SECTION

D

D-1

THE POSSIBLE EFFECTS OF TEMPERATURE ON THE
FECUNDITY OF GRAND BANK HADDOCK

By

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ABSTRACT

Observations on the fecundity of haddock were made from ovaries collected during the springs
of 1957-1961. Certain year-to-year differences in fecundity of fish of the same size and age were
observed. These differences are attributed to the effect of temperature at certain critical per-
iods during the initial development and early maturation of the ova.

INTRODUCTION

During the springs of 1957-1961, in the course of surveying the haddock (*Melanogrammus aegle-
finus* (L.)) population of the Grand Bank (ICNAF Subarea 3), material was collected to study the
fecundity of this species. All specimens were taken from an area along the southwest slope of the
Bank (Fig. 1), where haddock are usually heavily concentrated during winter and spring.

Mature haddock of the Grand Bank generally spawn during May and June, so the ovaries were col-
lected a month or two earlier in March-April. At that time the opaque yolky eggs could be readily
distinguished from the minute grey-coloured ova. Ovaries which were so advanced as to contain large
translucent eggs were not used in the investigation.

The method of preservation in Gilson's fluid was essentially the same as that used by Simpson
(1951) for North Sea plaice. The fecundity estimates were obtained from actual counts of yolky ova
in egg samples from the ovaries. These samples were obtained by fractioning the egg contents of
the ovary with a whirling vessel, the description and operation of which has been given by Wiborg
(1951).

During the course of the investigation year-to-year differences in fecundity of fish of the
same size and age were observed. The significance of these results is discussed in relation to the
possible effects of temperature at certain critical periods during the initial development and
early maturation of the ova.

RESULTS

Fecundity estimates were made for 229 Grand Bank haddock during 1957-61. The data were treated
by applying a logarithmic transformation to the 2 variables and expressing the relationship between
log fecundity and log length in the form

$$\log F = n \log L + \log k.$$

The observations are shown as a, scatter diagram in Fig. 2 together with the fecundity-length curve
for the combined data.

For any one length of fish the fecundity is shown to vary between wide limits. This variation
is much greater than would be expected due to sampling errors and tends to mask any annual dif-
ferences in fecundity that otherwise might be apparent. This aspect is better shown by comparing
the geometric means of the fecundity-at-length data with the values taken from the fitted log-log
regression (Table 1). The data of 1957, being the more substantial, follow closely the fitted
curve as would be expected. The 1958 data are quite irregular for haddock between 44 and 51 cm,
but only 23 observations were made in that year. The 1959 data follow closely the shape of the
fitted curve but, except for the value at 48-49 cm, are consistently below it throughout its en-
tire length. The 1960 fecundity values are in most instances greater than those calculated from the
curve, while those of 1961 are irregular, being based on only 16 fish.

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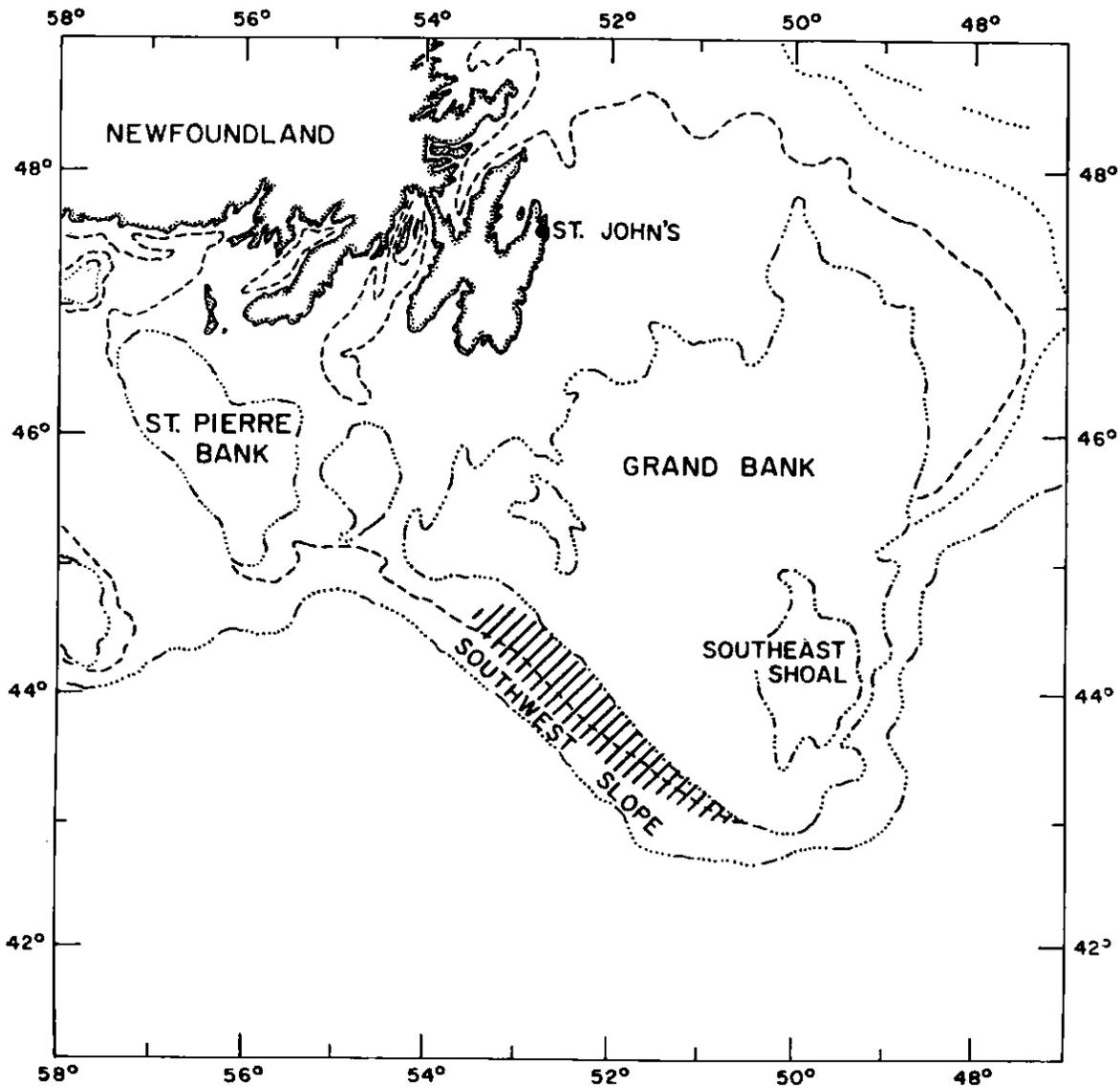
Fig. 1. Map of the Grand Bank showing the approximate location of the winter and spring
concentrations of haddock.

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DEPTH SCALE:
      30 fathoms  (55 m)___.._____..._____..._____...
      50 fathoms  (91 m)___._.._____.._.._____.._.._
     100 fathoms (183 m)___ __ __ __ __ __ __
     200 fathoms (366 m).............................
   1,000 fathoms (1,830 m)__.........._____........._____
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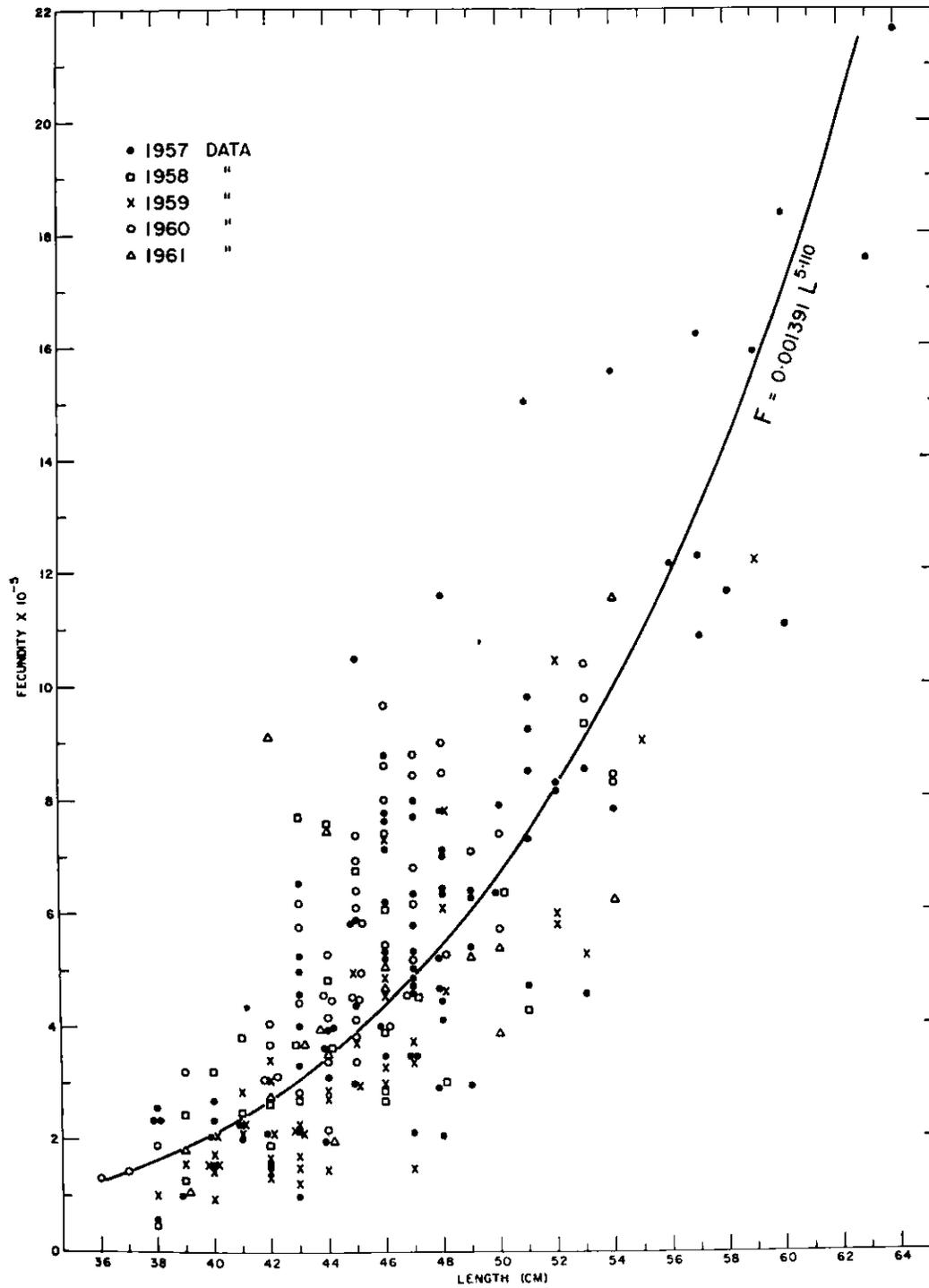
Fig. 2. Individual fecundity estimates for Grand Bank haddock by length and year of
capture together with the fitted regression line.

TABLE 1. GEOMETRIC MEAN FECUNDITIES BY LENGTH AND YEAR OF CAPTURE FOR FEMALE HADDOCK OF THE GRAND BANK, 1957-61.

Length 2-cm intervals	Geometric mean fecundities in thousands of ova (Figures in parenthesis are numbers of specimens)						Range of estimates ('000)	Fecundity calculated from curve ('000)
	1957	1958	1959	1960	1961	1957-61		
36-37	–	–	–	137(2)	–	137(2)	131-144	134
38-39	152(5)	176(2)	127(2)	143(3)	138(2)	148(14)	48-320	176
40-41	211(6)	310(3)	175(9)	–	–	205(18)	95-380	228
42-43	306(10)	327(5)	190(12)	363(8)	450(3)	284(38)	101-909	292
44-45	415(10)	543(4)	290(6)	460(17)	375(4)	418(41)	146-1044	369
46-47	524(21)	381(5)	360(8)	666(12)	484(2)	504(48)	148-963	462
48-49	521(16)	298(1)	600(3)	727(4)	520(1)	546(25)	205-1156	572
50-51	814(8)	520(2)	–	647(2)	456(2)	680(14)	388-1500	704
52-53	713(4)	931(1)	660(4)	1002(2)	–	755(11)	455-1041	859
54-55	1100(2)	–	900(1)	834(2)	846(2)	916(7)	621-1551	1040
56-57	1269(4)	–	–	–	–	1269(4)	1085-1616	1248
58-59	1357(2)	–	1216(1)	–	–	1308(3)	1216-1588	1493
60-61	1422(2)	–	–	–	–	1422(2)	1102-1834	1773
62-63	1748(1)	–	–	–	–	1748(1)	–	2093
64-65	2158(1)	–	–	–	–	2158(1)	–	2460

N	92	23	46	52	16	229	No. of fish
n	4.913	3.635	5.724	5.515	4.110	5.110	Regression coefficient, n
$\log k$	-2.5189	-0.4098	-3.9843	-3.4423	-1.2525	-2.8566	Intercept, $\log k$
r	0.81	0.60	0.88	0.80	0.67	0.79	Correlation coefficient, r

In order to test the significance of the between-yearly differences in intercept (log fecundity adjusted to a common log body length) and in slope (rate of increase of log fecundity with log length), an analysis of covariance was used according to Snedecor(1956). The F-value derived from the ratio of mean square for adjusted means to mean square for common regression measures the significance of the sample differences in intercept. The F-value derived from the ratio of mean square for regression coefficients to mean square within samples measures the degree of variability in the regression coefficients or slopes.

