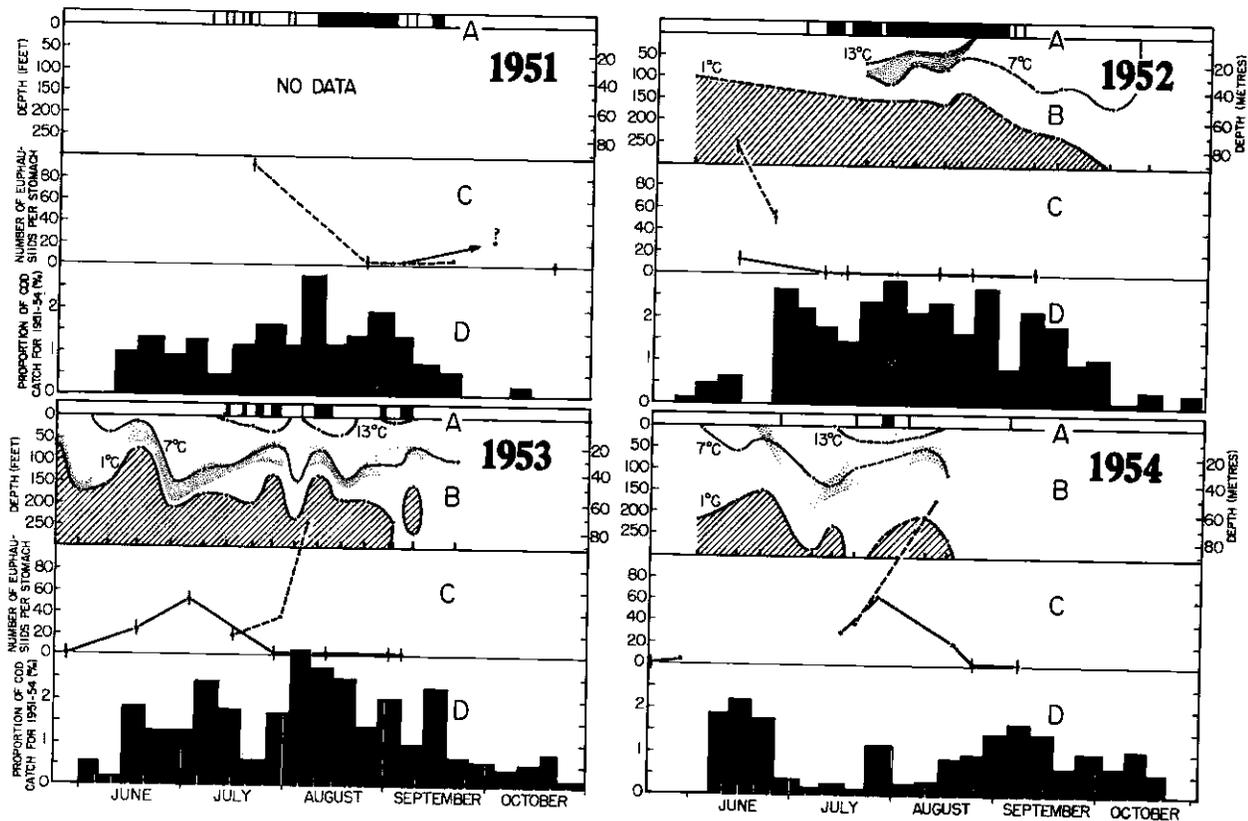


Fig. 6. Seasonal distribution from 1951 to 1954 of (A) days when the surface water temperature at Grande-Rivière wharf was  $14^{\circ}\text{C}$  (average for warmest month of the year from 1938 to 1956) or higher, (B) the depth distribution of three isotherms and the thermocline (stippled areas) at 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). *Zoologicheskii 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 Holsteinborg 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<sup>1</sup>

## ABSTRACT

At St. John's from mid-June to early August cod caught in the commercial fishery at 13-38 m fed almost entirely on capelin. From August 19 to 27 November the cod from the commercial fishery, now at 55-130 m, fed mainly on bottom invertebrates especially crustacea. Spider crabs were over 10% of the crustacean food. Although capelin were not important as food at this time, cod and some 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 at various depths.

On the offshore part of the Labrador Shelf in late July-early August the largest concentrations of cod were in cold water and associated with heavy feeding on adult capelin, whereas in deeper and warmer water other cod schools may have been held together by feeding especially on scaled lancet fish and on lantern fishes. The size of the food was related to the size of the fish, the largest fish feeding mainly on cod and wolffish 35 cm or over in length. The fish prey was evidently obtained by pursuit and taken tail first.

The early April cod concentrations on the eastern slope of Hamilton Inlet Bank were mainly non-feeding and were held together by pre-spawning and post-spawning schooling. The early May mainly post-spawning concentrations in the same area were feeding more heavily, almost entirely in portions of cod discarded by trawlers and this may have helped to hold the schools together or at least make them more related to the bottom.

On the northern Grand Bank in late March the food of the main concentrations in cold water was adult and young capelin.

On Flemish Cap in late March cod concentrations were feeding mainly on young cod at the shallow and young redfish at the greater depths.

Haddock on the Southeast Shoal of the Grand Bank in July-August accumulate, often in great numbers, 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 St. 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 the 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 remainder mainly bottom food.

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
		<i>m</i>		<i>no.</i>	<i>cm</i>	<i>cc</i>
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, line-trawl and handline	1,291	31-150	59,890

TABLE I. (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)	<i>Cyrtodaria stigmata</i>	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 pre-spawning cod, not expected to spawn for a month or two, and were feeding well, the large and medium

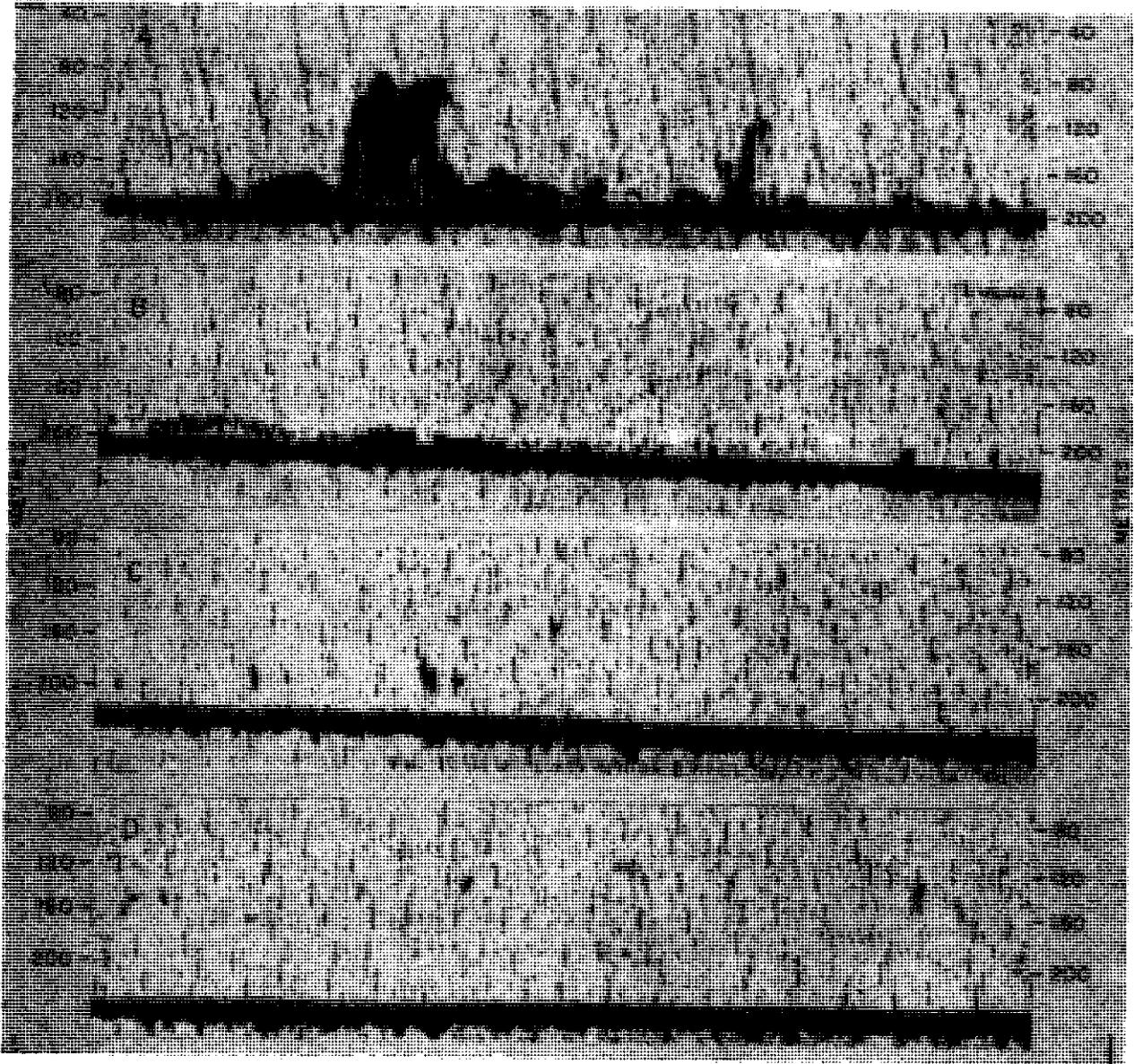


Fig. 1. Echo-sounder records of cod and very likely capelin, northern Grand Bank, 28 March 1961. A, half-hour tow at 185-190 m (3,610 kg cod); D, half-hour tow at 230 m (1,340 kg cod); B and C, ranging from end of A to beginning of D.

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

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 air-bladder 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.

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

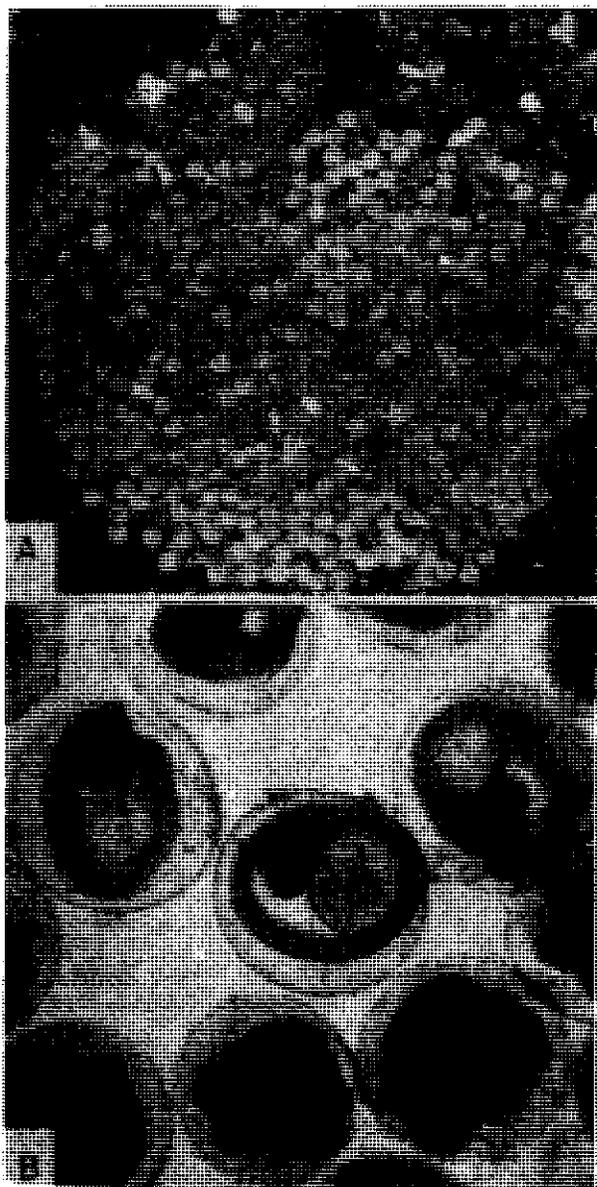


Fig. 2. A, sand and capelin eggs and B, developing capelin eggs from stomachs of haddock from the Southeast Shoal of the Grand Bank. A, August 1950 and B, 15 July 1951. From Pitt (1958).

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.