No significant difference was indicated between the regression coefficients of the yearly samples, but a significant difference at the 1% level resulted when the test was applied to measure the variability in intercepts. It has already been noted that the fecundity averages for 1959 are nearly all less than the values taken from the fitted curve. In an analysis of covariance of the data, omitting the fecundity estimates for 1959, neither the regression coefficients nor the intercepts are significantly different. Similar tests were applied by omitting the data of the years 1958, 1960 and 1961 individually, but the results were essentially the same as those in the first test. Consequently the variation shown by the first test is due in large part to the inclusion of the 1959 data.

Because of the great variation in year-class survival as shown by the age distribution of the samples collected for fecundity estimates in the years 1957-61 (Table 2), an analysis of the data is rendered difficult in so far as making comparisons between years and ages are concerned. However, despite the inadequacy of the data with regard to age, some indication of the annual variation in haddock fecundity by length and age is shown in Table 2, the last three columns of which give the geometric mean lengths of fish and fecundity estimates by age together with the corresponding fecundity values as calculated from the curve of Fig. 2. The similarity of the observed and calculated fecundity values for 1957 and 1958 must be noted. In 1960 the observed fecundity values for ages 5-11 are considerably greater than those calculated from the curve. In 1961 except for age 8, the observed and calculated values are reasonably similar considering the small numbers of observations involved.

TABLE 2. GEOMETRIC MEAN FECUNDITIES BY YEAR OF CAPTURE, AGE AND LENGTH
FOR FEMALE HADDOCK OF THE GRAND BANK, 1957-61.

Year of capture	Age (yr)	Geometric mean fecundities in thousands of ova by 4-cm length intervals (figures in parenthesis are numbers of fish)								Geometric mean		Fecundity calculated from curve ('000)
		36-39	40-43	44-47	48-51	52-55	56-59	60-63	64-67	Length (cm)	Fecundity ('000)	
1957	5	153(5)	249(10)	390(1)	–	–	–	–	–	40.5	220(16)	227
	8	–	298(6)	471(30)	605(24)	928(5)	1216(2)	1102(1)	–	47.7	550(68)	527
	11	–	–	–	–	455(1)	1267(3)	–	2158(1)	57.7	1148(5)	1380
	15	–	–	–	–	–	1588(1)	–	1791(2)	60.6	1720(3)	1780
1958	5	–	246(1)	–	–	–	–	–	–	41.0	246(1)	243
	6	176(2)	290(6)	447(3)	–	–	–	–	–	42.3	298(11)	283
	9	–	764(1)	446(6)	432(3)	931(1)	–	–	–	46.8	496(11)	480
1959	4	–	154(1)	–	–	–	–	–	–	40.0	154(1)	213
	6	127(2)	190(6)	290(3)	–	–	–	–	–	42.1	198(11)	277
	7	–	183(14)	314(10)	527(2)	578(1)	1216(1)	–	–	44.3	267(28)	360
	10	–	–	728(1)	778(1)	736(4)	–	–	–	50.9	742(6)	735
1960	4	48(1)	–	–	–	–	–	–	–	38.0	48(1)	163
	5	153(3)	402(1)	–	–	–	–	–	–	38.2	195(4)	170
	7	320(1)	326(3)	608(8)	843(1)	–	–	–	–	44.4	514(13)	363
	8	–	385(4)	481(18)	645(3)	–	–	–	–	45.2	481(25)	400
	11	–	–	731(3)	720(2)	914(4)	–	–	–	50.1	805(9)	673
1961	6	138(2)	273(1)	339(3)	–	–	–	–	–	42.3	242(6)	283
	8	–	578(2)	347(1)	536(1)	–	–	–	–	44.7	499(4)	377
	9	–	–	588(2)	449(2)	–	–	–	–	47.2	514(4)	500
	12	–	–	–	–	846(2)	–	–	–	54.0	846(2)	990

For 1959, on the other hand, the fecundity estimates as observed for ages 4, 6 and 7 are substantially below the calculated values, whereas the observed and calculated values for age 10 are similar. Examination of the catch records reveals that the 1959 specimens were taken in depths between 86 and 270 m (47 and 148 fathoms), while the samples in the other years were taken in depths between 77 and 183 m (42 and 100 fathoms). The records further reveal that most of the haddock age 7 and younger were taken in less than 183 m (100 fathoms), but most of the 10-year-olds were caught

in deep water over 183 m (100 fathoms), where they probably migrated at an earlier age and where they were not as liable to be affected by the violent changes in environmental conditions that often occur at shallower depths along the southwest slope of the Grand Bank (Templeman and Hodder, this symposium). The significance of the fluctuations in fecundity observed in 1959 and 1960 is discussed in the next section.

DISCUSSION

It has been shown that considerable variation in fecundity of Grand Bank haddock may occur from year to year. In particular, the 1959 fecundity estimates for fish of the same size and age were in general substantially lower than the averages for the 5 years combined (1957-61), while in 1960 the fish appeared to be generally more fecund. Such variation in annual egg-production has not previously received much attention. The most important work in this regard is that of Bagenal (1957) on long rough dabs (*Hippoglossoides platessoides*) for the years 1954, 1955 and 1956. He points out that the fecundity in 1955 was significantly lower than that in 1954 and 1956, even after allowance was made for length differences. Similar significant differences were evident for fish condition. He does not offer any other explanation for this except to point out that the differences were not due to differences in the age structure of the population.

In discussing the variation in individual fecundity of plaice (*Pleuronectes platessa*), Simpson (1951) observes that there are at least two critical periods in which the number of eggs to be laid may be influenced: one is the period when the germinal epithelium is being laid down during the first year of life, and the other is either the time when the new primary oocytes are being formed each year or when the eggs to be laid in the next spawning season are separated from the mass of resting oocytes. He discounts the first possibility, since it might determine the fecundity potential of the fish for life. Simpson's second critical period should really be called the second and third critical periods, for a considerable period of time might elapse between the formation of the primary oocytes and the separation from the mass of resting oocytes of the batch of ova for spawning in a subsequent spawning season.

Reibisch (1899) and Franz (1910) point out that once maturity is first reached two or three years elapse between the formation of oocytes and the final liberation of the resulting eggs, the eggs to be spawned in any winter being separated from the resting oocytes during the summer immediately preceding spawning. Raitt (1933) has thoroughly reviewed the literature with regard to intra-ovarian egg-groups. From this and from his own observations on North Sea haddock he concludes that in ripening ovaries two separate groups of ova are present (opaque-yolked and transparent-yolkless eggs), the first group to be laid in the approaching spawning season and the second to be laid in the following or possibly succeeding years.

1. In the following discussion, we shall consider three possible critical periods. Assuming that the period of intra-ovarian development is two years and that the critical period is the time of formation of the oocytes, it is possible that the low fecundity of haddock in 1959 and the high fecundity in 1960 might be the result of environmental conditions existing during the springs of 1957 and 1958 respectively. Templeman (1958, 1959, 1960) from hydrographic evidence points out that during the summers of 1957 and 1959 bottom temperatures on the southern Grand Bank were unusually low, whereas in 1958 they were generally above normal. Further evidence to support this statement is given by Templeman (this symposium) for a hydrographic station (No. 27) located off St. John's in the coastward part of the Labrador Current. The mean surface to bottom (175 m; 96 fathoms) water temperatures for the period January to May of the years 1955-59 are given below. Also given for comparison are the mean January-March air temperatures at St. John's Airport as compiled from air temperature records of the Meteorological Division of the Canadian Department of Transport (Anon., 1950-62).

| Year | Mean Temperature (°C) | |
	Water	Air
1955	-0.62	-3.0
1956	-0.35	-2.9
1957	-1.19	-5.8
1958	-0.21	-1.1
1959	-1.03	-6.0
1950-62	-0.65	-3.3

During the winter months haddock are generally concentrated along the southwest slope of the Grand Bank in depths greater than 90 m (50 fathoms). At this time the shallower parts of the bank are completely covered with cold water of less than 1°C and often there is much water below 0°C. In a year like 1957, when an unusually large volume of cold water flowed southward along the east coast of Newfoundland and covered the Grand Bank for a longer-then-normal period, the haddock were forced deeper and became heavily concentrated along the narrow southwest slope. The resulting over-crowded conditions, in which lack of food supposedly restricts growth, as argued by Lack (1954), pro-bably had the effect of reducing the fecundity of haddock two years later in 1959. In 1958, on the other hand, the higher-than-normal temperature conditons that existed throughout most of the area caused the haddock concentrations to be dispersed from their winter-quarters a month or more earlier than usual, thus favouring good growth in the spring and early summer and consequently greater egg-production two years later in 1960. Hydrographically, the years 1955 and 1956 were more or less typical of the average conditions in recent years. Conditions in 1959 were somewhat similar to those of 1957, but the small number of fecundity observations in 1961 are not sufficient to show whether or not the fecundity was lower than average in that year.

If, as Reibisch (1899) and Franz (1910) suggest, the eggs to be spawned in an approaching spaw-ning season are separated from the resting oocytes during the preceding summer, and if we consider this period as the critical one, then the environmental conditions existing in 1958 and 1959 may have been responsible for the low fecundity of 1959 and the higher-than-average estimates for 1960. Assuming that, for a particular ovary, the surface area of the lamellae on which egg growth takes place is limited (by the size of the ovary), it follows that the number of eggs for spawning in the following spring is related not only to the size of the ovary but also to the size of the eggs at the time when the limit of coverage of the basic surface area of the lamellae is reached. If this is so, fecundity might be related to the function of growth which these eggs undergo during the period in the summer when they are being separated from the resting oocytes. Therefore, in a year when growth conditions are favourable (e.g. 1958), it is possible that fewer large oocytes will occupy the available surface area of the ovarian lamellae and result in lower fecundity at spawning time of the following year. If conditions are unfavourable, thus restricting egg growth, a larger number of small oocytes may now occupy the surface area of the ovarian lamellae with the end result of higher fecundity in the next spawning season.

3. Perhaps the egg-production of individual fish in any one spawning season is the result of environmental conditions during the few months immediately preceding spawning. Vladykov (1956) for speckled trout (*Salvelinus fontinalis*) in Quebec lakes says that an abundant food supply for adults during several months preceding spawning resulted in higher fecundity at spawning time. Scott (1962) carried out experimental diet restriction on rainbow trout (*Salmo gairdneri*) and found that starva-tion during the months preceding spawning influenced the number of eggs by increasing the rate of atresia. Although there is no evidence at present to indicate that follicular atresia plays a very important role in the fecundity of those marine fishes which produce large numbers of small pelagic eggs, it is possible that severe food restriction during a period of several months preceding spaw-ning may induce some reabsorption of ova. To this extent overcrowding during the winter and spring of 1959, caused by the abnormally-low temperature conditions, may have resulted in low fecundity at spawning time in that year. However, the unusually low temperature conditions in 1957 cannot by this hypothesis be related to the normal fecundity estimates for that year.

Much of the above discussion is speculative, since the effect of such factors as temperature on the processes of growth and reproduction is not fully understood.

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D-2

RELATION OF PERIODS OF SUCCESSFUL YEAR-CLASSES OF HADDOCK ON THE GRAND BANK TO PERIODS OF SUCCESS OF YEAR-CLASSES FOR COD, HADDOCK AND HERRING IN AREAS TO THE NORTH AND EAST

By

Wilfred Templeman[1]

ABSTRACT

In the period 1942-58 for which information is most complete, there were years or two or three adjacent years when successful year-classes of cod, haddock and herring were produced in Greenland, Iceland and the Norwegian to Barents Sea area. There were also intervening years or groups of years when successful year-classes were relatively scarce. The more scanty data for cod and herring from previous years back to 1912 also indicate that certain years or adjacent years were more favourable than others for the production of good year-classes throughout this region.

For cod in the years 1912-45, good year-classes occurred at West Greenland in the same years which also produced successful year-classes at Iceland. In more recent years, good year-classes of cod at West Greenland may often occur independently to or may occur one year later than good year-classes at Iceland.

For the years since 1942, successful year-classes of West Greenland and East Greenland cod usually have occurred one year after a successful year-class of Grand Bank haddock. For this period, also, Icelandic cod, haddock and herring tended to have good year-class survival in the same year as Grand Bank haddock with a tendency, also, for equally successful year-classes of haddock and herring and smaller year-classes of cod to occur one year and occasionally two years later than successful year-classes of Grand Bank haddock.

Arcto-Norwegian cod, haddock and herring in recent years generally had successful year-classes one or two years after Grand Bank haddock. The haddock year-class relationships between the two areas were closest and were generally one year apart. In an earlier period, 1912-44, when West Greenland cod may have been largely derived from Icelandic spawning, good year-classes of Atlanto-Scandian herring usually occurred one year after a good year-class of West Greenland cod. In more recent years, with the success of West Greenland year-classes of cod more dependent on spawning in West Greenland waters, the tendency has been for successful year-classes of Atlanto-Scandian herring to occur in the same year as a successful year-class of West Greenland cod.

In recent years successful year-classes of Grand Bank haddock, with one exception, have occurred only in years with low iceberg numbers.

A complete explanation of all the relationships described cannot be offered at present and some of the inter-related occurrences appear to be too close together in time. However, the occurrence of good year-classes of different species over such a wide area, usually in the same sequence of years, indicates more than unrelated local phenomena and argues for an inter-relationship through and variations in the Gulf Stream which may affect the southern Grand Bank through eddies and intermingling with Grand Bank-Labrador Current water and through its North Atlantic Current branches affect the Icelandic, Greenland and the Norwegian-Barents Sea areas.

INTRODUCTION

The haddock of the southern Grand Bank are at the northern extremity of their spawning range on the continental shelf in this area and are subject to great variations in year-class strength. It is the purpose of this paper to compare the timing of the successful year-classes of haddock on the southern Grand Bank with that of successful year-classes of cod, haddock and herring in Greenland, Iceland and the Arcto-Norwegian area.

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Much of the information on year-class strength has been obtained from the following papers: for cod and haddock, Tåning (1931, 1936), Sund (1936), Raitt (1936, 1948), Thompson (1929, 1939), Rollefsen (1954), Hansen (1939, 1949, 1954), Jónsson (1954), Baranenkova (1960), and for herring, Sund (1943).

The remaining information on year-class success especially in recent years has come mainly from papers too numerous to mention in detail in such a short paper, by many authors in many years in Annales Biologiques and ICNAF Proceedings. Among these the following authors have supplied most of the information: for West Greenland cod, Hansen, Jónsson, Rasmussen, Meyer, Rúivo, and Quartin, and Bratberg; for East Greenland cod, Meyer, Hansen and Jónsson; for Icelandic cod, Fridriksson and Jónsson; and for Arcto-Norwegian cod, Rollefsen, Lundbeck, Meyer and Maslov.

For haddock, additional year-class information, mainly from Annales Biologiques, has been obtained for Iceland from Baranenkova, Meyer and Fridriksson; and for the Arcto-Norwegian area from Baranenkova, Maslov, Meyer, Lundbeck and Saetersdal.

For herring, the information has come mainly from papers in Annales Biologiques by Fridriksson for the Icelandic area and by Devold for the Norwegian area.

The iceberg numbers south of 48°N in the eastern Newfoundland area in Table 1 are from the various Bulletins of the U.S. Coastguard giving the Ice Patrol Reports for the years 1902-61.

The following people have assisted by giving their opinions on year-class strengths for certain of the species and areas: Dr Paul Hansen, Mr Jón Jónsson, Mr Jakob Jakobsson, Mr Steinar Olsen, Mr O.J. Østvedt, Mr John Corlett and Mr John Gulland.

It is inevitable, however, that there will be some errors in the list of year-class strengths both from failure to have or to assess the complete information. For the Arcto-Norwegian cod data, apart from the most recent years, we have depended largely on Norwegian assessments based chiefly on the skrei, but in recent years there has been an increasing proportion of this Arcto-Norwegian stock caught as immature fish. There are differences in our list of successful year-classes of this stock and that of Seryakov (MS, 1962) and an unpublished list by Mr John Gulland. Our list will doubtless need correction at some future date when there are enough published data to make a critical comparison.

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RELATION OF OCCURRENCE OF SUCCESSFUL YEAR-CLASSES OF
COD, HADDOCK AND HERRING IN VARIOUS AREAS

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1: Haddock, Grand Bank

Only for recent years since 1942 is a good approximation possible of the relative success of haddock year-classes in the Grand Bank area. In this period there have been two very successful year-classes, 1949 and 1955, three moderately successful, 1942, 1946 and 1952 and three of modest survival, 1947, 1953 and 1956. In the remaining years only small or very small numbers of young haddock survived.

2: Cod, Haddock and Herring, West Greenland — Barents Sea since 1942

For the period 1942-58 there are years, or two or three adjacent years, when successful year-classes of cod, haddock and herring are produced over much of the area under discussion from West Greenland to the Barents Sea. There are, also, intervening years or groups of years when successful year-classes are relatively scarce. Especially is this true if only the abundant and very abundant year-classes are considered (Table 1).

Two especially successful years for survival of young were 1950 and 1956 with, especially for 1950, some success in each adjacent year. There was, also, fair success in 1942, 1945, 1947, 1948 and 1953.

The 1950 and 1956 successes in year-class survival occurred one year after the production of the two most successful and very abundant year-classes of haddock on the Grand Bank. The 1947, 1948, 1953 and 1957 years of moderately successful survival occurred one year after an abundant or moderately abundant survival of haddock year-classes on the Grand Bank. The moderate success in

TABLE 1. SUCCESSFUL YEAR-CLASSES.

* moderately abundant
** abundant
*** etc.very abundant

Year-class	Grand Bank haddock	Cod				Haddock		Herring			Iceberg numbers south of lat. 48°N Nfld. area	Relative total year-class strengths all species -not including G. Bank	
		West Green-land	East Green-land	Iceland	Arcto-Norwe-gian	Iceland	Arcto-Norwe-gian	Icelandic spring spawners	Icelandic summer spawners	Atlanto-Scandian stock		Total	Total abundant to very abun-dant only
1962	...	...	...	...	***?	...	...	...	...	...	...		
61	...	...	...	...	...	...	***?	...	...	...	115		
1960	...	*?	...	...	**?	...	...	...	...	**(*?)	253		
59	...	...	...	...	*	...	*	...	...	**(*?)	693		
58	...	*	...	...	*	**	...	...	...	...	1	0	2
57	*	**	...	*	**	**	*	**	...	...	931	4	6
56	****	**	**	***	...	*	**	...	***	...	80	15	16
55	...	...	...	...	*	*	...	...	*	...	61	3	5
54	*	**	**	...	*	...	*	...	...	...	312	0	2
53	**	...	*	...	...	**	**	**	*	...	56	6	7
52	...	...	*	*	*	**	...	**	**	...	14	0	3
51	...	**	**	*	*	***	****	**	*	*****	6	6	8
1950	****	**	*	*	**	***	...	*	*	...	460	20	22
49	...	...	...	...	**	...	***	...	**	...	47	7	10
48	*	***	...	...	*	...	...	...	...	*	523	5	5
47	**	...	**	...	...	**	...	...	...	...	63	5	7
46		...	...	...	...	...	...	...	...	...	430	2	2

TABLE 1. cont'd.

Year-class	Grand Bank haddock	Cod				Haddock		Herring			Iceberg numbers south of lat. 48°N Nfld. area	Relative total year-class strengths all species —not including G. Bank	
		West Green-land	East Green-land	Iceland	Arcto-Norwe-gian	Iceland	Arcto-Norwe-gian	Icelandic spring spawners	Icelandic summer spawners	Atlanto-Scandian stock		Total	Total abundant to very abun-dant only
1945	...	**	*	****	...	**	...	*	*	...	1,087	11	8
44	...	...	...	*	*		...	...	...	*	700	3	0
43	...	...	...	*	*		...	...	...	**	840	4	2
42	**	**	**	***	*		...	...	...	...	30	8	7
41	...	...	...	...	...		...	...	...	...	2[a]	0	0
1940	*?	...	...	...	...		...	*	...	...	10[a]	1	0
39	...	...	...	...	...		...	...	...	...	850[a]	0	0
38	...	...	...	...	...		...	...	...	*	660[a]	1	0
37	*?	***	...	**	***		***	...	...	**	470	8	8
36	*?	***	...	**	*		...	...	...	...	22	6	5
35	*?	***	...	**	*		...	...	...	**	875	3	2
34	*?	...	...	**	*		...	...	...	*	576	8	7
33	*?	*	...	**	*	*	...	...	...	*	216	4	2
32	*	*	...	**	*	**	...	...	...	...	514	6	2
31	...	...	...	...	**	...	...	...	...	**	13	6	4
1930		...	...	...	**	...	...	...	...	...	475		
29		...	...	...	*	...	...	...	...	...	1,351		
28		...	...	...	*	...	...	...	...	...	515		
27		...	...	*	*	...	...	...	...	...	389		
26		**	...	...	*	**	...	...	...	*	345		
25		...	...	...	...	*	...	...	...	...	109		
24		**	...	***	...	...	...	...	...	...	11		

TABLE 1. cont'd.

Year-class	Grand Bank haddock	Cod				Haddock		Herring			Iceberg numbers south of lat. 48°N Nfld. area	Relative total year-class strengths all species —not including G. Bank Total abundant to very abundant only
		West Greenland	East Greenland	Iceland	Arcto-Norwegian	Iceland	Arcto-Norwegian	Icelandic spring spawners	Icelandic summer spawners	Atlanto-Scandian stock		Total
1923										**	236	
22	***	***		****	*	**					523	
21					*	*					746	
1920				*	*						445	
19					***						317	
18	**				***					*	199	
17	**	**		*	***	*					38	
16					*	*					54	
15				*	**						468	
14											731	
13	*?	*?		*	**					*	550	
12				*							1,019	
11											396	
1910	*?	*?									50	
09											1,024	
08						*					222	
07											638	
06											405	
05						*					845	
04					**	*				*****	265	
03						*					802	
02											41	

a = approximate from figure.

1942 and 1949 was in the same year with an abundant survival of haddock on the Grand Bank and in 1951, two years after a very abundant haddock year-class on the Grand Bank. Only the 1945 success in the Greenland and Icelandic areas appears to be unrelated to a recent successful haddock survival on the Grand Bank.

2.1 West Greenland and East Greenland Cod. In recent years there is an excellent relationship between the occurrence of an unusually successful year-class of cod in West Greenland and the success of survival of Grand Bank haddock. All five abundant to very abundant year-classes of West Greenland cod since 1946 came the year after a moderately abundant to very abundant year-class of Grand Bank haddock. Four of these came one year after an abundant to very abundant Grand Bank haddock year-class and only one of three moderately abundant Grand Bank haddock year-classes was followed by an abundant year-class of cod in West Greenland.

One successful year-class of West Greenland cod, that of 1942, occurred in the same year as a successful year-class of Grand Bank haddock and another, that of 1945, was apparently not related to a successful year-class of Grand Bank haddock.

All the abundant year-classes of East Greenland cod have occurred in years when there was also an abundant survival of West Greenland cod but there have been other years of moderate survival, two of three being in the same year as an abundant to very abundant year-class of Grand Bank haddock. Cod of the East Greenland area have not been so intensively investigated as those of West Greenland and the year-classes cannot be assessed with as great accuracy.

2.2 Icelandic Cod, Haddock and Herring. In recent years since 1942 better than average year-classes of Icelandic cod have some tendency to occur in the same year and magnitude as successful year-classes of Grand Bank haddock, and usually moderately abundant year-classes occur the year afterward (in 1944, two years afterward). The very abundant 1945 year-class appears to be unrelated to the success of a year-class of Grand Bank haddock.

The recent information on year-classes of Icelandic haddock begins with 1945. Although these haddock usually have better than average year-classes in the same years as the Icelandic cod and in the same years with good survival of haddock on the Grand Bank, there is also a tendency in some cases for Icelandic haddock, like the Greenland cod, to have a successful year-class one year later than that for Grand Bank haddock (in 1951, two years later).

Icelandic herring show some tendency, but more for the summer than for the spring spawners, to have successful year-classes in the same year as the Grand Bank haddock but there is also some tendency for a good year-class to occur a year later and in one case two years later. The year-class of 1945, generally successful in the Greenland and Icelandic area and not represented by haddock success on the Grand Bank, was also moderately successful for Icelandic herring. In the Icelandic area the success of survival of herring, although having some relationship to that of cod, has still more agreement with that of haddock. There appear, however, to be less good year-classes of herring, unless different criteria are used for judging herring. It is especially close to the time of the very abundant Grand Bank haddock year-classes of 1949 and 1955 that unusually successful year-classes of herring appeared at Iceland. Lesser year-classes of haddock on the Grand Bank were not followed by exceptional year-classes of Icelandic herring.

2.3 Arcto-Norwegian cod and haddock and Atlanto-Scandian herring. The variations in survival of the Arcto-Norwegian cod do not seem to be as extreme as those of West Greenland cod, or there is a tendency to assess more of the year-classes of Arcto-Norwegian cod as moderately abundant. The moderately abundant to very abundant year-classes of Arcto-Norwegian cod in recent years between 1942 and 1958 usually occurred one or two years after a moderately abundant to very abundant year-class of Grand Bank haddock.

All six moderately abundant to very abundant year-classes of Arcto-Norwegian haddock between 1948 and 1957 occurred one year after a moderately abundant to very abundant year-class of Grand Bank haddock. In all cases except one there is a qualitative relationship, the moderately abundant and the more abundant year-classes of Norwegian haddock following one year after moderately abundant and more abundant year-classes, respectively, of Grand Bank haddock. In the remaining case the 1948 very abundant year-class of Arcto-Norwegian haddock can be considered either as following one year after the moderately abundant year-class of Grand Bank haddock or two years after an abundant year-class, that of 1946.

For the Atlanto-Scandian herring the 1904 and the 1950 year-classes were so large that all other year-classes suffer by comparison and for nine and eight years respectively after these two year-classes no even moderately abundant year-class appeared. Between 1942 and 1950, however, the four moderately abundant to very abundant year-classes of Atlanto-Scandian herring appeared one to two years after an abundant to very abundant year-class of Grand Bank haddock.

3: Successful Year-classes before 1946

For the period earlier than 1942 the years when successful year-classes of Grand Bank haddock occurred are in doubt since the information is too general. Information on year-class strengths is also lacking for many of the other areas and species. There is good information for West Greenland, Icelandic and Arcto-Norwegian cod and Atlanto-Scandian herring and some for Icelandic haddock.

All eleven moderately abundant to very abundant year-classes of West Greenland cod between 1912 and 1945 occurred in the same year as a moderately abundant to very abundant year-class of Icelandic cod, but not all successful year-classes at Iceland were also exceptional year-classes at West Greenland. Of 12 moderately abundant to abundant year-classes of Atlanto-Scandian herring between 1912 and 1944, eight occurred one year after, one occurred in the same year (or two years after) and two two years after the occurrence of a moderately abundant to very abundant year-class of West Greenland cod. In the period since 1944 when the success of cod year-classes in West Greenland has depended more on spawning in West Greenland, of four successful year-classes of Atlanto-Scandian herring three have occurred in the same year as a successful year-class of West Greenland cod.