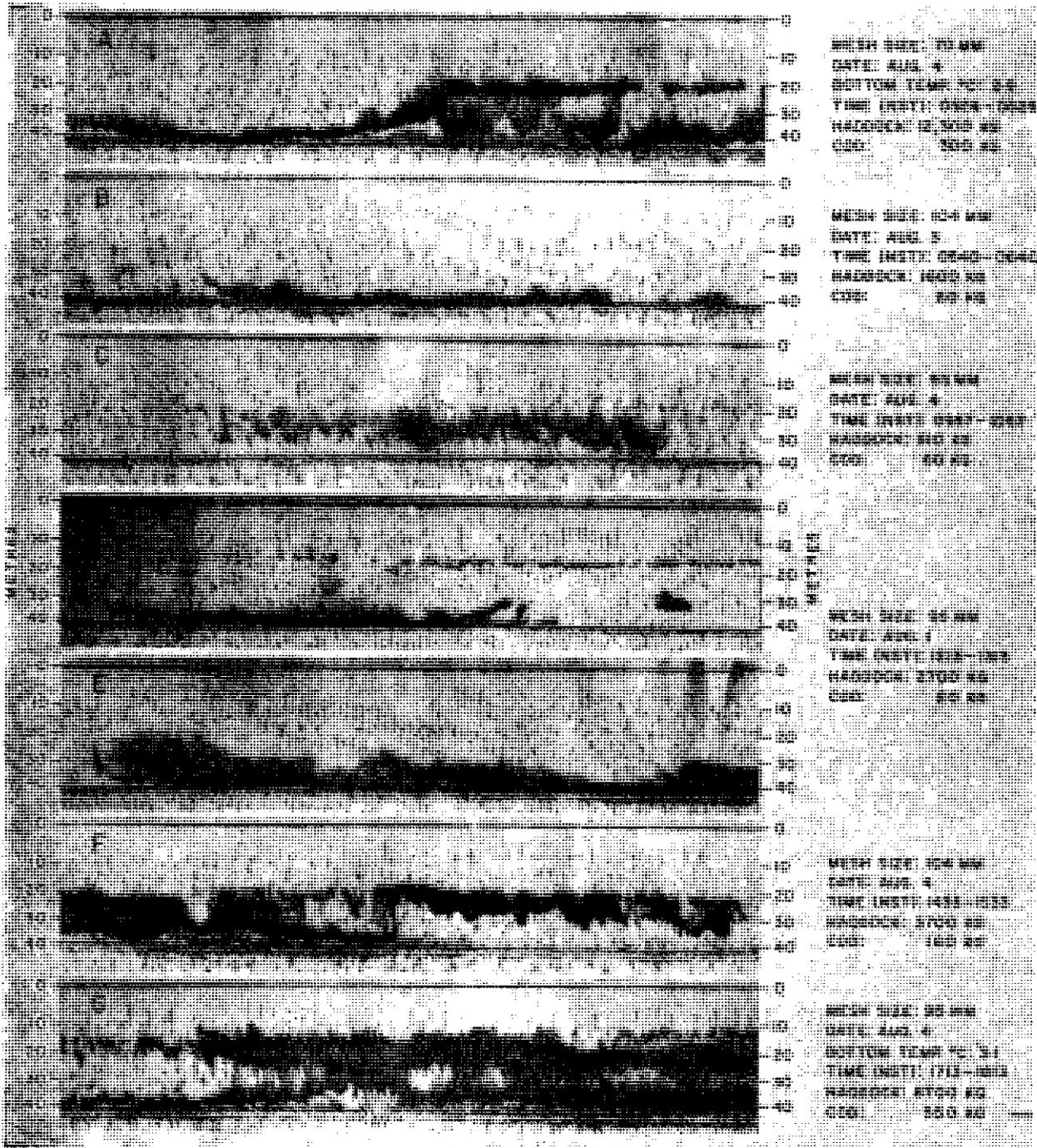


Fig. 3. Surface to bottom echo-sounder records of capelin, haddock and cod and catches of haddock and cod in 60-min bottom otter-trawl tows of the *A.T. Cameron* in 40-46 m, 1-4 August 1959, on the Southeast Shoal of the Grand Bank at  $44^{\circ}09'-44^{\circ}11'N$ ,  $49^{\circ}42'-49^{\circ}46'W$ . (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.)

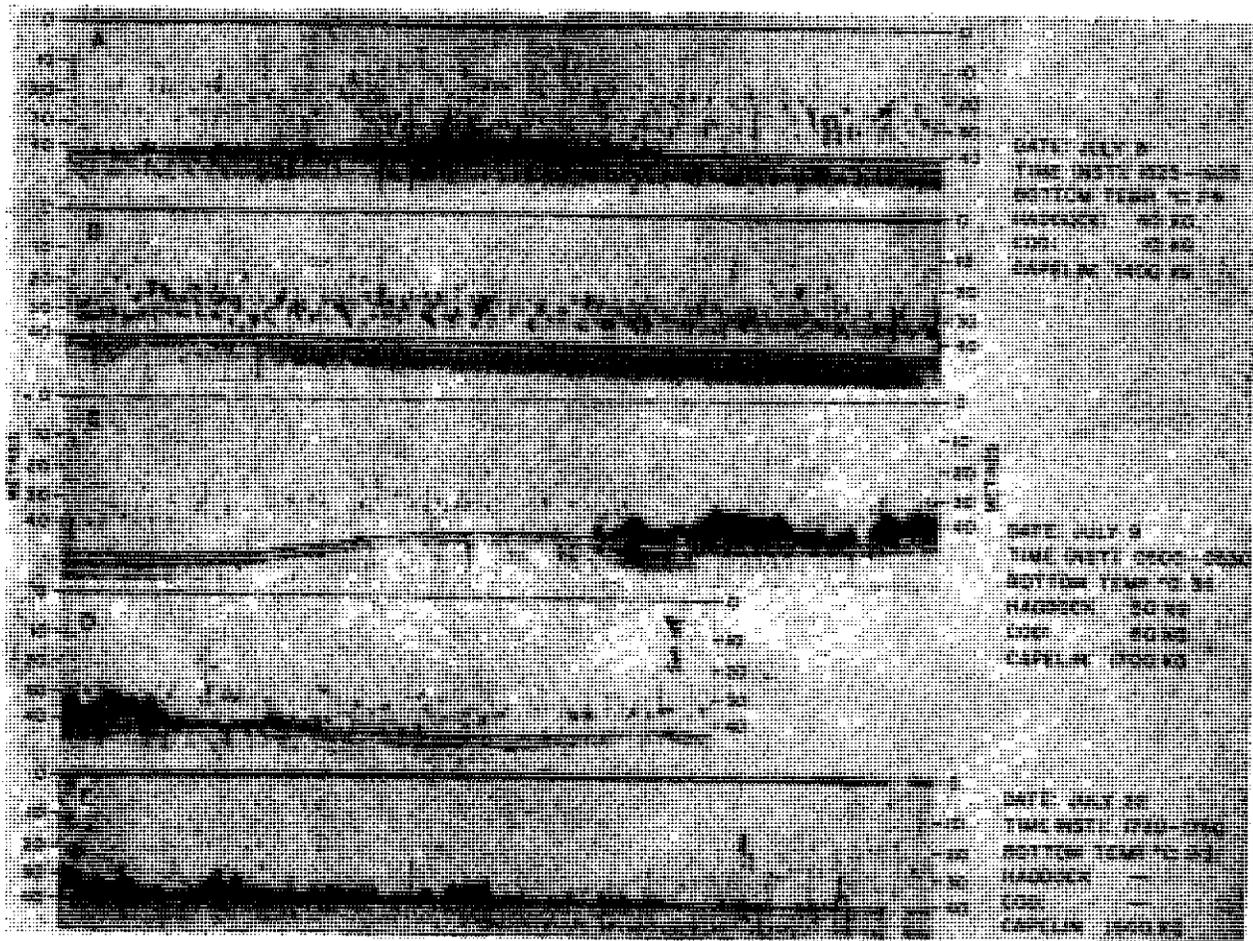


Fig. 4. Surface to bottom echo-sounder records of capelin, haddock and cod in half-hour to 1-hour otter-trawl tows of the *A.T. Cameron* on the Southeast Shoal of the Grand Bank in 38-51 m, 8-22 July, 1961 at  $44^{\circ}03'-44^{\circ}12'N$ ,  $49^{\circ}40'-49^{\circ}45'W$ . (The portions A, B; C, D; 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.)

#### ACKNOWLEDGEMENTS

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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,<sup>1</sup>

## 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<sup>2</sup>/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

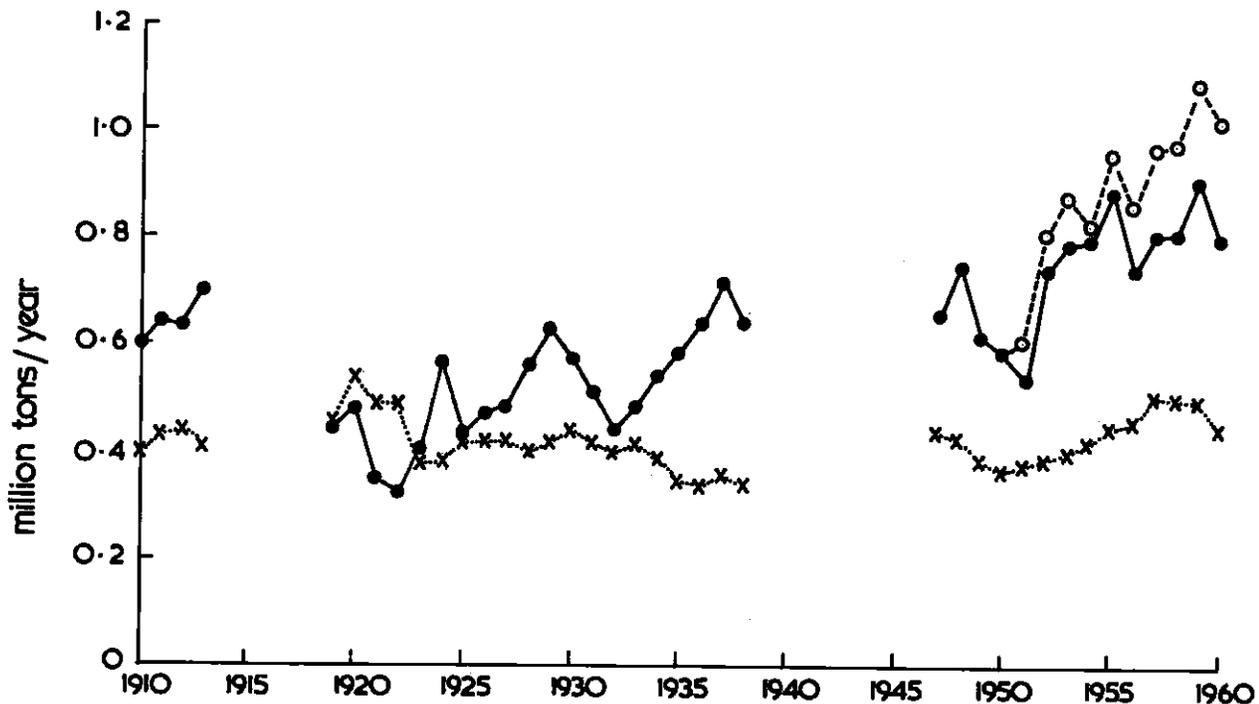


Fig. 1. Fish yields from the North Sea: ...x... demersal; —●— pelagic; - - o - - pelagic plus industrial fisheries.

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  $0.43 \times 10^6$  tons/year. The pelagic fisheries show a general increase especially when the industrial landings are included. A value of  $1.0 \times 10^6$  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  $3.3 \times 10^5$  km<sup>2</sup>, these yields are 0.13 and 0.30 g C/m<sup>2</sup>/year for demersal and pelagic respectively.

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  $0.17 \text{ g C/m}^2/\text{year}$ . 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, 1961a). A very tentative value of 0.5 is used here to make the total yield  $0.6 \text{ g C/m}^2/\text{year}$ .

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.

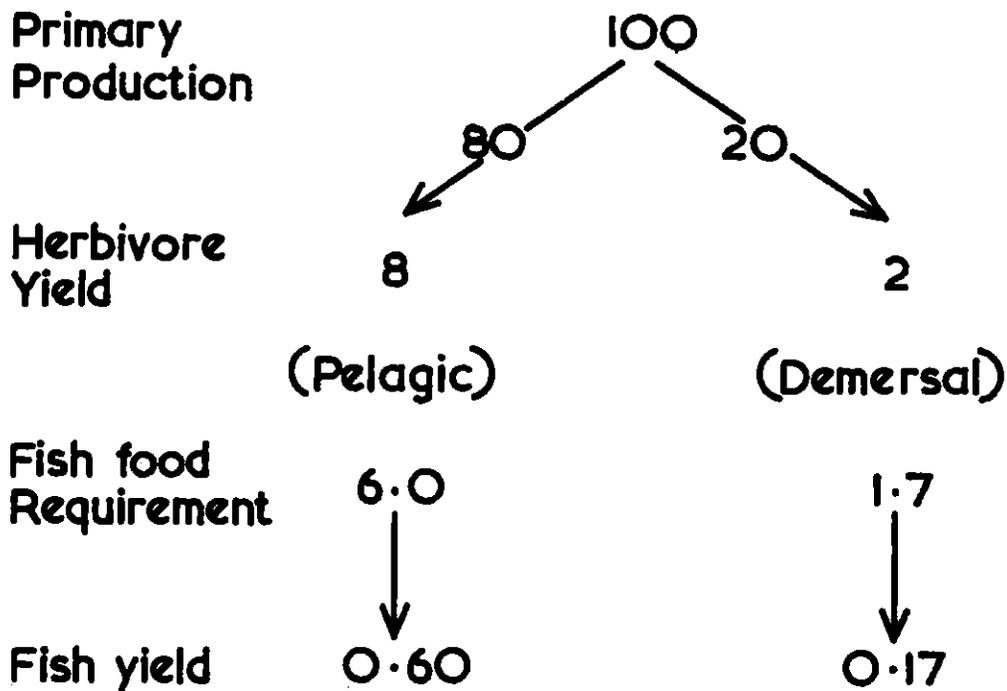


Fig. 2. The herbivore yield deduced from primary production compared with fish food requirement deduced from fish yield (g carbon/year).

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<sup>2</sup> 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<sup>2</sup>. 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<sup>2</sup> 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<sup>2</sup> 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<sup>2</sup> 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<sup>2</sup>.

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<sup>2</sup> 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<sup>2</sup> 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<sup>2</sup>. The macrobenthos in the poorest area (Fladen) is about 0.6 g C/m<sup>2</sup> and in more inshore areas (excluding bottom areas within the euphotic zone) about 1.6 g C/m<sup>2</sup>; giving a rough average of 1 g C/m<sup>2</sup>.

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<sup>2</sup>/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<sup>2</sup>/year.

Ignoring the bacterial populations (which should not be done) the ratio of benthic production to the value of 20 g C/m<sup>2</sup> 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.

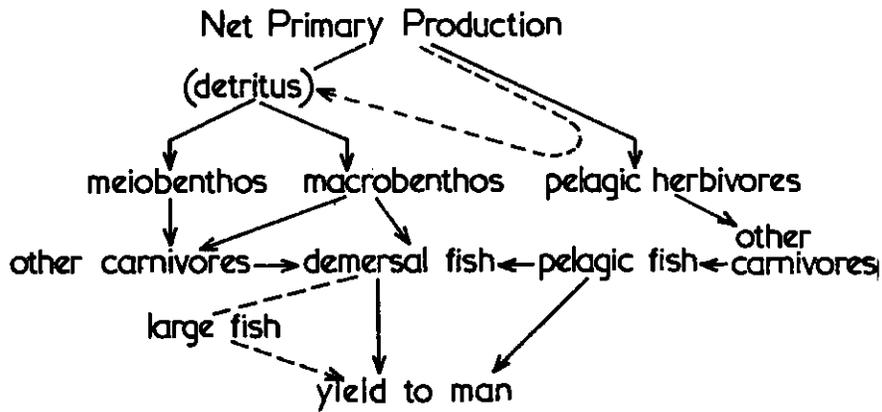
### 4. Carnivorous Benthos

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

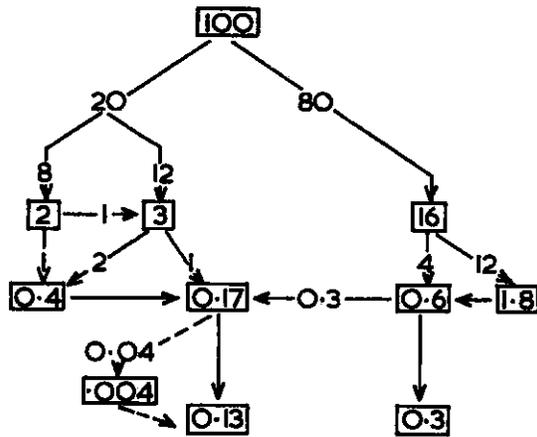
	Fish	Crustacea	Annelids	Molluscs	Echinoderms
Haddock (31-35 cm)	12	42	12	12	28
Whiting (21-25 cm)	32	43	16	8	-

Central N. Sea

(a)



(b)



(c)

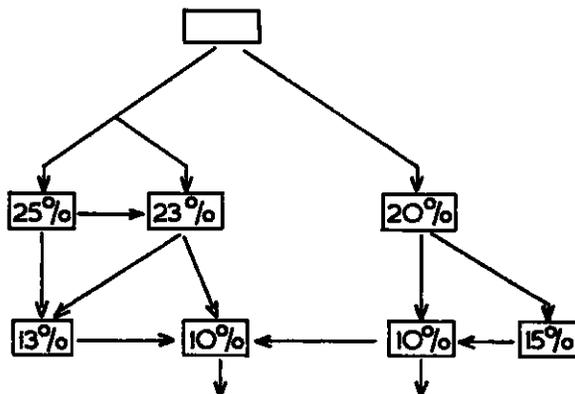


Fig.3. Schematic representation of; (a) simplified food web, (b) production by each group, (c) ecological efficiency of each group.

The fish were *Anmodytes*, *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.

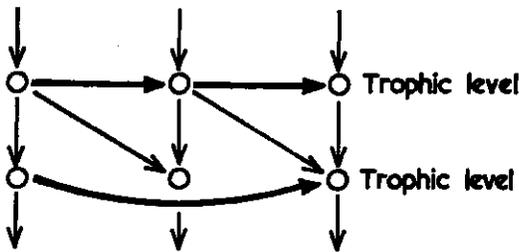


Fig. 4. Part of a generalised food web.

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.

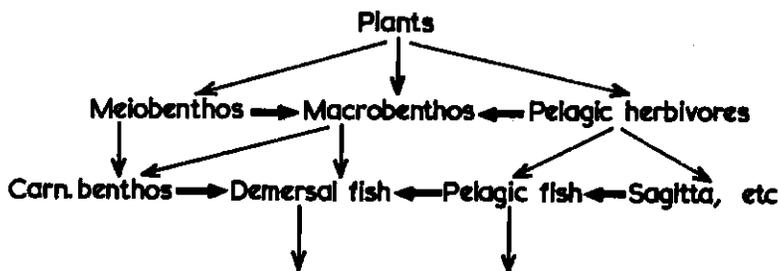


Fig. 5. The general pattern of Fig. 3 expressed as a food web of the type shown in Fig. 4.

Finally, in Fig. 5 the web in Fig. 3a 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

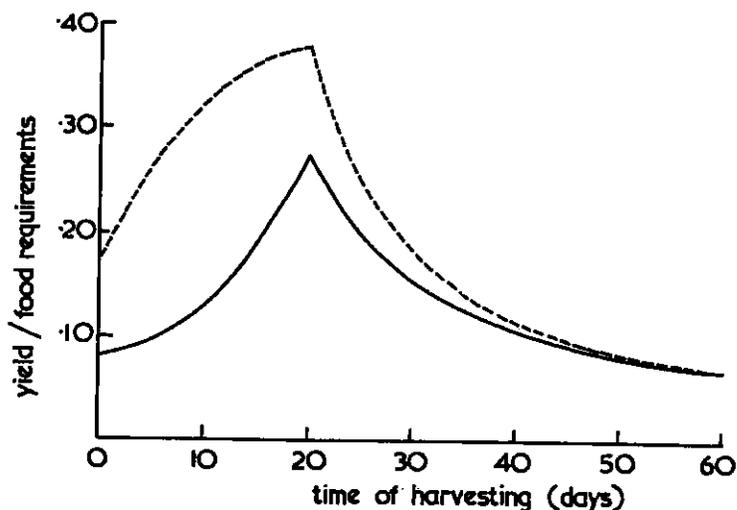


Fig. 6. The calculated efficiencies for a hypothetical *Calanus* with reproductive ratios of 100 ( - - -) and 10 (—).

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<sup>2</sup>. 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<sup>2</sup>. 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<sup>2</sup>. At a trophic level efficiency of 10% this would require a plant production of 110 g C/m<sup>2</sup>, but at 20% the required part of the production would be only 55 g C/m<sup>2</sup>. 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

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

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.

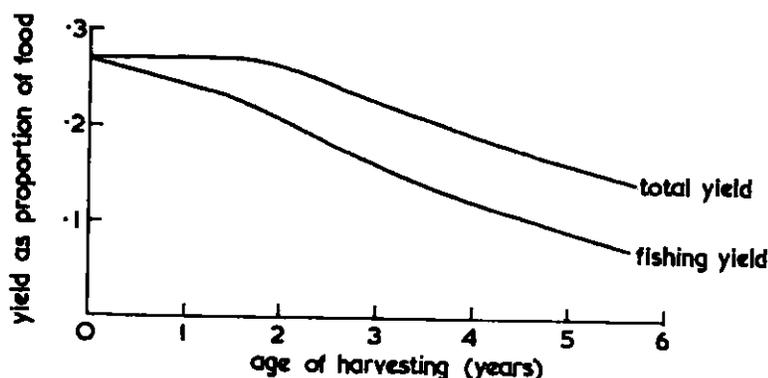


Fig. 7. The yields of haddock per unit of food requirement.

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 1961a). 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

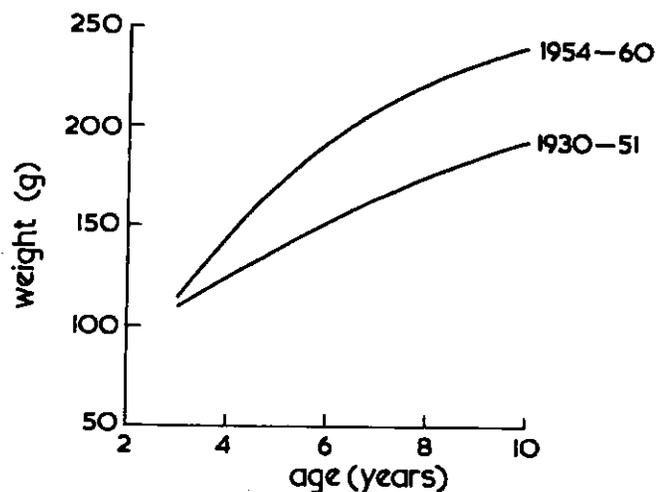


Fig. 8. The age-weight relations for herring used in the calculations (see text).

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.

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.

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

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		

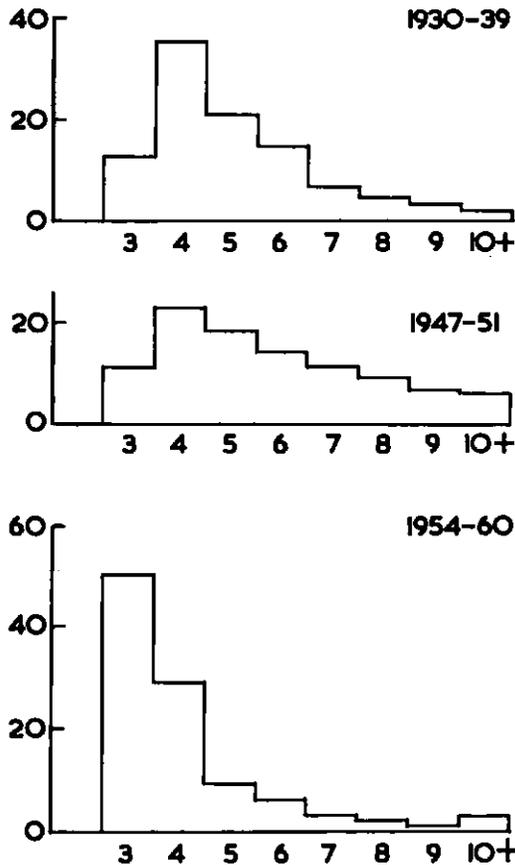


Fig. 9. Percentage are composition of herring in the Northern North Sea.