ICEBERG NUMBERS AND SUCCESS OF YEAR-CLASSES OF
GRAND BANK HADDOCK

Seven out of eight moderately abundant to very abundant year-classes of Grand Bank haddock since 1942 occurred in years when there were low iceberg numbers (less than 100) passing south of 48°N in the eastern Newfoundland area (Table 1). The exception, 1946, had an average iceberg number (430). Nine of the years between 1942 and 1960 were low iceberg years (1-80) and seven of these had moderately abundant to very abundant year-classes of Grand Bank haddock. Ten of the years between 1942 and 1960 were moderate to high iceberg years (253-1,087) and only one of these years had a successful haddock year-class on the Grand Bank.

DISCUSSION AND CONCLUSIONS

1: Introduction

As near as we can determine, the main periods of spawning for the populations of fish under consideration are:

Grand Bank haddock	May – June
West Greenland cod	March – <u>April</u> – May
East Greenland cod	April – May
Icelandic cod	Mid-March – mid-April
Icelandic haddock	Mid-April – mid-May
Icelandic spring spawning herring	March – April
Icelandic summer spawning herring	July – August
Arcto-Norwegian cod	Late February – <u>March</u> – mid-April
Arcto-Norwegian haddock	May and presumably earlier
Atlanto-Scandian herring	February – March

Tåning (1931) remarked on the apparent agreement between Norway, Iceland and West Greenland in the years when dominant year-classes of cod were produced, except that not all of the dominant year-classes in the other two areas were also dominant at West Greenland.

The apparent interrelationships of the occurrence of good year-classes in the Greenland, Iceland and Norwegian to Barents Sea areas in the year or two following, or in the case of Iceland sometimes in the same year as, a good year-class survival of Grand Bank haddock suggests a hydrological or meteorological sequence of favourable situations for survival in these areas.

Success of year-classes will also depend especially on drift and survival for several months following spawning.

Mr Floyd M. Soule (personal communication, 6 March 1963) says that if the oceanographic conditions on the Grand Bank are affected by the North Atlantic eddy, conceivably conditions off southwest Greenland might be affected a year later subject to the many opportunities for modification en route. Hermann (1951; MS, 1961) found a correlation between successful year-classes of cod in West Greenland and higher than usual bottom temperatures on Fylla Bank in June. Kislyakov (1961) found a correlation between success of year-class survival of Arcto-Norwegian cod and the mean temperature and also the surface temperature of the water mass on the spawning grounds off the west coast of Norway. Higher-than-usual temperatures produced the more successful year-classes. These correlations may indicate a direct relationship between temperature and survival, or it may be that the higher temperatures are indicative of some other factor such as water transport acting directly or in concert with temperature.

2: Drifts across the Atlantic

Five of the surface drift bottles liberated in and near the Gulf of Maine in July and August 1922-23 were found on the European side of the Atlantic in the Azores, France, Ireland and England 12-14 months later (Bigelow, 1927).

In the Annual Reports of the Newfoundland Fisheries Research Commission (1934) and of the Newfoundland Fisheries Research Laboratory (1936) surface drift bottles liberated in the Newfoundland area in 1932-33 at southern Labrador, northern Grand Bank and the mid-east coast of Newfoundland were reported from Ireland (2) and from Scotland (1) in 343, 371 and 339 days after liberation. Others liberated in the Newfoundland area in 1932-34 were recovered in Ireland (4), Scotland (5) and the Azores (1) in 421-470 days and at the Faroes (1) 436 days, and in Norway (2) 470 and 511 days after liberation.

Dr R.W. Trites of the Fisheries Research Board of Canada's Atlantic Oceanographic Group, has supplied (20 June 1963) information on periods between release of surface drift bottles in the Canadian Atlantic area by the Fisheries Research Board of Canada Biological Station, St. Andrews, N.B. and recovery in some of the countries on the European side of the Atlantic. Omitting occasional abnormally short and unusually long periods the average times between release and recovery of these bottles were as below:

Area	Number drift bottles	Avg days release to recovery		
		1st 25%	1st 50%	All bottles
Ireland	54	228	246	356
Scotland	15	302	339	393
Iceland	9	328	374	417
Norway	18	383	452	537

These average periods are maximal since some bottles would not be recovered immediately they drifted ashore. Dr Trites estimates that with drift bottles ballasted so that they barely float the speed of drift is probably not more than 20% in excess of the speed of the upper metre of water and that the average times of transatlantic passages of drift bottles indicated above are reasonably representative of water motion in the upper metre.

Dodimead and Hollister (1958) for drift bottles liberated in the Eastern Pacific found that the current speeds estimated from drift bottles were generally comparable to the average speeds calculated from the geopotential topography.

The leptocephali of the European eel (*Anguilla vulgaris*) take two years to drift from the Western Atlantic west of 50°W (the longitude of the southern tip of the Grand Bank but with the main distribution 10-15° of latitude further south) to the coastal banks of Europe west of the British Isles (Schmidt, 1925).

Helland-Hansen and Nansen (1909) say that the temperature effect of a large amount of warm Atlantic water should appear off Lofoten one year later and in the Barents Sea two years later than off Sognefjord in southwestern Norway.

3:    Relation of Relative Year-class Successes to Speed of Current Drift

It is apparent from the foregoing that it is possible that a hydrological effect due to the Gulf Stream system effect on the southern Grand Bank such as a greater volume transport of this warm water may affect the Icelandic area a little over a year later, the Norwegian area approximately two years later and the western Barents Sea area over which the Arcto-Norwegian cod and haddock stocks drift about three years later than the Grand Bank effect. It is possible that there may be also some persistence of the effect for a later period and that on the Grand Bank the effect may both begin much earlier and continue considerably later than the time of its actual main effect on haddock year-class survival.

The occurrence in recent years of good year-classes of cod in West Greenland one year after those of Grand Bank haddock (actually a little less than one year since West Greenland cod spawn more than a month earlier than Grand Bank haddock) seems to allow a minimal time for transfer of warm water from the Gulf Stream system. The occurrence of some good year-classes of cod, haddock and herring at Iceland and more occasionally in West and East Greenland in the same year as the success of year-class survival of Grand Bank haddock is unlikely to be due to transport of the same water which led to the haddock success unless the beginning of the build-up of the passage of suitable water south of the Grand Bank occurred in the year previous to the year of the successful Grand Bank year-class. The Icelandic year-class successes in haddock and herring one and sometimes two years after the Grand Bank success could presumably be due to water transfer between the two areas.

The occurrence of good year-classes of Arcto-Norwegian cod and haddock, and to a lesser degree Atlanto-Scandian herring, one year after a good year-class of Grand Bank haddock again seems to be too short a time for actual water transport between the two areas unless the actual water mass changes south of the Grand Bank begin many months previously to the May-June-August period when Grand Bank haddock year-class survival is likely to be affected. The relationship of the year-class survivals in the Grand Bank and Norwegian areas which are separated by two years has a greater probability.

The occurrence of abundant to very abundant year-classes of Grand Bank haddock had such a reg-ular periodicity of three years between 1946 and 1955, with a four-year period between 1942 and 1946, that instead of a Greenland-Barents Sea relationship of successful year-classes of cod, haddock and herring usually one to two years after the occurrence of a successful year-class of Grand Bank haddock (with often successful year-classes of these fish at Iceland and of Grand Bank haddock in the same year), the relationship might be that of a good year-class occurrence in the West Greenland-Barents Sea areas three to five years after a Grand Bank haddock success.

Opposed to this view is the occurrence of the best groups of year-classes in the West Greenland-Barents Sea areas one year after the most successful Grand Bank haddock year-classes of 1949 and 1955. However, the presumption that the related effect is one to three years after a Grand Bank success would transfer most of the cases of year-class success at Iceland and Greenland occurring in the same year as a Grand Bank success to an occurrence three or two years after a Grand Bank success, and would also provide a relationship between the 1945 successes at Iceland and Greenland and the 1942 success on the Grand Bank.

The occurrence between 1912 and 1945 of good year-classes of cod at West Greenland, always in the same, but not in all, years when there were good year-classes of cod at Iceland, may often be due to the drift of cod larvae from Iceland (Tåning, 1934, 1937; Hansen, 1949, 1954) and argues for a stronger water and cod egg and larval transport from Iceland to West Greenland in some years than others.

During the period when cod year-class success at West Greenland coincided with and often, at least, largely depended on cod year-class success at Iceland, the success of year-classes of Atlanto-Scandian herring (occurring usually one but sometimes two years after a year-class success of West Greenland cod) could be due, also, to the same stronger than usual (or otherwise more suitable than usual) North Atlantic water transport which produced the successful West Greenland year-classes of

cod. Due to the longer time required for water transport to Norway than to Iceland the Norwegian herring development and larval drift area is affected a year and occasionally two years later. In recent years, with a greater dependence of the West Greenland cod stock on spawning in West Greenland itself (Hansen, 1954), there is more coincidence in year-class success in the same year for West Greenland cod and Atlanto-Scandian herring. This agrees with the idea that water transported from a common source will arrive later on the West Greenland than on the Icelandic cod spawning grounds, and may arrive off Norway at approximately the same time as off West Greenland.

A complete explanation of all the relationships described cannot be offered at present and some of the interrelated occurrences appear to be too close together in time. However, the occurrence of good year-classes of different species over such a wide area in the same years and groups of years indicates more than unrelated local phenomena and argues for an interrelationship through the Gulf Stream which may affect the southern Grand Bank through eddies and intermingling with Grand Bank-Labrador Current water and through its North Atlantic Current branches affect the Icelandic, Greenland and the Norwegian-Barents Sea areas.

It is possible that in the periods of change in water transport and temperature the favourable effect on year-class survival may be at or near the peak of transport or temperature in one area and also before and after the peak in another area and that thus the apparent timing differences in year-class survival may be explained. Although the main effects appear to be related there are also likely to be some local effects which will occasionally produce or interfere with the production of a successful year-class in a local area.

Often in fisheries research what has appeared to be a good correlation has shown no correlation at a later period. Thus, our confidence cannot be too great in the apparent correlations in year-class timing and in year-class iceberg relationship discussed in this paper. However, the greater tendency for successful haddock year-classes on the southern Grand Bank to appear in low rather than in high iceberg years seems to occur too often to be fortuitous. Mr Floyd Soule (personal communication 6 March 1963) says that there are great year-to-year variations in the numbers of bergs calved in West Greenland. Once calved they are affected in varying degrees by the factors which prevent 98 to 99% of them from reaching positions south of 48°N in the vicinity of Newfoundland. In addition to variations in the transportation system such factors as stranding and melting are important. Each of these is the result of a number of interrelated items which still have to be evaluated. Mr Soule's best estimate of the travel time of bergs, from parent glacier point in West Greenland to the Newfoundland area, is three years.

It is not possible at the present time to say why iceberg numbers south of 48°N should be related to the success of haddock year-classes on the southwestern Grand Bank. Schell (1962) showed that stronger than usual northwesterly winds off the Newfoundland and Labrador coasts and relatively low temperatures over Newfoundland in the months from December to March produce greater than average berg counts off Newfoundland in the following months, mainly April to June. The opposite conditions – lighter northwesterlies and higher temperatures are related to lower than average berg counts. Thus temperature and related winds may be factors in haddock year-class survival on the Grand Bank.

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D-3

CHANGES IN GROWTH, FEEDING AND DENSITY OF GULF OF ST. LAWRENCE COD[1]

By

A. Carl Kohler[2]

ABSTRACT

Growth rates of southwestern Gulf of St. Lawrence cod increased from 1952 to 1955 and de-
creased from 1957 to 1959. Laboratory studies showed that within limits food consumption increases
with increasing water temperature and growth increases with increasing food consumption. Field
studies showed no major changes in water temperature in the period 1952-59, but during the fast-
growth years there was a lower density of large cod (herring eaters) and greater availability of
food for cod in the form of moribund herring due to an epizootic. The changes in growth rate were
related to the latter two environmental factors.

D-4

TEMPERATURE AND GROWTH OF COD IN ICELANDIC WATERS

By

Jon Jonsson[1]

ABSTRACT

The hydrographical conditions around Iceland are characterized by a gradual decrease in temperatures along the coast, the temperature being highest off the south coast and lowest off the east coast. This very much affects the growth and distribution of marine animals in these waters.

The immature cod in Icelandic waters provides a good example of a strong positive correlation between temperature and growth.

Four stations with a range in temperature from 3.57°C to 8.51°C are analyzed and the temperature differences are correlated to differences in the lengths of the various agegroups. The temperature coefficients found this way are in agreement with values found by laboratory tests.

Numerous tagging experiments have shown that the Icelandic cod is rather stationary during its first years of life and does not undertake extensive migrations until it reaches maturity. The main spawning areas are located in the warm waters off the south and southwest coasts, and from there the eggs and larvae drift clockwise around the Island. The fish in the various coastal areas are therefore practically all derived from the same spawning population.

There is a gradual decrease in temperature from highest off the southwest coast to lowest off the northeast and east coast. In August the mean temperature at 50 m is about 9°C in Faxa Bay (southwest coast), but below 5°C off the east coast. This difference in temperature greatly affects the distribution and growth of marine organisms in the various coastal areas.

The growth of the cod in Icelandic waters is a good example of this and in order to examine this problem further we shall analyse some samples of cod taken by the R/V *Maria Julia* in 1950. All the stations were worked during the period 14 to 31 August. Figure 1 shows the location of the stations. Table 1 shows the average lengths of the age groups with the average temperature at 50 m in July-August of 1948-50 at four fixed hydrographical sections nearest the locality where the fish were caught. These averages should therefore give, as far as temperature is concerned, the differences in the environment in which the fish has lived the past three years before capture.

Figure 2 shows a very strong positive correlation between temperature and growth. It therefore does not seem unreasonable to view the data as resulting from a huge experiment conducted by Nature to rear fish under different temperature conditions.