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 it 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 (1961b) 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 Co-operative 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., Copenhagen*, 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. 1961a. The effect of fishing on the Downs stock of herring in the North Sea. *ICES, C.M. 1961*, Herring Symposium, Paper No. 25.
- 1961b. 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.*, I: 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<sup>1</sup>

## 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 pallasi 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

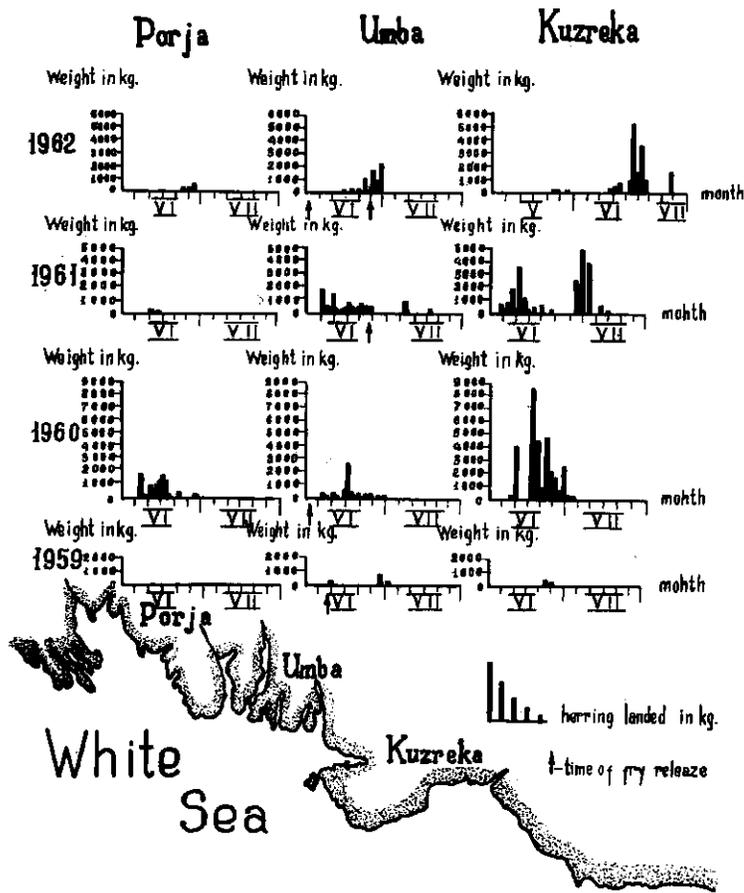


Fig. 1. Quantities of herring delivered in 1959-62 to the factory nearest to the Uмба River (the White Sea).

As seen from the figure the least quantity of herring was delivered to the factories of Uмба, Porja and Kuzreka in 1959. The lack of herring possibly accounted for the good survival of the young 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 portion 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 a result of a longer littoral period of life and lesser mobility in comparison with the young pink salmon.

In 1963 a special experiment was carried out in the same Bay aimed at finding the rate of destruction of the young pink and chum salmon by young cod, *Gadus morhua morhua* Linné. The results of this experiment have brought further evidence that the chum salmon are eaten by young cod much more intensively, so we have a right to assert that it is completely inadvisable to release the young chum in those parts of the littoral area where there are many predators. In the littoral zone of the White Sea the number of predators is smaller, and therefore the young chum is observed for a considerably longer time than in the Barents Sea.

#### CONCLUSION

As a result of field observations and laboratory investigations we have come to the conclusion that the main factor governing the numbers of pink and chum salmon returning to the rivers of the north European part of the USSR is the relationship of Far Eastern salmon to the ichthyofauna of 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<sup>1</sup>

## 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 Sphyrinidae, 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 filets.

Herrington, Bearse, and Firth (1940) reported on abundance and distribution of *Sphyrion*, and the frequency of occurrence of its embedded remains in redfish filets from the Gulf of Maine. Bigrelli 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 parasites 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

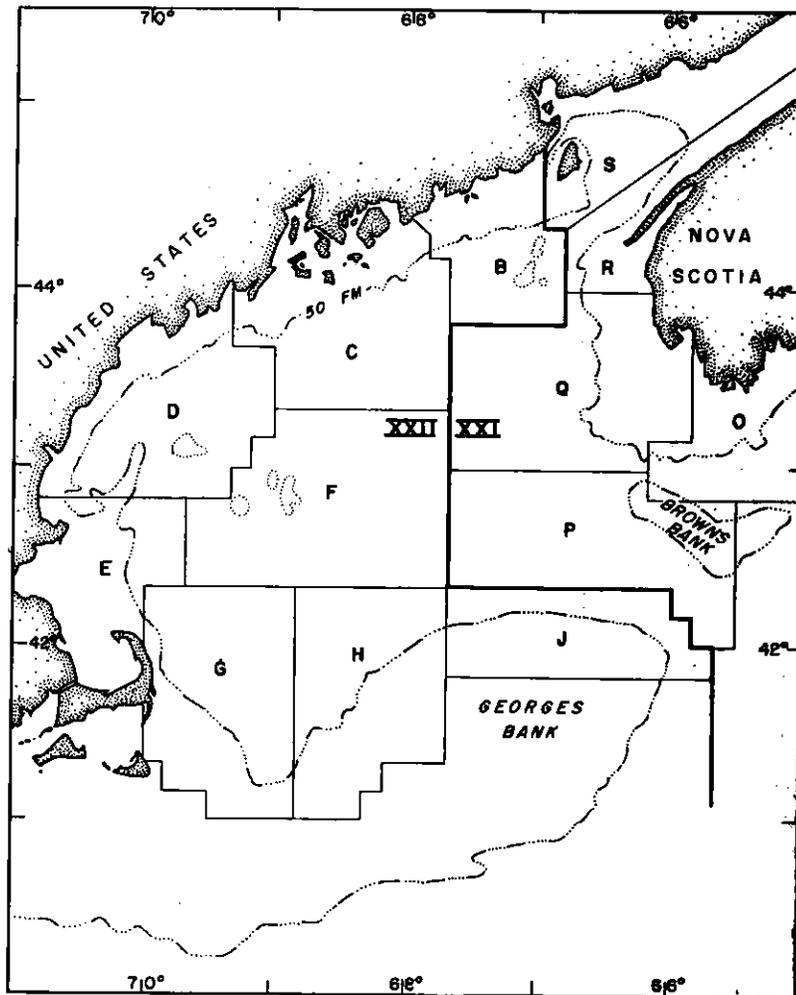


Fig. 1. Statistical subareas of the Gulf of Maine.

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	
C	36	26	22	8	4	-	1	2	-	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	14	54	80	53	33	23	36	24		
G									16	3	4	1	4	4	8	4	14	3	8	7	
H	22	23	25	13	16	6	7	-		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

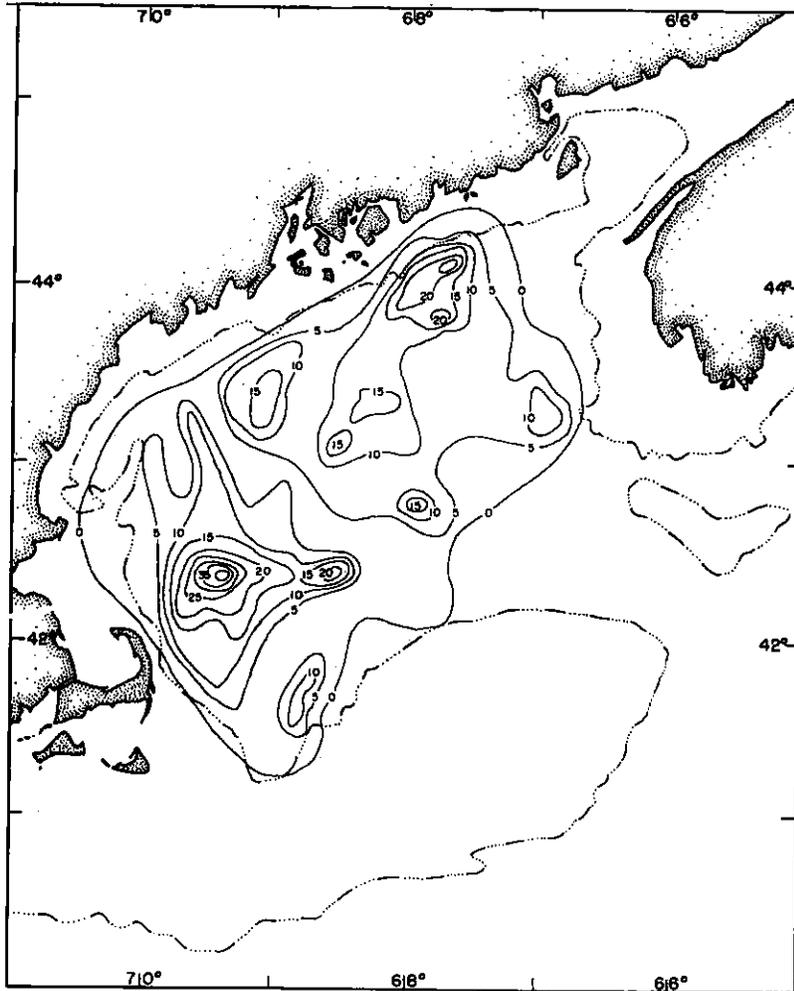


Fig. 2. Distribution of redfish with first stage infestation of *Sphyrion lumpi* in the Gulf of Maine, 1943-47.

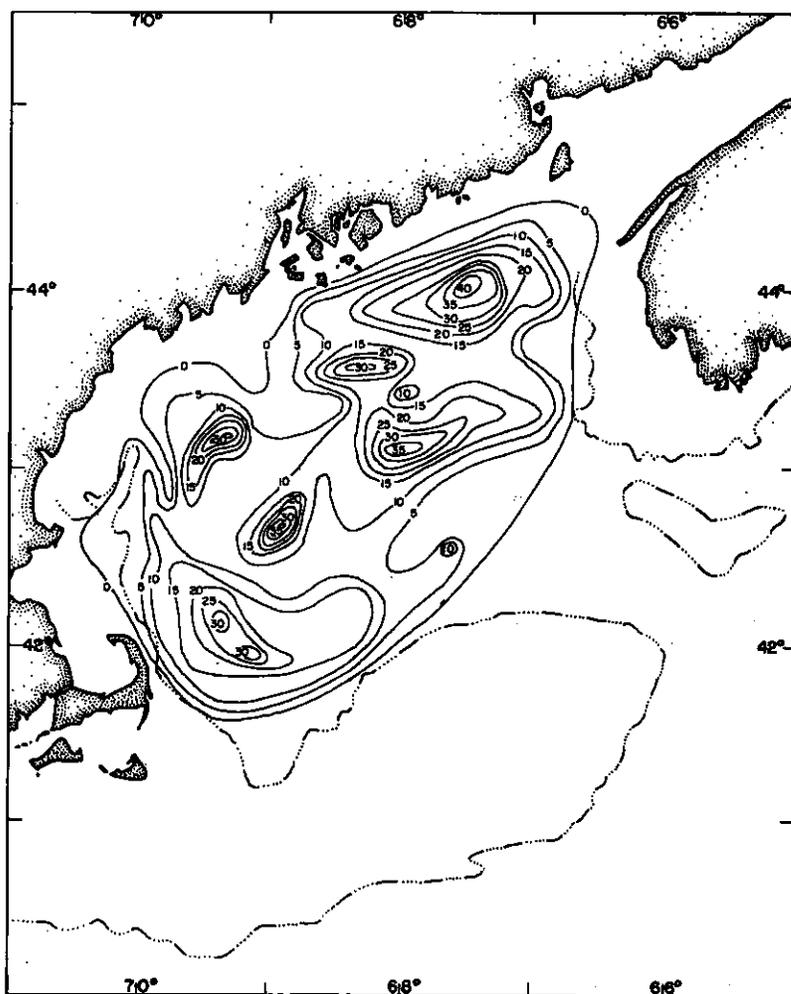


Fig. 3. Distribution of redfish with first stage infestation of *Sphyrion lumpi* in the Gulf of Maine, 1957-62.

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 *Sphyron* ON REDFISH IN SOUTHERN GULF OF MAINE, SUBAREAS XXII, E, F, AND G, 1943-47. MALES AND FEMALES SEPARATED.