Tackling the problem from this point of view, we can see if our data are in any agreement with laboratory experiments about the effect of temperature on the growth of living organisms. We have to assume, among other things, that the availability of food has been the same in all areas and there is no reason to believe otherwise.

Van't Hoff has shown that the rate of an inorganic process increases exponentially with increasing temperature, *i.e.* the rate of the process increases as x^n, n being the difference in temperature and x the socalled *temperature coefficient*. Generally we can say that when $n=10$, then $x=2$, *i.e.* the speed of the process is doubled with an increase of 10°C in temperature.

Numerous investigations made on the effect of temperature on the rate of growth in living organisms have shown a similar effect of temperature as stated by Van't Hoff.

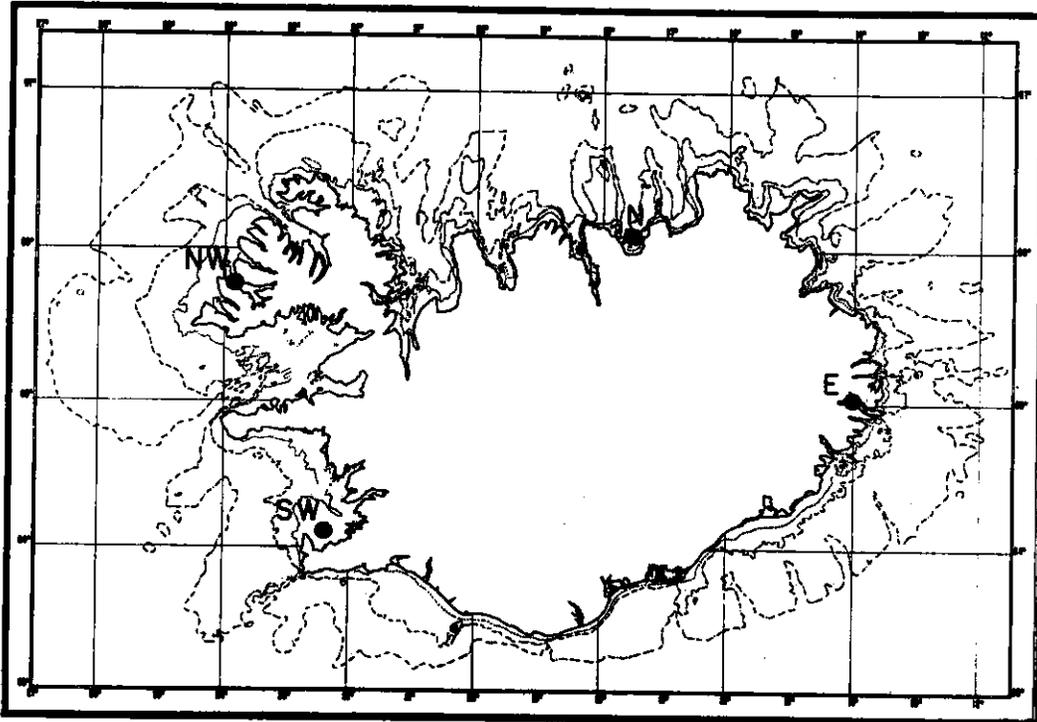[1]   Fisheries Research Institute, Reykjavik

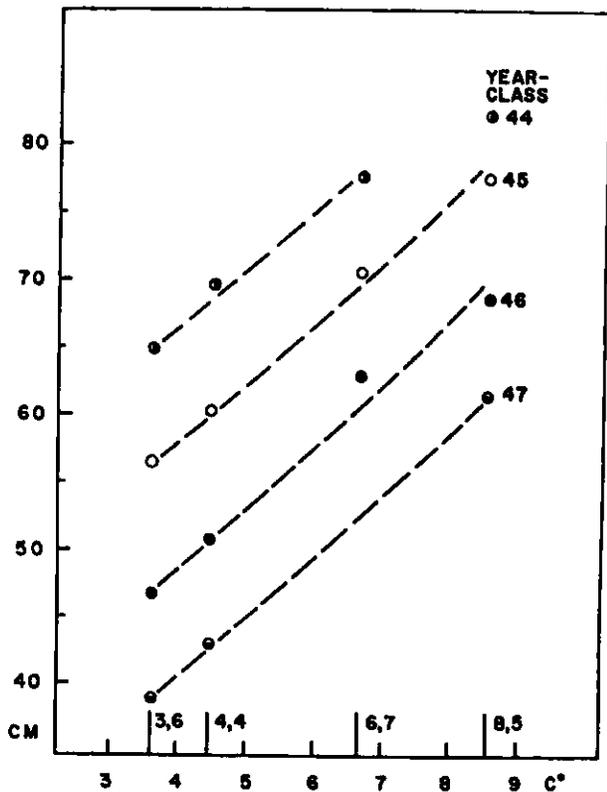Fig. 1. Location of stations where otolith material was collected.

Fig. 2. Average temperatures at 50 m in July-
August 1948-1950 and the lengths of
the age-groups 3-6 (1944-1947 year-
classes) of cod in August 1950.

From Table I we can calculate the Q_1, or the
temperature coefficient for one centigrade and
make use of the following equation:

$$\frac{V_{(t+n)}}{V_t} = x^n \text{ or } \log V_{(t+n)} - \log V_t = n. \log x$$

As an example we can compare the lengths of
age-group 4 from the areas N and SW and get the
following:

$$\frac{\log 68.7 - \log 51.0}{4.07} = \log x, \quad \log x = 0.0318, x = 1.07$$

In the same way we can compare other temp-
eratures and other age-groups, and the values for
Q_1 thus found are shown in Table 2.

The table shows, first, that the Q_1 is high-
est for the younger age-groups, and decreases for
the older ones. This may be explained by' the fact
that a part of the older fish is already mature
and the effect of maturity has set in. Second,
we see that the values of Q_1 are relatively higher
when we compare the lower temperature areas, $i.e.$
the change in temperature in the cold water seems
to have a greater effect than in the warm waters.

In his work on growth and form, D'Arcy
Thompson (1942) gives some values for the Q_1 found

TABLE 1.--TEMPERATURE (°C) AND THE LENGTH (CM) OF THE AGE-GROUPS
3 TO 6 AROUND ICELAND IN AUGUST 1950.

Areas	Mean temp. °C	Age-groups			
		3	4	5	6
SW	8.51	61.6	68.7	77.6	81.2
NW	6.66	--	58.0	70.5	77.8
N	4.44	43.4	51.0	60.5	68.7
E	3.57	39.2	46.9	56.6	65.0

TABLE 2.--VALUES OF Q_1 FOUND FOR VARIOUS TEMPERATURE DIFFERENCES AND VARIOUS AGE-GROUPS.

Areas	Diff. in temp.	Age-groups				
		3	4	5	6	mean for 4-6
SW and E	4.94	1.095	1.080	1.066	1.046	1.064
SW and N	4.07	1.090	1.076	1.063	1.041	1.060
NW and E	3.09		1.071	1.074	1.060	1.068
NW and N	2.22		1.060	1.071	1.058	1.063
SW and NW	1.85		1.096	1.053	1.023	1.057
N and E	0.87	1.124	1.101	1.080	1.066	1.082
Avg		1.103	1.081	1.068	1.049	1.066

by laboratory experiments in various plants and animals. The following figures are taken from his work (page 231):

Yeast 1.13, lupin 1.16, maize 1.20, pea 1.09, echinoids 1.08, drosophila 1.12, frog (segmentation) 1.08, frog (tadpole) 1.13. The average for these experiments is 1.12.

We therefore say that our "natural experiment" without any scientific control is in a rather good agreement with laboratory tests.

This material was not originally collected with such calculations in view and the number of fish in some age-groups is rather small. Laboratory experiments on Q_1 have been criticised by some workers and the problem is of course very difficult, but without taking the figures found for Q_1 too seriously, we certainly must admit that they give us the strongest impression of the relationship between the growth of the fish and their environment. Other factors, of course, may influence the growth, but at present only the temperature can be expressed by numerical values.

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D-5

SOME PROBLEMS OF ZOOPLANKTON PRODUCTION
AND THE PROBLEMS OF FISHERIES

By

Wladyslaw Mankowski[1]

ABSTRACT

From observations made on zooplankton production in the Southern Baltic and on the biology of
two plankton-eating fish, sprat and herring, from 1951-62, the author shows that the amount of fat
in sprat, the length of herring in its first and second year of life, the rate of growth of both
species and the condition of herring depend on production of zooplankton. These relationships
were most conspicuous in the years 1955-1957. Hydrological conditions, particularly the temperature
of water, seem to be the factor regulating these phenomena. After severe winters the production of
zooplankton and the amount of fat in sprat, condition of herring and the rate of growth are poor;
after mild winters they are good.

Studies, carried out for many years on production of zooplankton in the southern Baltic, though
sometimes based on incomplete annual cycles, enabled us to establish the course of zooplankton pro-
duction in particular years. As a further step an attempt was made to compare acquired data with
some elements of the biology of the plankton-eating fish, sprat and herring. The following elements
were taken into consideration:

(1)   Fat contents (for sprat);

(2)   Length (L_1, L_2) and the rate of growth

       (t_2 for herring and t_2, t_3 , t_4 for sprat);

(3)   Condition (Fulton's weight-growth coefficient for herring).

The observations cover the period of twelve years (1951-62). It was impossible to obtain the
same data for all the elements shown above.

The first few years of the period (1951-54) do not show anything particular. The production of
plankton (Fig. 1) and such elements of the biology of the above mentioned fish, which were recorded
from the observations, $i.e.$ fat contents of sprat, the length of herring (L_1 and L_2 - Fig. 2 and 3)
and Fulton's coefficient K, remain on an average level.

The years 1955-58 are the most interesting period. Plankton production reached its highest and
lowest values and was followed by similar fluctuations in values of some of biological features of
plankton-eating fish.

The first year, 1955, must be considered a good one. Good production of plankton caused con-
siderable accumulation of fat in sprat and good condition of herring, as well as good growth rate
of both species.

Lowest plankton production was in the year 1956. It was characterised by a continuing and con-
siderable fall of fat contents of sprat, which at the beginning of 1956, with an accumulation from
1955, was large. The decrease of fat contents of sprat lasted unusually long, and in July had
dropped to a very low value, the lowest one in the whole period of observations (about 3%). The
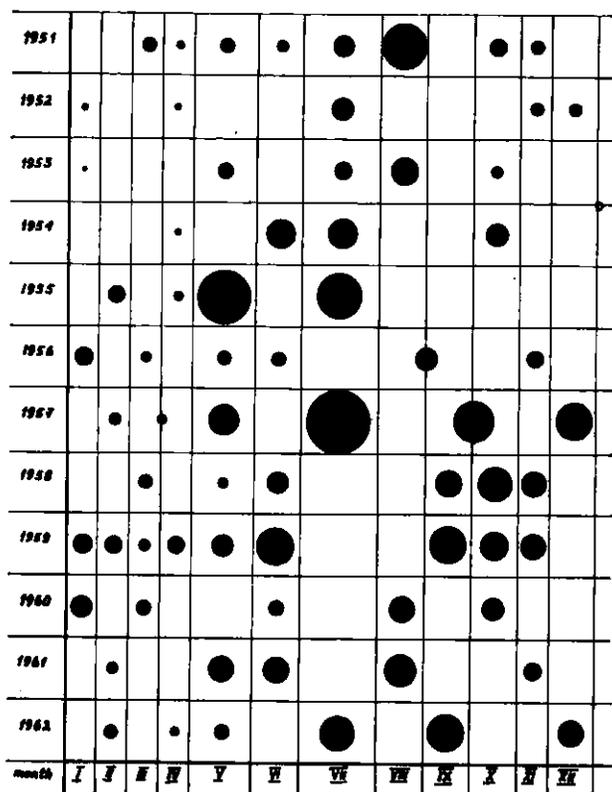
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Fig. 1. Mean biomass of the plankton in Gdansk region in g/1m² of the sea surface.

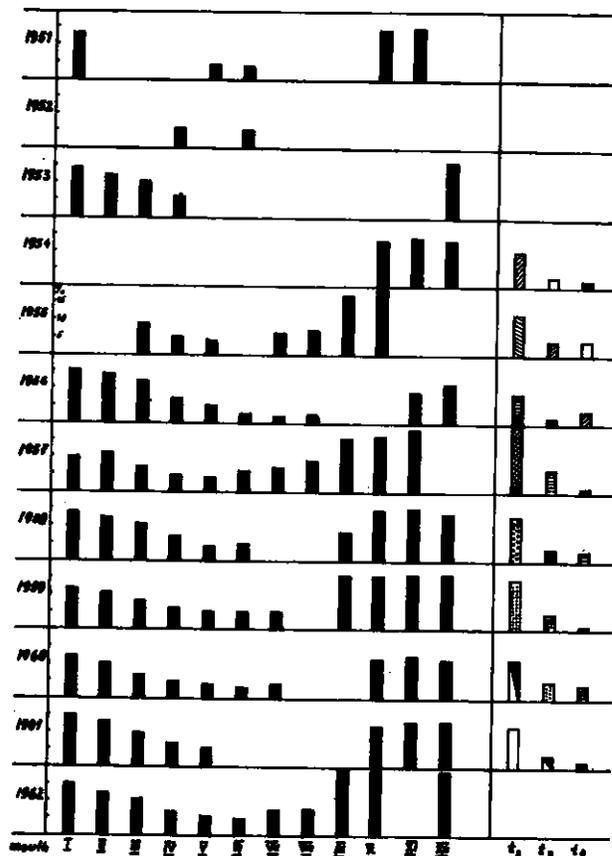Fig. 2. Fat content (in %) and rate of growth (t_2, t_3, t_4) of sprat in the southern Baltic.

delayed restoration of fat and the small quantities of plankton resulted in the fat content of sprat reaching (towards the end of the year) only 12%, quite small in view of the recorded 19% in 1955. Also the rate of growth in 1956 was smaller than the rate in both preceding and following years.

Similar behaviour was observed in 1956 for both the spring and autumn spawning herring. The coefficient K dropped to its lowest value. The same was true for the length reached by herring from the autumn spawning of the previous year and spring spawning of 1956. Thus the length increase of this herring was small.

This year of poor nourishment, 1956, was followed by the best one in plankton production, the year 1957. The amounts of plankton were enormous. All the biological indexes of plankton-eating fish reached their highest values. The fat contents of sprat in spite of their low level (12%) at the beginning of the year decreased only to about 5%. This decrease stopped in May and fat restoration on the basis of the rich plankton reached 18% towards the end of the year. The highest value was also recorded for length increase of sprat of the first and second age-group (t_2 and t_3).

Herring reacted in a similar way to the amount of nourishment. The fish of zero group reached good growth, whereas the fish of group I reached the average long-term length, owing to an exceptionally fast length increase, which made up for the losses in 1956. Of particular interest was the increase of the coefficient of condition of herring to the highest value during the period of observations.

In the next period the values for plankton production were rather average, which was evidenced by the good fat contents (to 16%) and the average length increase of sprat. Herring size and coefficient of condition showed similar values.
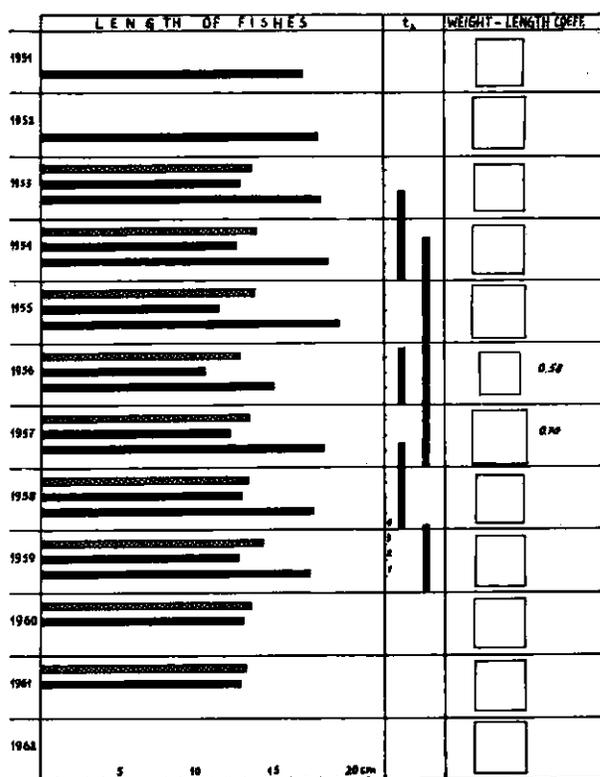
Fig. 3. Length (L), rate of growth (t₂) and weight-length coefficient of spring (solid black) and autumn (cross hatched) herring in the southern Baltic.
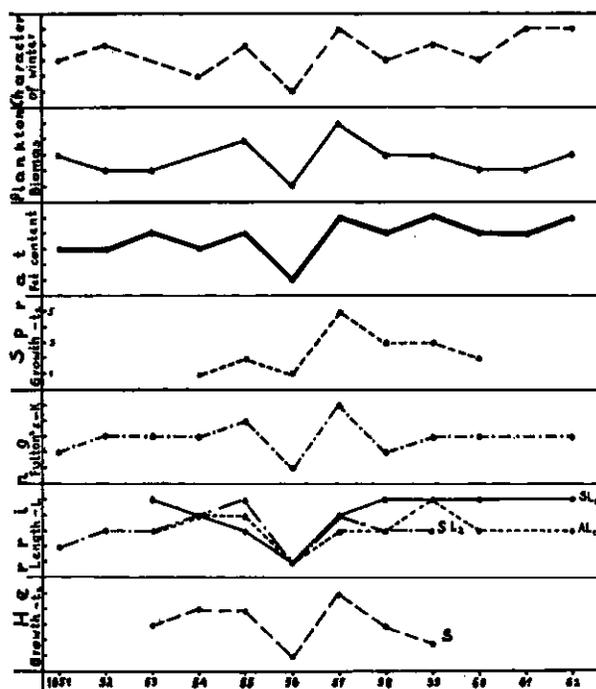

Fig. 4. Plankton production in the southern Baltic and its effect on the biology of the sprat and herring. Scale for the character of winter: 1-very cold; 2-cold; 3-mean; 4-mild; 5-very mild. Scale for the other features: 1-very small; 2-small; 3-mean; 4-good; 5-very good.

The mean biomass of zooplankton and the above elements have been brought into a five-grade scale (Fig. 4), in which the lowest and the highest values were taken as the lowest and the highest grades of the scale. It was possible in this way to bring all the elements into a common diagram. Such tabulation allows quick comparison and shows the relation between plankton production and biology of plankton-eating fish.

The question arising from this analysis, is: what is the basic source of the plankton production? Characteristic winter conditions in the sea are shown in Fig. 4 and the following table

WINTER SEA WATER TEMPERATURES

Depth	25 March 1956	5 April 1957	18 March 1958
m	^{o}C	^{o}C	^{o}C
0	-0.20	4.90	1.15
10	-0.15	3.20	1.15
20	-0.28	3.20	1.18
30	-0.15	2.90	1.10
40	-0.20	2.80	1.10
50	-0.20	2.60	1.22
60	-0.30	2.80	1.25
70	4.70	2.80	1.62
80	5.40	4.40	2.00
90	5.27	4.40	2.10
100	5.50	5.00	3.20

points to the fact that the most severe winter was in 1956, whereas the mildest winters were in 1955 and 1957. Is temperature of the waters the main and direct factor regulating all the above phenomena, or are we witnessing only their coincidence? Is water temperature an indirect factor which affects the balance of biogenic salts in the sea, which in turn affect the basic production and further links of life? These questions require further and thorough analysis.

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D-6

COD GROWTH AND TEMPERATURE IN THE NEWFOUNDLAND AREA

By

A.W. May[1], A.T. Pinhorn[1], R. Wells[1] and A. M. Fleming[1]

ABSTRACT

Growth of cod from various parts of the Newfoundland-Labrador area is described by the von Bertalanffy growth equation. Variations in growth are related to the varying influence of the Labrador Current in terms of increasing surface temperatures and decreasing volume of cold water (less than 0°C) from north to south. Values of the growth parameters K and L_∞ are shown to be related to latitude. The highest values of K and lowest values of L_∞ are found in the cooler waters of higher latitudes, while the reverse is true in warmer waters to the south. This does not conform to most of the findings in the fisheries literature. Some possible reasons for these differences are discussed.

INTRODUCTION

Annual growth of fishes represents the excess of food intake over that necessary for general maintenance requirements and, in the case of mature individuals, for production of the genital products. As such, the yearly growth increment is governed by the complex interaction of factors influencing availability of food and its assimilation to form new somatic tissue in the organism. The former category includes those factors which govern distribution and abundance of predator and prey, while the latter includes those affecting metabolism. Temperature makes its effects felt in both directions and has probably received most attention, both in the laboratory and in nature.

While the effects of temperature on growth can be observed with relative ease in controlled laboratory experiments, they are difficult to isolate in studies of natural populations. Of all the physical and biotic factors which influence growth, temperature is certainly the one most easily measured, and the one for which the greatest amount of accurate and long-term data is available. Even so, a study relating temperature to growth in the sea may be little more than qualitative because of the difficulty of obtaining a temperature measure which is representative of an oceanic area and, particularly, of the immediate thermal environment of the fish which inhabit that area. Taylor (1958, 1959, 1960) has approached the problem by using mean annual air and surface temperatures as indicators. Experimental evidence relating temperature and growth has been reviewed by Brown (1957).

In the present study geographical variations in growth of cod from the Newfoundland-Labrador area are related to temperature differences in the various localities under consideration.

MATERIALS AND METHODS

The assembled growth data cover at least eight more or less distinct stocks of cod, as reviewed by Templeman (1962b), occupying ICNAF Subareas 2 and 3 as well as Division 4R. These include the Labrador-Newfoundland stock, the Flemish Cap stock, the Grand Bank stock, the Avalon-Burin stock, north and south St. Pierre Bank stocks, the Borgeo Bank stock and the West Newfoundland stock. The geographical limits, seasonal distribution and migration routes of these are illustrated in Fig. 5 of Templeman (1962b).

In the present study, since it was not always possible to separate data relating to the various stocks, the analysis has proceeded on an area rather than a stock basis. In fact, these criteria have similar effect except for the Newfoundland south coast area where intermingling of several stocks is known to occur at various times throughout the year.

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The otolith collections and length data include both inshore and offshore material collected during the period 1960-62 (Table 1). The offshore data represent random samples of research vessel catches by otter trawl having the codend lined or covered with small-meshed netting. These vessels generally fished one or more series of standard depths from the shallowest depth available to at least 375 m, and sometimes to more than 700 m. The inshore collections represent random samples by various gears from the inshore commercial catches at fishing centres along the Newfoundland and Labrador coasts (Fig. 1). Where both inshore and offshore material were available only the offshore
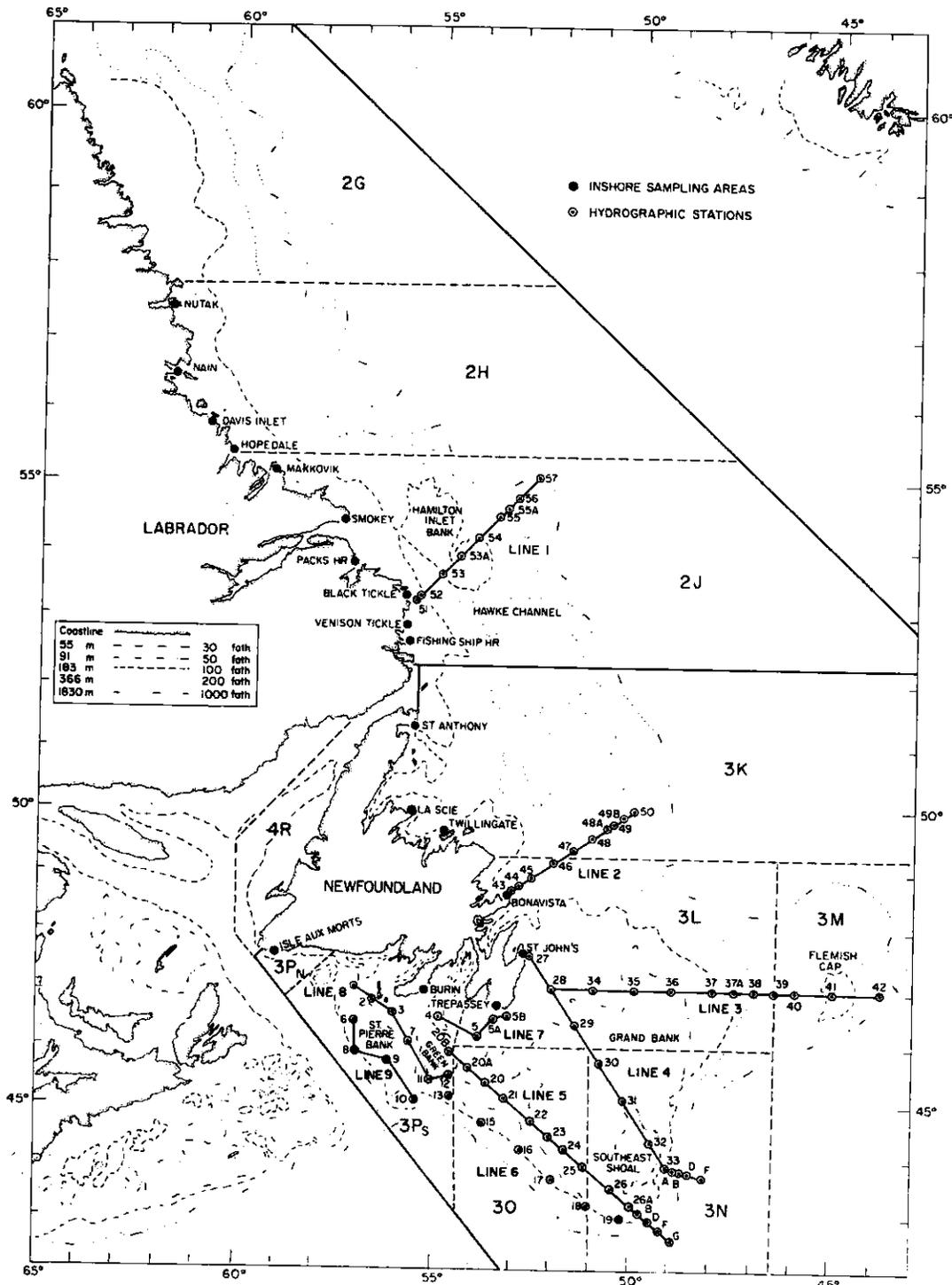
Fig. 1. Area map showing ICNAF Divisions, hydrographic stations, inshore sampling stations and place names mentioned in the text.

data were used to compute mathematical growth curves, with the exception of Division 3Ps where the offshore data were scanty for the older ages.

TABLE 1.   OTOLITH COLLECTIONS DURING 1960-62 IN THE NEWFOUNDLAND
AREA REPRESENTED IN THE LENGTH-AT-AGE PLOTS OF FIG. 2.