Month	1943			1944			1945			1946			1947			TOTAL			
	No. fish sam-pled	No. fish para-sit.	No. fish sam-pled	No. fish sam-pled	No. fish para-sit.														
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	-	-	628	42	6.7	
Apr.	130	7	258	19	73	0	49	2	91	2	601	30	5.0	-	-	601	30	5.0	
May	179	13	313	9	693	32	453	31	283	24	1,921	109	5.7	-	-	1,921	109	5.7	
June	281	5	433	10	314	5	159	2	241	9	1,428	31	2.2	-	-	1,428	31	2.2	
July	196	2	583	8	265	4	409	12	360	7	1,813	33	1.8	-	-	1,813	33	1.8	
Aug.	916	7	370	3	422	8	166	18	286	11	2,160	47	2.2	-	-	2,160	47	2.2	
Sept.	136	1	331	1	453	3	232	10	394	2	1,546	17	1.1	-	-	1,546	17	1.1	
Oct.	201	0	356	7	64	3	305	4	230	5	1,156	19	1.6	-	-	1,156	19	1.6	
Nov.	304	9	382	8	138	1	54	0	48	5	926	23	2.5	-	-	926	23	2.5	
Dec.	72	0	108	12	-	-	-	-	41	7	221	19	8.6	-	-	221	19	8.6	
Total	3,021	102	3,362	99	2,915	102	1,878	81	2,064	79	13,240	463	-	-	-	13,240	463	-	
Per- cent inci- dence	3.38		2.94		3.50		4.31		3.83		3.50		4.31		3.83		3.50		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	-	-	622	60	9.6	
Apr.	145	3	342	22	127	0	51	2	109	9	774	36	4.7	-	-	774	36	4.7	
May	221	17	287	10	807	52	490	78	317	37	2,122	194	9.1	-	-	2,122	194	9.1	
June	369	20	567	22	386	9	241	6	459	16	2,022	73	3.6	-	-	2,022	73	3.6	
July	304	5	817	12	335	6	491	31	440	10	2,387	64	2.7	-	-	2,387	64	2.7	
Aug.	759	8	430	11	678	30	234	30	314	7	2,415	86	3.6	-	-	2,415	86	3.6	
Sept.	189	0	419	4	447	14	368	38	406	12	1,829	68	3.7	-	-	1,829	68	3.7	
Oct.	248	3	444	25	136	10	395	9	370	6	1,593	53	3.3	-	-	1,593	53	3.3	
Nov.	296	1	468	10	162	3	46	1	52	0	1,024	15	1.5	-	-	1,024	15	1.5	
Dec.	98	1	92	16	-	-	-	-	59	8	249	25	10.0	-	-	249	25	10.0	
Total	3,273	130	4,138	165	3,535	180	2,365	199	2,636	112	15,947	786	-	-	-	15,947	786	-	
Per- cent inci- dence	3.97		3.99		5.09		8.41		4.25		4.93		8.41		4.25		4.93		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 sam-pled sit.	No. fish para-sitized	No. fish sam-pled sit.	No. fish para-sitized	No. fish sam-pled sit.	No. fish para-sitized	No. fish sam-pled sit.	No. fish para-sitized	No. fish sam-pled sit.	No. fish para-sitized	No. fish sam-pled sit.	No. fish para-sitized	No. fish sam-pled sit.	No. fish para-sitized
MALES														
Jan.	148	7	275	39	294	20	158	26	-	-	296	37	1,171	129
Feb.	874	59	326	78	153	7	102	9	364	122	53	-	1,872	275
Mar.	800	140	334	57	321	59	326	77	313	70	188	53	2,282	456
Apr.	588	77	369	48	459	74	150	18	-	-	115	6	1,681	223
May	466	84	246	60	149	25	212	44	700	152	416	28	2,189	393
June	315	26	239	7	295	27	-	-	468	97	456	79	1,773	236
July	326	5	213	18	165	13	117	8	142	24	149	15	1,112	83
Aug.	251	11	169	7	248	18	241	27	199	18	422	11	1,530	152
Sept.	277	11	243	36	350	58	-	-	54	19	34	-	958	124
Oct.	281	21	83	7	-	-	191	13	-	-	-	-	555	41
Nov.	214	14	128	12	59	12	92	2	-	-	-	-	493	40
Dec.	90	6	-	-	99	15	-	-	170	28	-	-	359	49
Total	4,630	461	2,625	369	2,592	328	1,589	224	2,410	530	2,129	289	15,975	2,201
Per-cent inci-dence	9.96	14.1	12.7	14.1	14.1	22.0	13.6	13.8						
FEMALES														
Jan.	152	4	325	51	206	11	142	19	-	-	304	40	1,129	125
Feb.	826	54	374	82	147	2	98	7	336	106	47	-	1,828	251
Mar.	700	106	366	53	381	57	274	48	287	55	210	54	2,218	373
Apr.	712	114	331	41	441	59	150	10	-	-	85	5	1,719	229
May	534	87	354	74	151	23	188	29	600	160	384	46	2,211	419
June	435	56	261	5	305	34	-	-	532	102	465	63	1,998	260
July	374	12	287	18	135	10	183	9	158	21	151	14	1,288	84
Aug.	349	15	231	8	252	23	259	25	201	25	478	71	1,770	167
Sept.	323	7	257	31	550	95	-	-	46	22	66	-	1,242	155
Oct.	319	41	117	6	-	-	209	29	-	-	-	-	645	76
Nov.	286	22	172	19	41	2	108	7	-	-	-	-	607	50
Dec.	110	10	-	-	101	9	-	-	130	20	-	-	341	39
Total	5,120	528	3,075	388	2,710	325	1,611	183	2,290	511	2,190	293	16,996	2,228
Per-cent inci-dence	10.3	12.6	12.0	11.4	11.4	22.3	13.4	13.1						

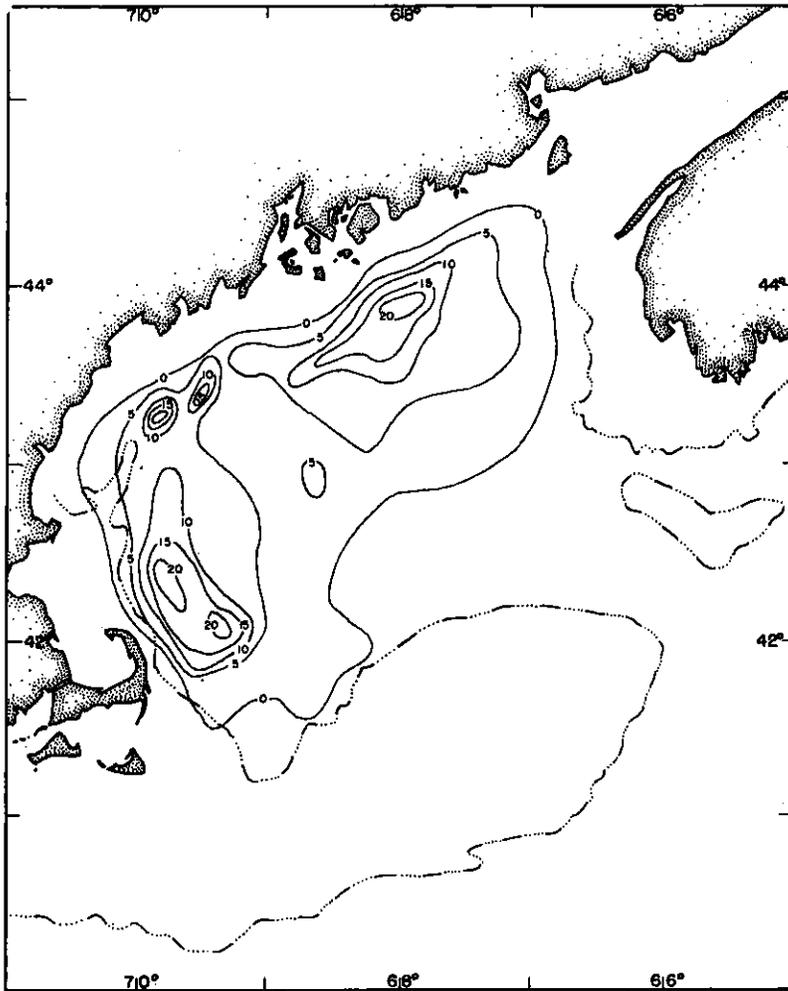


Fig. 5. Distribution of redfish with third stage infestation of *Sphyrion lumpi* in the Gulf of Maine, 1943-47.

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).

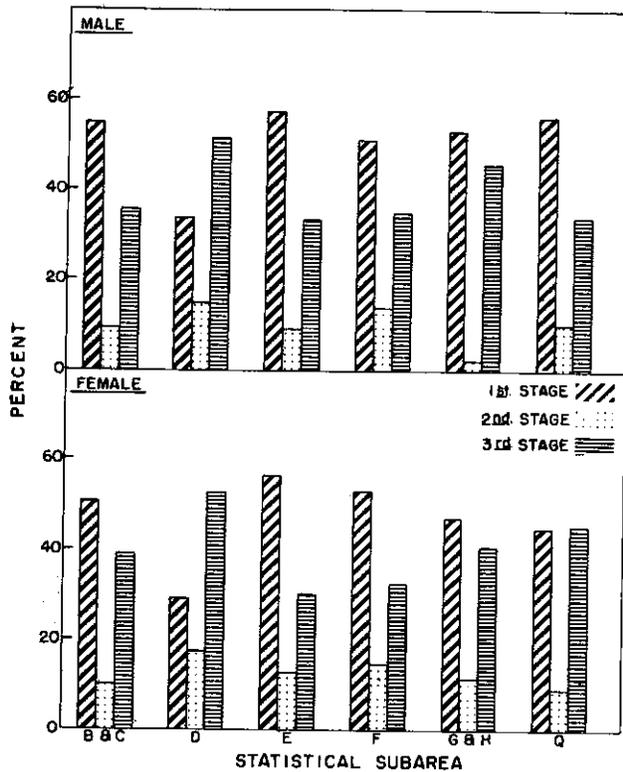


Fig. 6. Percent composition of parasitized redfish having three stages of infestation. Average values for the period 1943-51, by statistical subarea, for males and females separately.

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

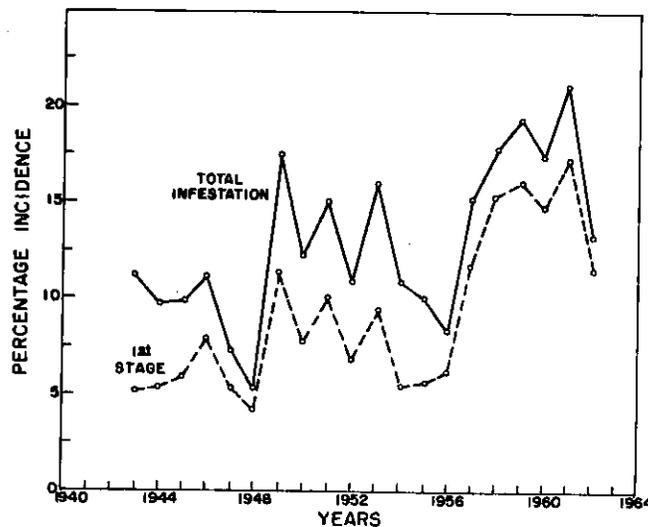


Fig. 7. Variation in annual average percentage incidence of live *Sphyrion* and total parasite infestation on Gulf of Maine redfish, males and females combined, during 1943-62.

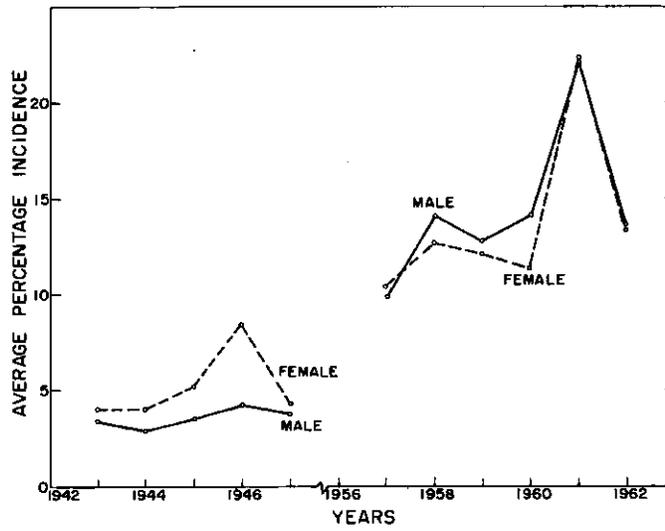


Fig. 8. Variation in annual average percentage incidence of live *Sphyrion* on redfish, males and females separated, in subareas XXII E, F, and G, southern Gulf of Maine, in 1943-47 and 1957-62.