ICNAF Division	Stocks	Pairs of otoliths		Ages used to fit growth curve
		Inshore	Offshore	
2H	Labrador-Newfoundland	1,149	1,176	3-15
2J	Labrador-Newfoundland	1,870	1,580	3-15
3K	Labrador-Newfoundland	3,792	1,004	3-15
3L	Labrador-Newfoundland, Grand Bank, Avalon-Burin	2,596	1,279	2-14
3M	Flemish Cap	-	522	2-8
3N-O	Grand Bank	-	2,560	2-14
3Ps	St. Pierre Bank, Avalon-Burin, Burgeo Bank	2,340	684	3-14
3Pn	West Newfoundland, Burgeo Bank, Avalon-Burin	901	-	5-14
		12,648	8,805	

Lengths were measured to the nearest centimetre from snout to mid-fork. Ages were determined from otoliths, supplemented by scales in some doubtful cases. Most of the age reading was done by the authors, working on an area basis. The age reading technique is described in the summary by Keir (MS, 1960). An intramural otolith exchange programme revealed that no consistent differences in interpretation existed among the group and, in fact, that each age reader obtained best results for the area for which he was responsible, and therefore most familiar.

The collections were made at various times throughout the year in the various areas, though in most areas mainly between April and September. In such cases the age has been regarded as one-half year above that read from the otolith, since we have adopted the convention of using 1 January as the "fish's birthday". However, the collections in Divisions 3M and 3Pn were almost entirely in the January-June period, and for these areas no adjustment has been made.

Growth in each area has been described by the von Bertalanffy (1938) growth curve (Fig. 2) using the "trial L_∞" approach as described by Ricker (1958), P. 194-196. Aberrant averages at the younger ages and averages based on less than 10 fish have not been used in computing the curves.

The temperature sections of Fig. 4 and 5 are based on annual hydrographic surveys in July-August by research vessels of the St. John's Biological Station.
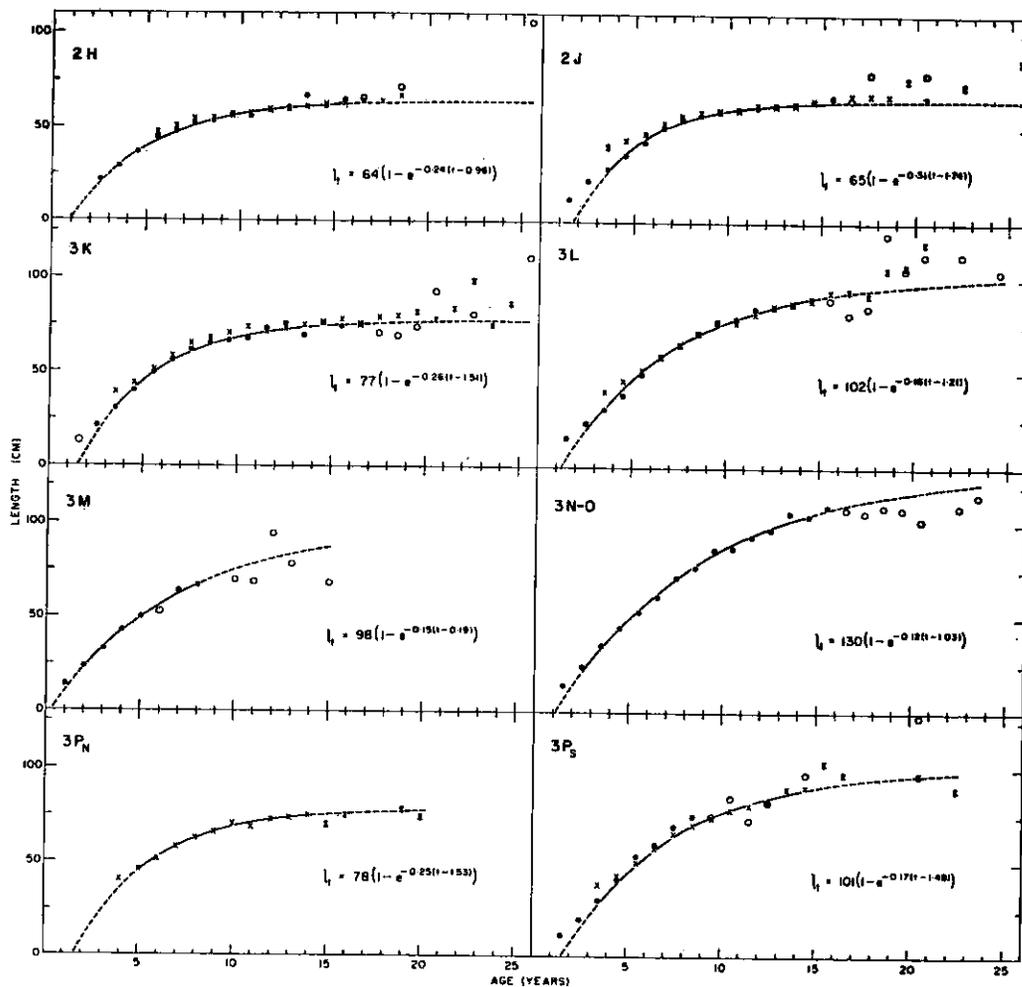
Fig. 2. Plots of average length at age and fitted von Bertalanffy growth curves for various areas. The curves are fitted to the offshore data only except in Divisions 3Pn and 3Ps. The circles represent offshore averages and the crosses inshore averages. Open circles, and crosses with a vertical stroke indicate averages based on less than 10 fish. The solid part of each curve represents the range of data on which the mathematical fit was based.

GROWTH OF COD

Plots of average length at age for each area under consideration are shown in Fig. 2. Inshore averages from mixed gear collections and offshore averages from research otter-trawl collections are shown separately. The von Bertalanffy growth curve is given for each area in the form

$$l_t = L_\infty \ (1-e^{-K(t-t_0)})$$

where l_t is length at age t, L_∞ is the theoretical maximum length, K is a constant determining the rate of change in length increment and t_0 is the hypothetical age at zero length. The various equations provide an adequate description of growth over the range of ages used to derive them.

Average lengths at the youngest ages represented in the inshore data tend to be artificially high because of selection by the various inshore gears (traps, longlines, handlines, jiggers and gillnets). Apart from this, and except for Division 3Ps, the inshore average lengths in those areas

bordering the coastline are similar to those derived from the offshore data in the same areas.
Thus the curves derived from the offshore data provide an adequate representation of the inshore
material as well, lending evidence to the hypothesis (Templeman, 1962b) that there is no inshore-
offshore stock separation in the areas concerned. With the exception of the youngest ages the off-
shore averages in Division 3Ps are generally higher than those inshore. These differences are un-
doubtedly a reflection of the fact that several stocks inhabit this area. Since the offshore (St.
Pierre Bank) growth data were very scanty beyond age 7 we have not considered this area separately.
Again, the Flemish Cap data were scarce beyond age 8, but it is reasonably certain that the iso-
lated cod population in this area does not alter significantly in composition throughout the year.
However, the values of K and L∞ calculated for the Flemish Cap stock must be regarded as provisional.

The offshore data almost always include some fish at the youngest ages, but the averages for ages
1 and 2, at least, are considered to be artificially high. Fish of these young ages are probably not
distributed randomly on bottom, and the trawl probably would select the largest individuals which
might tend to be distributed closer to bottom than the smallest. Thus the fish at age 1 have not been
used in computing the growth curves, and those at age 2 used only where large numbers were available.

It is evident from Fig. 2, that with the exception of Divisions 3N-O and 3Pn, the very old fish,
having values of average length at age consistently greater than the calculated value of L_∞, do not
adhere to the theoretical pattern of growth as described by the von Bertalanffy equation. Although
the average lengths at these ages are often based on very few fish, the pattern is consistent enough
that it cannot be dismissed as random variation in the data. Further, such a phenomenon has pre-
viously been reported from the Newfoundland area by Fleming (1960), and for other areas by Poulsen
(MS, 1957). Elucidation of this phenomenon requires further investigation, but it may possibly
be related to a change in diet beyond a certain size (Fleming, 1960; Templeman, this symposium).
Also, since it is more evident in the northern areas, the possibility of north-south separation
of fast- and slow-growing old fish is indicated.

Fig. 3. Comparison of growth curves from the
various areas.

The fitted curves are shown in relation
to each other in Fig. 3. The curves cross over
only at the youngest ages, and the general de-
cline in average length at age proceeding from
south to north is obvious. The curves for
Divisions 3K and 3Pn are seen to be closely
similar, as are those for Divisions 3L and 3Ps
(see also the equations of Fig. 2).

TEMPERATURE DISTRIBUTION

The single major factor influencing the
hydrography of the greater part of the area under
consideration is the effect of the Labrador Cur-
rent. The origins, extent and structure of the
Labrador Current are well documented (Smith,
et al., 1937; Dunbar, 1951; Bailey and Hachey,
1951; Hachey, et al., 1954). The shoreward
portion of this current, containing cold water
of Arctic origin, extends from the coastline
to the edge of the continental shelf, causing
bottom temperatures in summer in most areas (and
except where solar warming occurs close inshore)
to be less than 3°C in depths less than 300 m
(Fig. 4 and 5). The cold, central core of the
current tends to diminish in volume to seaward.
The seaward portion of the Labrador Current, ex-
tending to depths of 1,000 m or more over the
continental slope, contains warmer water of
West Greenland origin. Since most of the cod
stocks in the area spend their lives in water
of Labrador Current origin, any growth varia-
tions with temperature between areas should be
closely related to geographical variations in
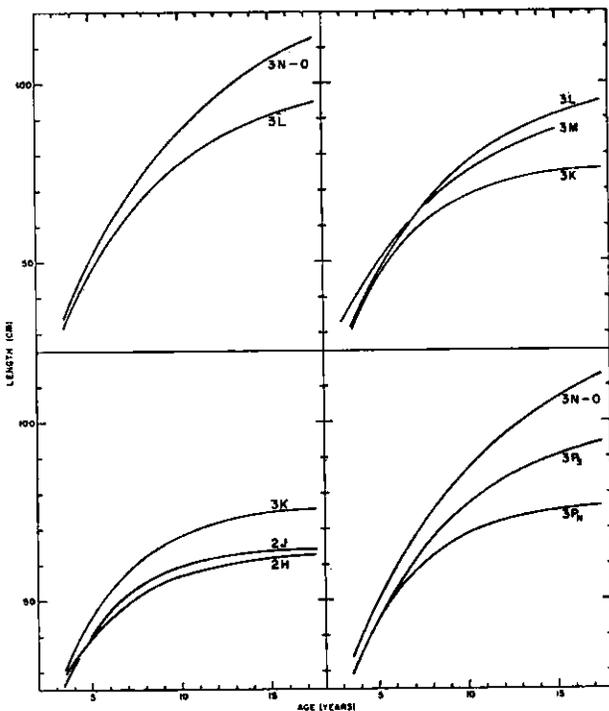temperature structure of the Labrador Current.

The difficulty of obtaining a temperature measure to represent the thermal environment of a species has previously been noted. Ideally one would need to know the geographical and depth distribution of a stock at all times throughout the year, and to obtain growth and hydrographic data at regular intervals and as changes in distribution occur. This is almost a physical impossibility, especially as in this area much of the ocean is covered by ice for part of the year.
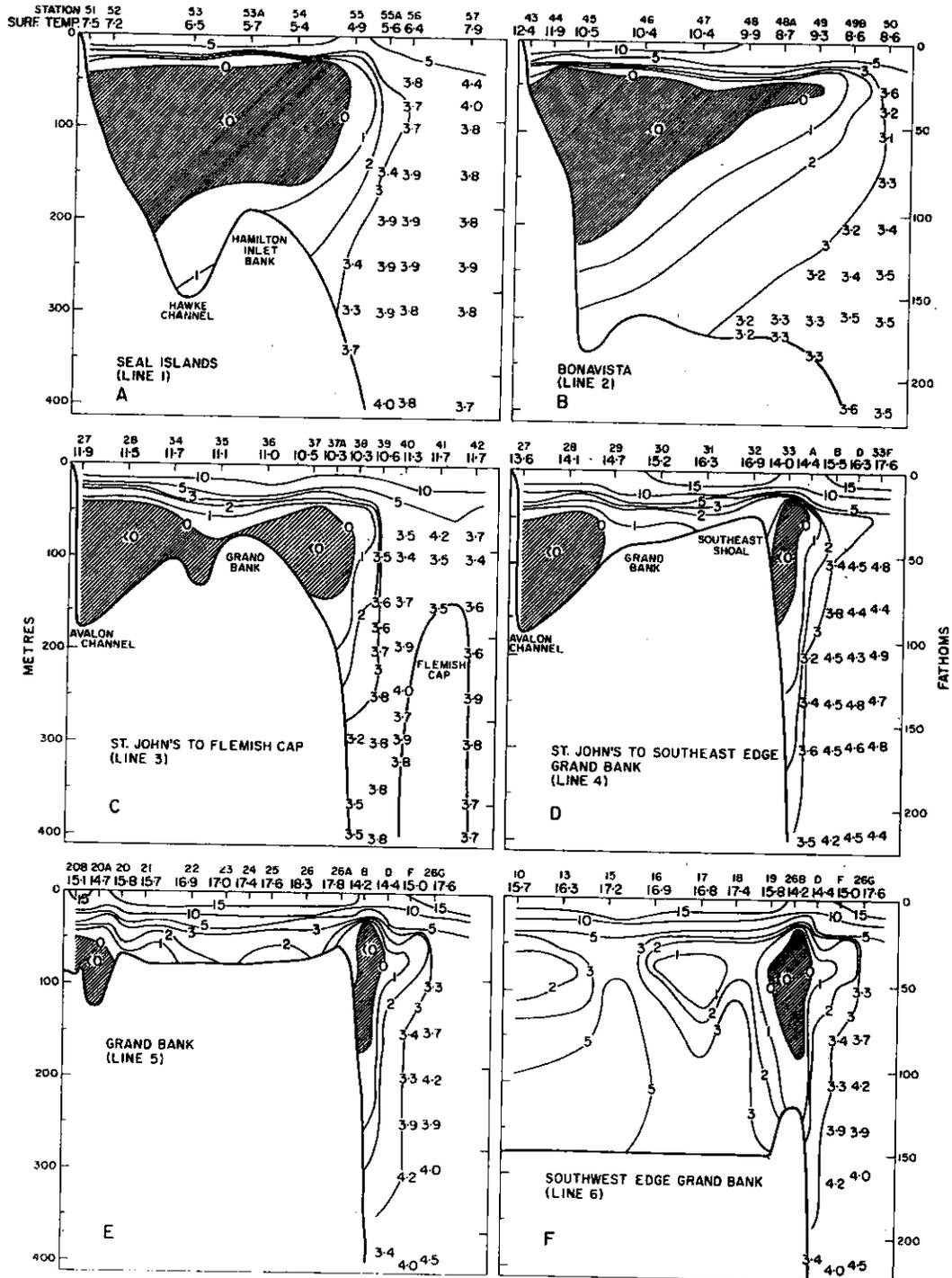