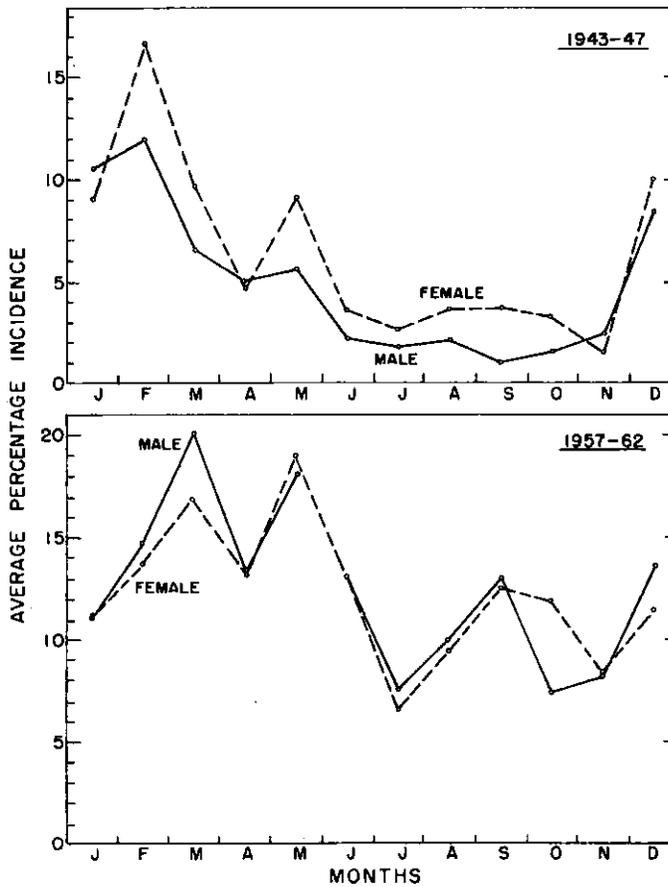


Fig. 9. Seasonal variation in percentage incidence of live *Sphyrion* on redfish in southern Gulf of Maine, subareas XXII E, F, and G. Average monthly values for 1943-47 and 1957-62 are given as percent of each sex parasitized.

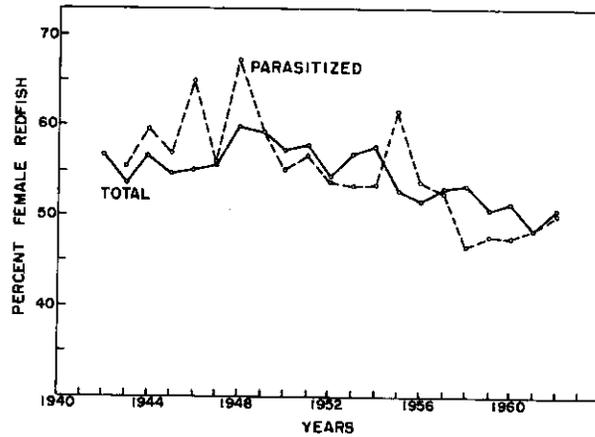


Fig. 10. Annual variations in percentage of female redfish in total Gulf of Maine sample and in samples infested with live *Sphyrion*.

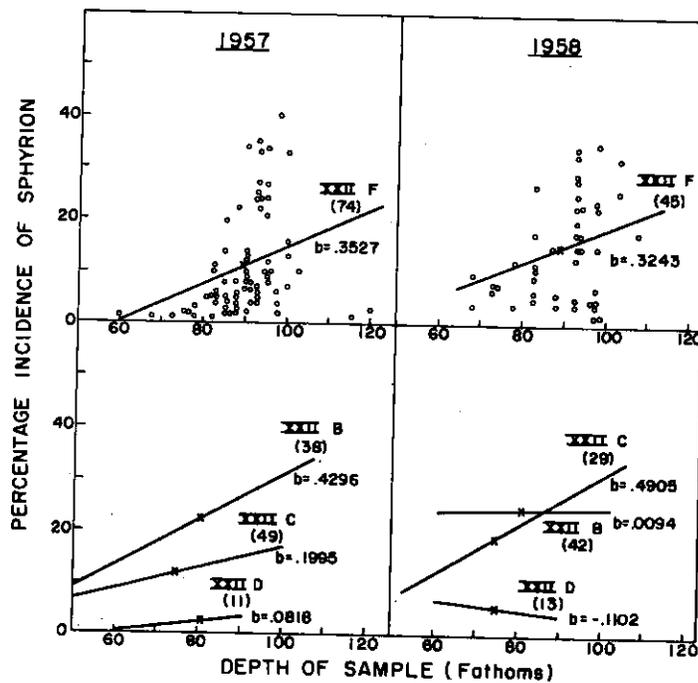


Fig. 11. Regression of percentage incidence of live *Sphyrion* on redfish in relation to depth of capture, by subarea, during 1957 and 1958. Number of samples from each subarea is shown in parentheses.

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.

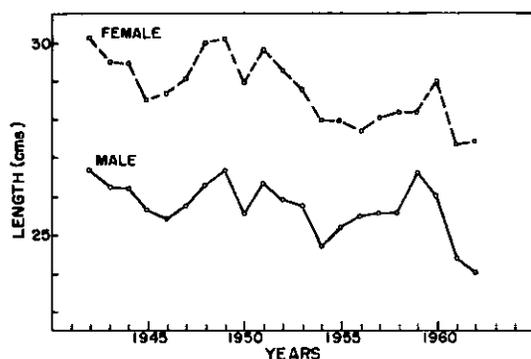


Fig. 12. Variations in mean length of redfish in the Gulf of Maine, 1942-62.

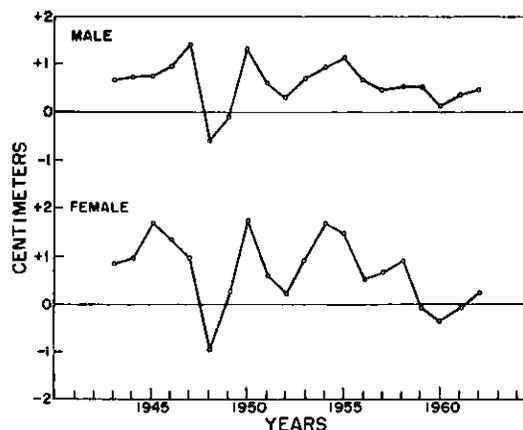


Fig. 13. Difference between annual mean lengths of parasitized redfish and total redfish sample from the Gulf of Maine, 1943-62. Zero lines represent mean lengths of total male and female samples.

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 <i>Sphyrion</i>							Second Stage Infestation (Sores)	Third Stage Infestation (Spots)	Total Sample
		1	2	3	4	5	6	7			
<b>MALES</b>											
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									
<b>FEMALES</b>											
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							417	
24	411	42	5	1				1		472	
25	524	65	8	3	1			9	4	617	
26	627	71	10	4	2	1	1	8	8	725	
27	693	108	16	3	1			5	4	841	
28	710	107	15	1	1			9	11	862	
29	695	101	15					14	14	852	
30	614	85	11	1	1			20	21	738	
31	550	80	11	4				19	17	700	
32	428	59	5	2				21	34	537	
33	409	49	4	3				21	22	508	
34	277	38	4	1				18	25	361	
35	166	23		2				19	22	226	
36	69	9						9	26	89	
37	17	5						5	6	27	
38	7	2						1	4	10	
39	3								1	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									

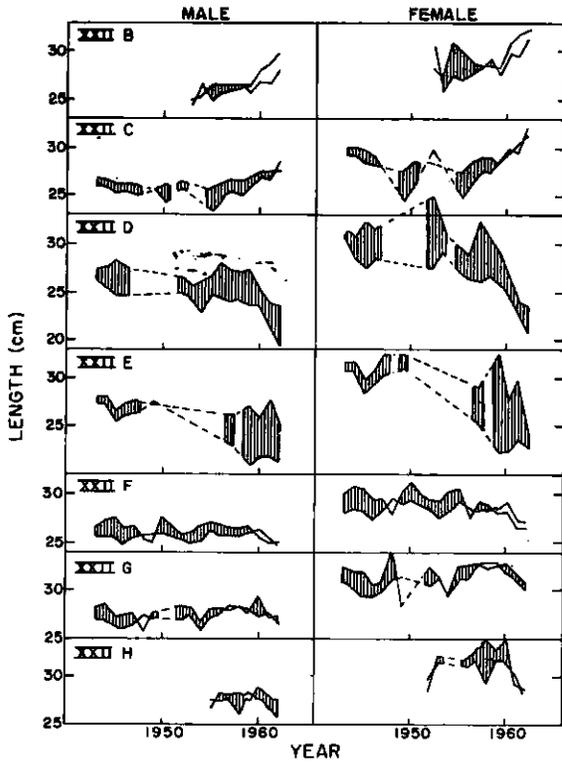


Fig. 14. Variation in mean lengths of parasitized redfish and total redfish sample, by statistical subarea, in the Gulf of Maine, 1943-62. Shaded area represents years when parasitized redfish were larger than the mean length of the whole redfish sample from that subarea.

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

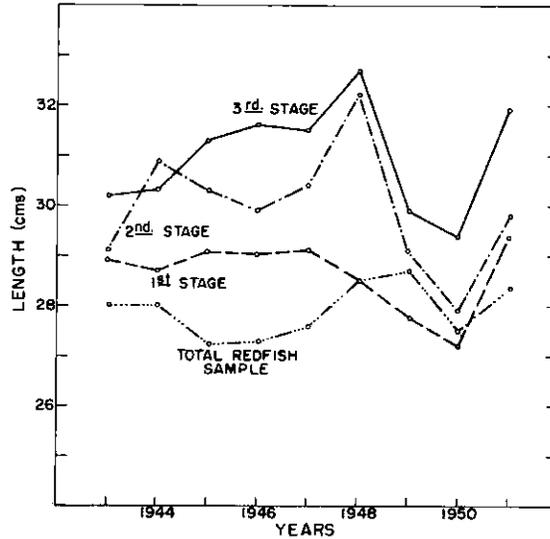


Fig. 15. Comparative annual mean lengths of redfish with first, second, and third stage infestations of *Sphyrion* and that of the total redfish sample from the Gulf of Maine, 1943-51.

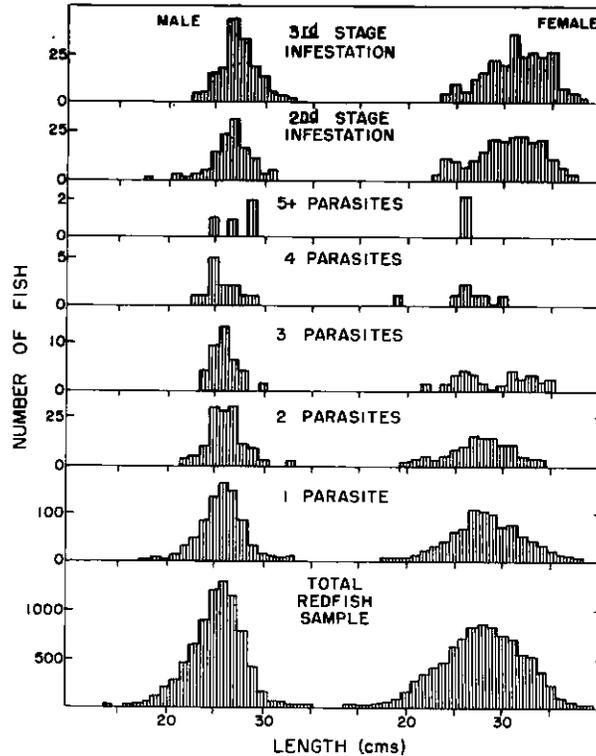


Fig. 16. Comparative size compositions of redfish, grouped as follows: nonparasitized; first stage infestation with 1, 2, 3, 4 and 5 or more live copepods; second stage infestation; and third stage infestation. Data are from statistical subarea XXII F, 1957-59, males and females separated.

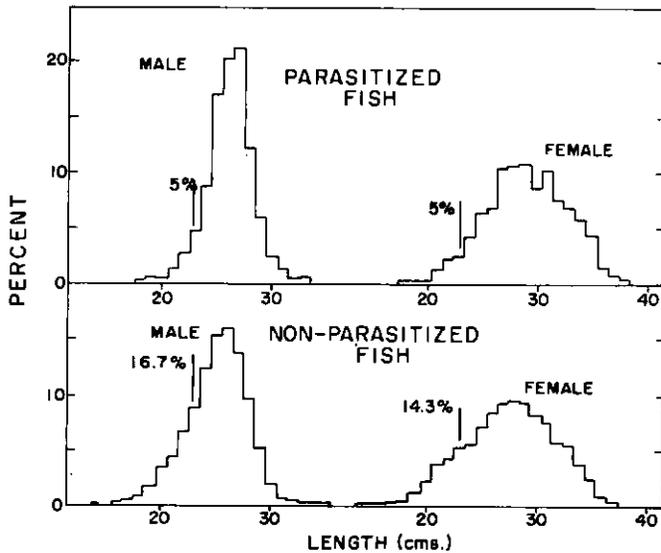


Fig. 17. Percent size composition of parasitized and nonparasitized redfish, sexes separated, in subarea XXII F, 1957-59.

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 composition 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 ‰ 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‰ 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

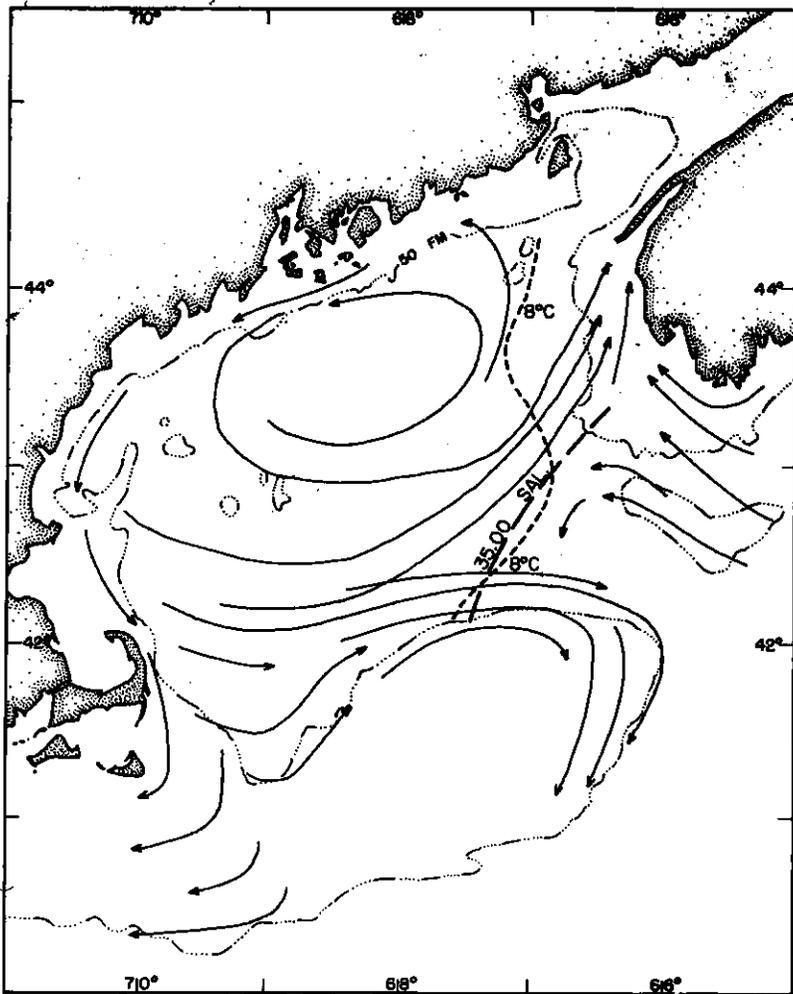


Fig. 18. Approximate location of 8°C bottom temperature and 35 ‰ salinity boundaries representing maximum penetration of ocean water into the Gulf of Maine (Data from Bigelow, 1927).

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. *Sphyron* 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 *Sphyron* 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 Sphyridae. *U.S. Nat. Mus. Proc.*, 55: 549-604.

C-7

DENSITY-DEPENDENT FOOD RELATIONSHIPS WITH  
REFERENCE TO NEW ENGLAND GROUND FISH

By

Roland L. Wigley<sup>1</sup>

## 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, had-dock 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 Borradalle (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 *Chrysomya*, 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,

<sup>1</sup> U.S. Department of the Interior, Fish and Wildlife Service, Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, Massachusetts, USA.

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 (Garlander, 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, *Rutilus*. 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.

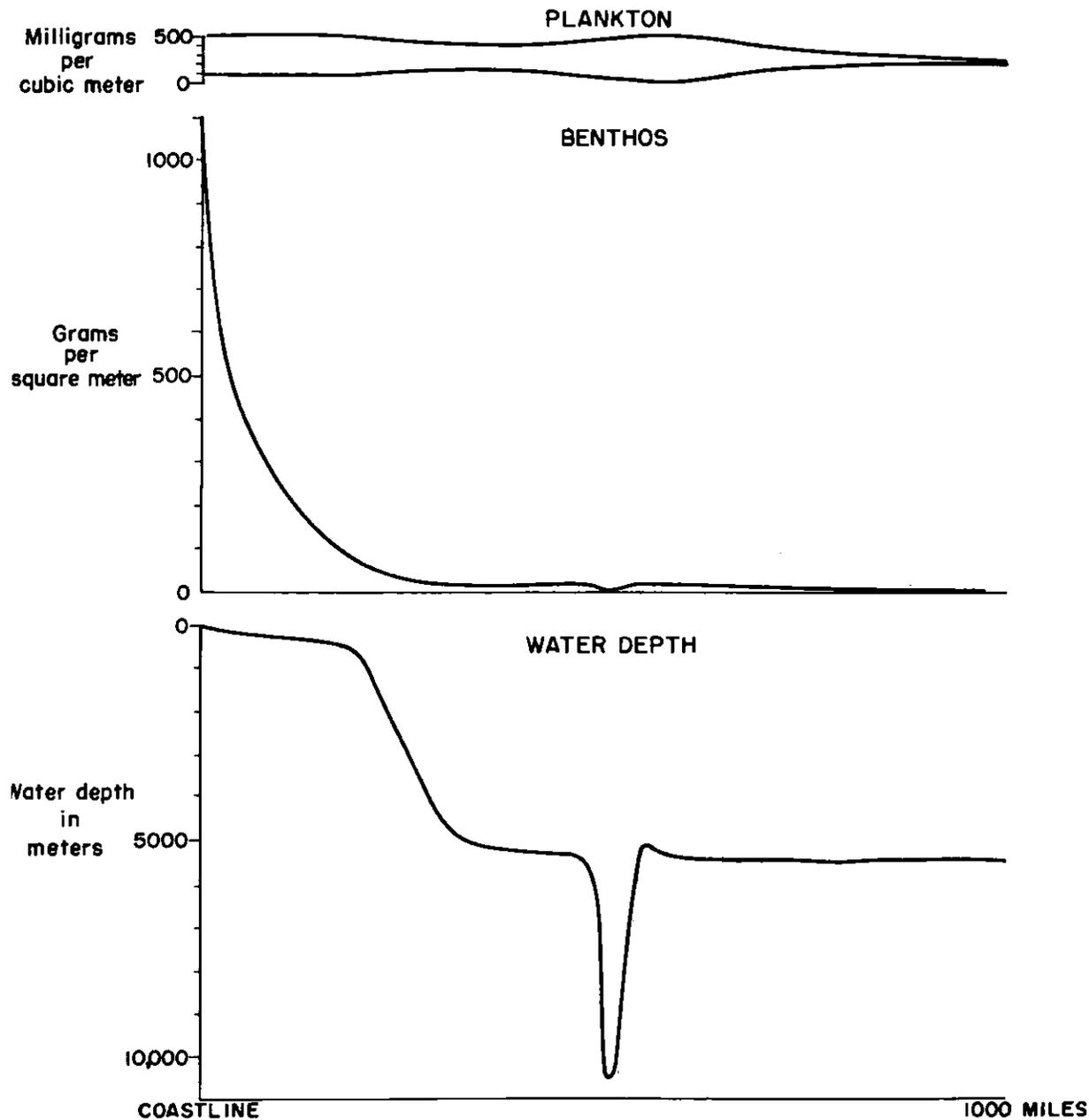


Fig. 1. Quantitative changes in the standing crop of plankton and benthos from shore to 1,000 miles offshore (modified after Zenkevich, 1956).

"Contagious distributions are the rule in nature. Sessile as well as motile animals settle or collect in favorable localities...." according to Allee *et al.*, (1949). Moreover, third in the list 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 surrounding areas tend to congregate."

The aggregation of fish and other aquatic organisms about their food is particularly pertinent to the subject of this report. The following few examples have been selected from the literature to exemplify 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. At the same time the trawl was also crammed with other animals." 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 GROUND FISH

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 in 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 second 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 the 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, *Pseudopleuronectes*; and American dab, *Hippoglossoides*. The spiny dogfish, *Squalus*, was abundant in research 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

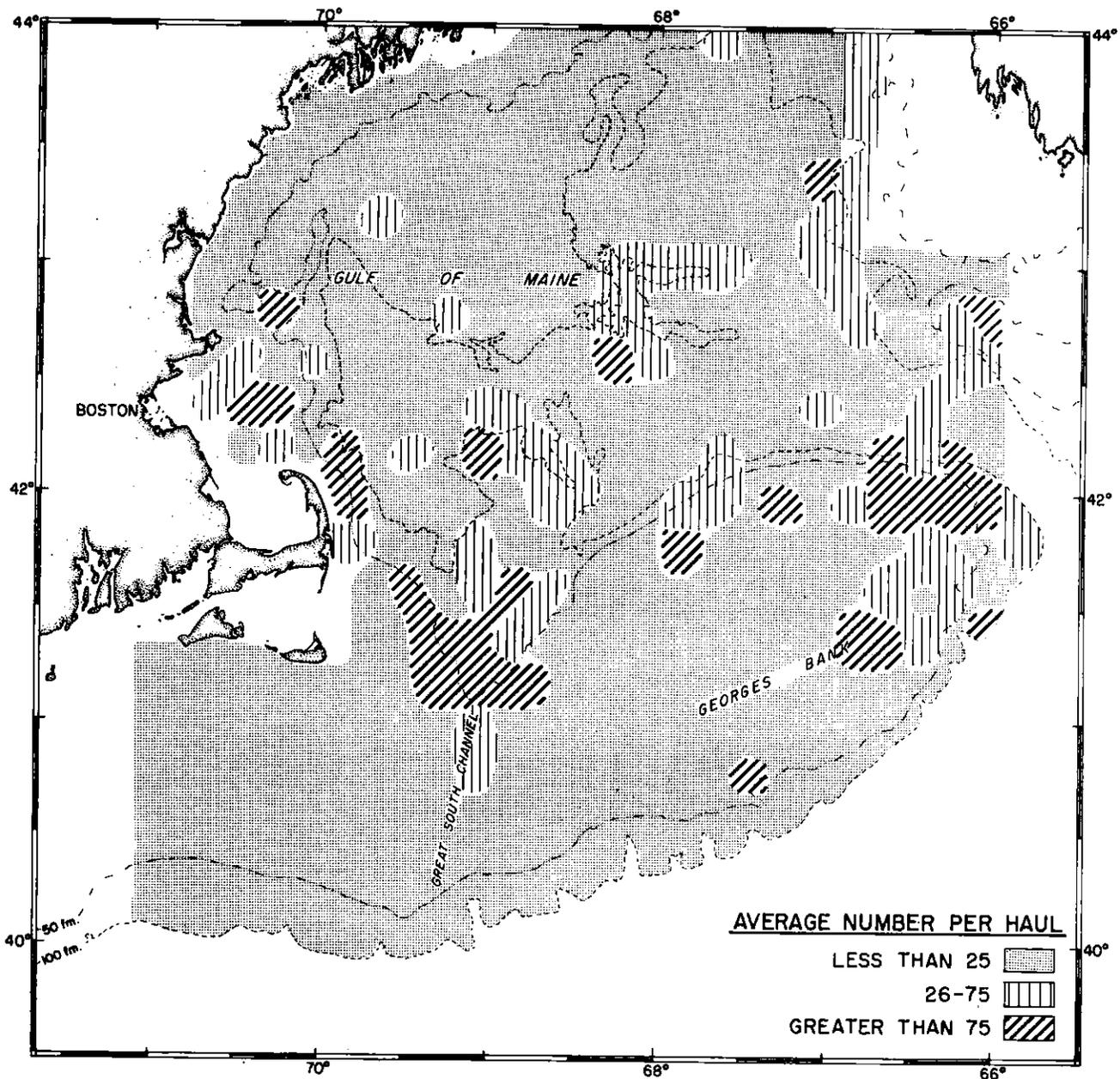


Fig. 2. Autumn density-distribution of haddock based on inventories conducted by research vessels *Albatross III* and *Delaware* from 1955 through 1961. Values are mean numbers of haddock caught per 30-min haul in a No. 36 otter trawl.

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

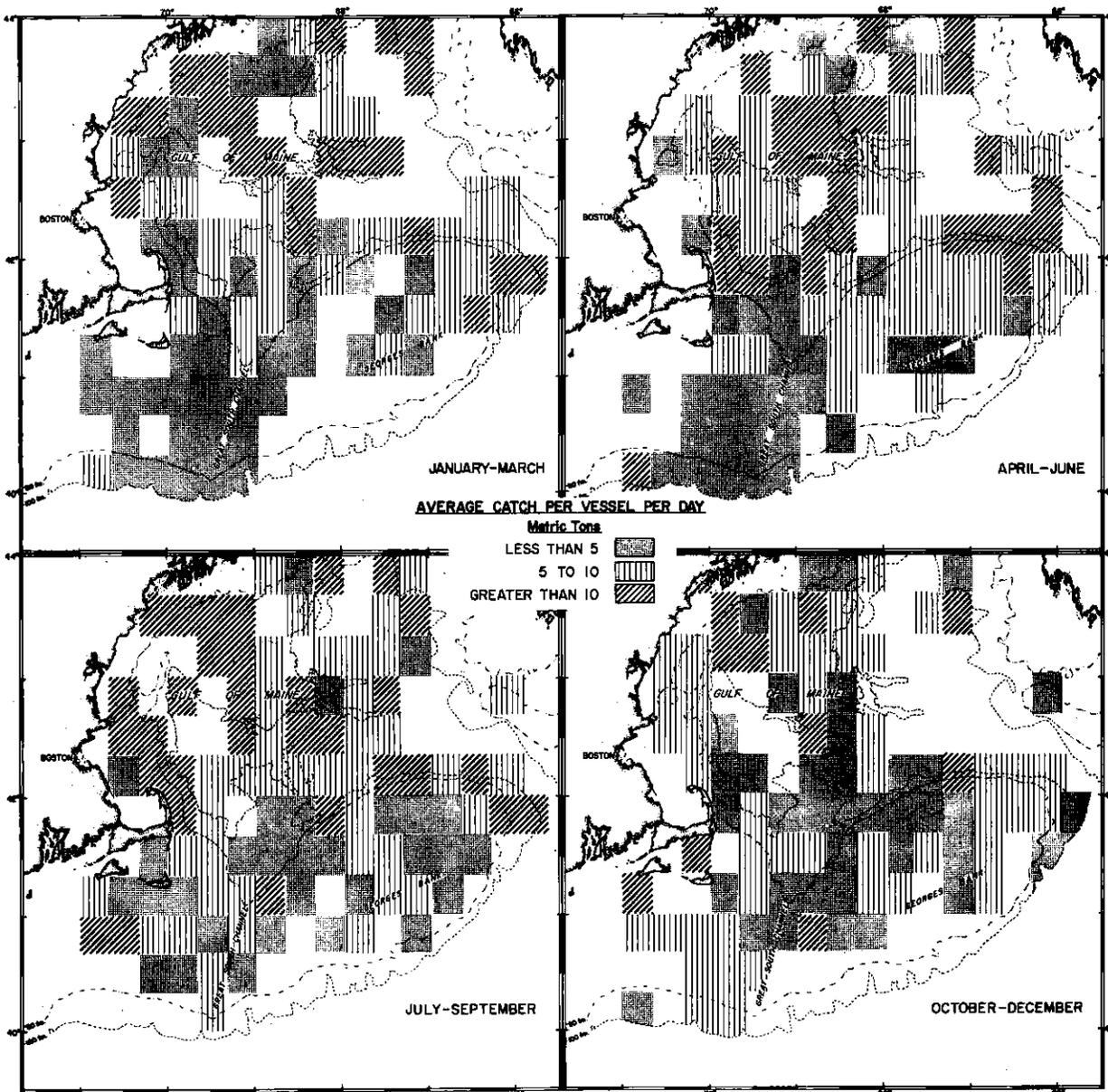


Fig. 3. Seasonal density-distribution of New England groundfish based on commercial landings statistics for 1962. Values are catch per vessel per day in metric tons.

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.

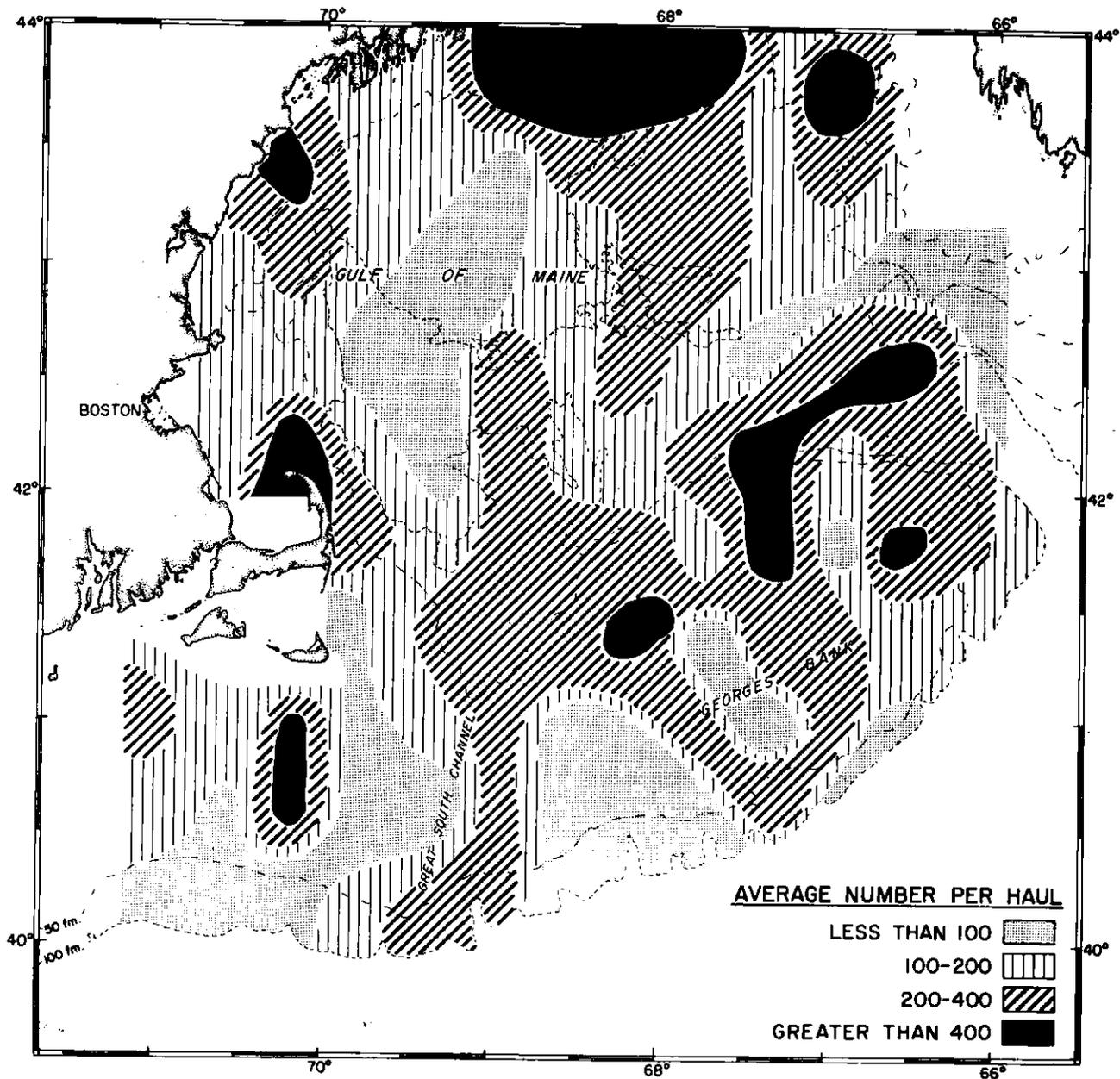


Fig. 4. Autumn density-distribution of New England groundfish based on inventories conducted by research vessels *Albatross III* and *Delaware* from 1955 through 1961. Values are mean number caught per 30-min haul in a No. 36 otter trawl.

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

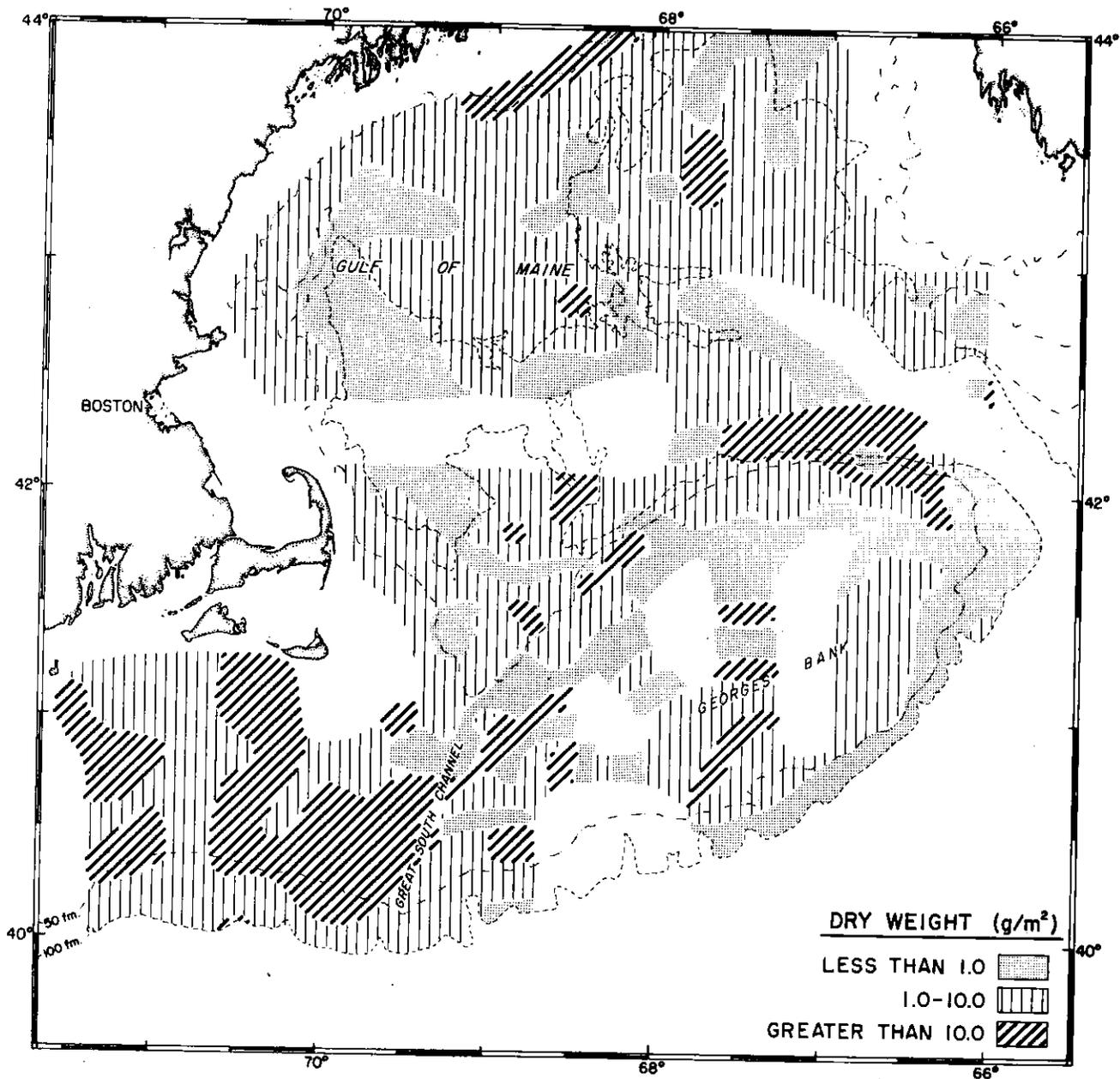


Fig. 5. Biomass of the macrobenthic invertebrate fauna collected with a Smith-McIntyre grab sampler. Values are dry weight (grams) per square meter.

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.

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## 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. Saunders 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.