Fig. 4. Average temperature profiles for July–August, 1959–63, over the continental shelf off Labrador and Newfoundland. The station positions are shown in Fig. 1.
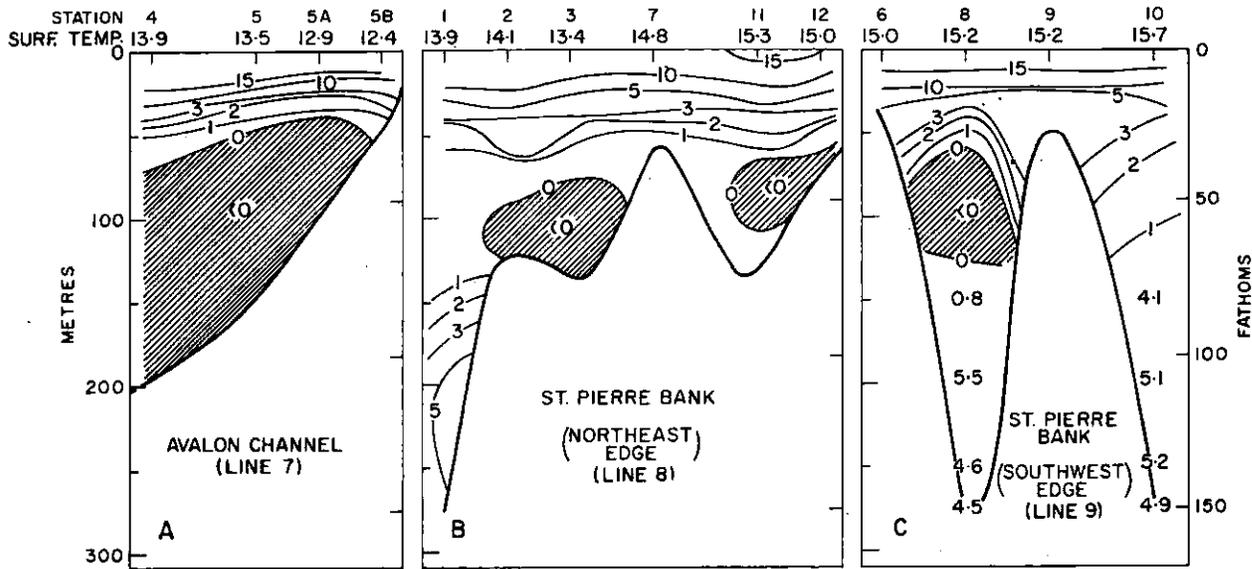
Fig. 5. Average temperature profiles for August, 1959-63, in the Avalon Channel-St. Pierre
Bank area. The station positions are shown in Fig. 1.

It can be shown that the volume of very cold water in the Labrador Current declines from north
to south in the area under consideration. Vertical temperature profiles during July-August for most
of the lines of hydrographic stations shown in Fig. 1 (Templeman, 1960, 1961, 1962a; MS, 1963) il-
lustrate these points. For present purposes temperatures at standard depths in these profiles have
been averaged for the period 1959-63, and the resultant average profiles are shown in Fig. 4 and 5.
The shaded portion of each profile represents water of temperature less than 0°C.

Figure 4A gives the vertical temperature distribution from the coast of Labrador in a north-
easterly direction across the Hawke Channel and Hamilton Inlet Bank. Water of temperature less than
0°C extends from depths of less than 50 m to more than 150 m from near the coast to the eastern edge
of Hamilton Inlet Bank. Bottom temperatures on the bank in depths to 300 m are less than 3°C. Some
solar warming is evident, though temperatures greater than 5°C are generally to be found only in the
upper 15 m.

In the section extending northeast from Cape Bonavista (Fig. 4B) the 5-degree contour is a little
deeper, mainly between 15 and 25 m, and temperatures above 10°C are present in the upper 10-15 m.
The volume of cold water on the inshore part of the section is about the same as on the Labrador line,
but becomes progressively less offshore.

On the section extending from St. John's to Flemish Cap (Fig. 4C), solar warming has pushed the
5-degree contour to 20-35 m over the Grand Bank and to 55 m over Flemish Cap. The 10-degree contour
extends between 15 and 25 m. Solar warming over the shallower parts of the Grand Bank causes the
0-degree contour to approach very close to the bottom. Also the Labrador Current divides into two
branches in this area, one passing westward through the Avalon Channel as seen in the inshore part
of the section, and the other sweeping around the eastern edge of the Grand Bank, as evidenced by the
volume of cold water between 50 and 150 m over the edge of the bank. The colder inshore part of the
Labrador Current does not extend to Flemish Cap, and fairly uniform temperatures (3.5 to 4.0°C) are
seen to be present at all depths below 100 m.

The section from St. John's to the southeast edge of the Grand Bank (Fig. 4D) again shows the
Avalon Channel branch of the Labrador Current as the volume of cold water on the inshore part of the
section, but the amount of cold water along the eastern edge of the bank is much reduced, and bottom
temperatures on the bank are higher than in the previous section (Fig. 4C). Temperatures in excess
of 15°C are present in the upper 15 m. A similar pattern is present in the Grand Bank section of
Fig. 4E, but with bottom temperatures over the shallower part of the bank about 1°C warmer. It
should be noted here that these two sections (Fig. 4D and 4E) and those of Fig. 4F and 5, are oc-
cupied 2-3 weeks later than the more northerly sections. Thus at stations 27 and 28 (Fig. 4C and 4D)

the average surface temperatures are seen to be higher in the later period (by 1.7°C and 2.6°C respectively), and at station 27 and 0-degree contour is about 10-15 m deeper.

In the section at 275 m along the southwest edge of the Grand Bank (Fig. 4F), the body of cold water is present only as an intermediate layer, representing the Labrador Current as it turns westward around the tail of the bank. Warmer water of Gulf Stream origin is present over the western part of the southwest edge.

Temperature profiles in the Avalon Channel and across the northeast and southwest edges of St. Pierre Bank are shown in Fig. 5. The Avalon Channel branch of the Labrador Current is seen to extend southward to St. Pierre Bank and cool water (less than 1°C) is present along the northeast edge for most of the area below 50 m (Fig. 5A, 5B). Temperatures in shallow water on top of the bank, and in deeper water along the southwest edge are moderately high (Fig. 5C). The core of cold water over the slope represents the Labrador Current water which flows southward from the Avalon Channel on each side of Green Bank, and turns westward around the southeast corner of St. Pierre Bank.

Comparable temperature data for the area represented by the Division 3Pn growth curve are not available, but these fish are mainly of the West Newfoundland stock, which spend most of the year (April-December) in the eastern and northeastern Gulf of St. Lawrence. A cold layer of water less than 0°C in temperature is present throughout the year in this area, having a maximum volume in spring and a minimum in autumn (Lauzier and Bailey, 1957). Comparing the temperature profiles given by these authors with those of Fig. 4 and 5, the vertical temperature distribution in this area during July-August would be most similar to that in Division 3K, as represented by the profile of Fig. 4B.
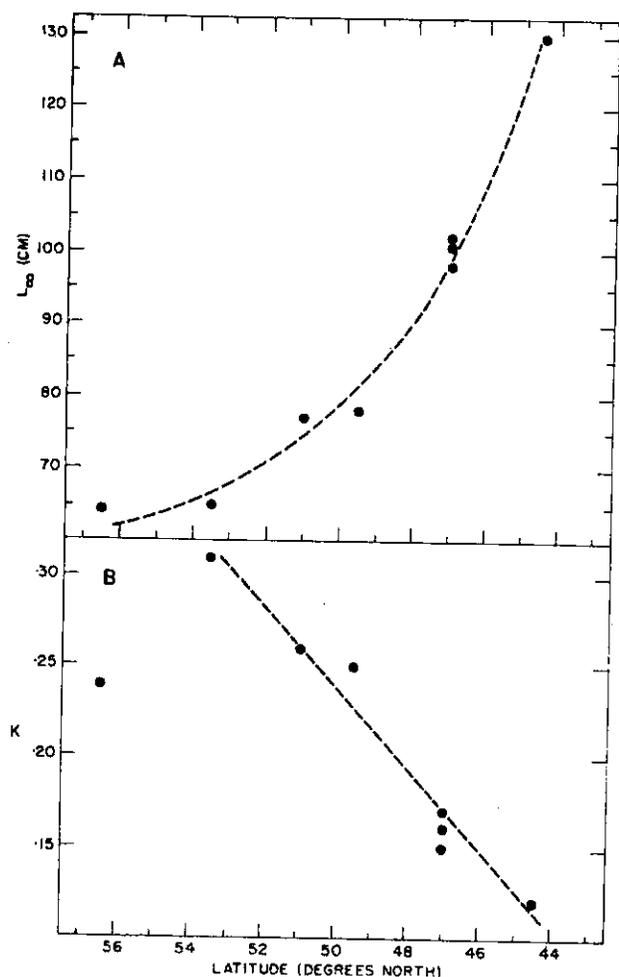

Fig. 6. Plot of data of Table 2 showing for the Newfoundland area the correlation between mid-latitude of ICNAF Divisions (except as indicated in text) and values of L_∞ and K derived from cod growth data.

RELATION OF TEMPERATURE AND GROWTH

We have seen in the previous sections that in the Newfoundland area, average length at age of cod tends to increase from north to south (Fig. 2 and 3), while the volume of cold water (less than 0°C) carried by the Labrador Current decreases in the same direction. This being so, an indirect correlation between temperature and growth appears to exist. However, lacking a temperature measure which would be comparable for all the areas considered, we have related values of L_∞ and K to the value of latitude (degrees North) which probably represents the centre of north-south distribution of the fish in each area (Fig. 6). L_∞ represents the theoretical maximum size of an average individual of the population, while K gives a measure of the average rate at which this size is reached.

We have chosen the approximate mid-latitude of each of the areas concerned except for Divisions 3Pn and 3Ps. Since fish in the former area are known to spend the summer and autumn (presumably the growing season) in the eastern and northeastern Gulf of St. Lawrence, the mid-latitude of Division 4R can be considered representative for present purposes. We have used age and length data for the inshore part of Division 3Ps to derive the growth parameters, and therefore chose the latitude of this inshore area to represent this particular group.

With the exception of the low value of K for Division 2H, the correlations of Fig. 6 are surprisingly good, and indicate, that for the area under consideration, latitude may serve as a measure of environmental opportunity for growth of the species. Stocks inhabiting similar latitudes (e.g. those of Divisions 3L, 3M and 3Ps)

exhibit similar growth patterns, though in Division 3M it cannot be said that this is related to temperature since temperatures in this area are not similar to those in Divisions 3L and 3Ps (Fig. 4C, 5B and 5C).

It is obvious from the plots of Fig. 6 that L_∞ and K are inversely correlated. This has been found to be fairly general for a variety of species (Beverton and Holt, 1959). For the present material, this means that fish from the northern areas approach their theoretical maximum length (L_∞) more quickly (high K values) than do those of the southern areas.

DISCUSSION AND CONCLUSIONS

Allee *et al.* (1949), discussing the Bergmann rule, observe that poikilothermous terrestrial animals tend to have their species and individuals with largest size in warmer climates. Clarke (1954), in effect, makes the same observation, *i.e.* that poikilothermous animals tend to be smaller in colder climates. The present data conform to this principle.

On the other hand Taylor (1958) makes the observation that "rapid growth is, in poikilothermic animals at least, generally incompatible with a long life span and, conversely, that large size and a long life span are often associated with the cooler temperatures of higher latitudes". Holt (1959) proposes that on theoretical grounds L_∞ should decrease slowly with increasing temperature, and that fish which approach their L_∞ rapidly, seemingly tend to have shorter lives than those which approach it at a slower pace. Taylor (1962) attributes to Pütter (1920) the observation that animals at higher temperatures should show more rapid growth but a smaller final size, and that animals at lower temperatures should grow larger.

Beverton and Holt (1959) have shown for a number of species groups that a positive correlation exists between longevity and ultimate size, and also between K (the rate at which this size is approached) and mortality. In general, a negative correlation is shown to exist between K and L_∞. The present data also show a negative correlation between K and L_∞, but the lowest L_∞ (and highest K) values are found in a cool, rather than a warm environment. Further, no relation is evident between longevity (as measured by the maximum age recorded in the samples) and L_∞. Beverton and Holt (1959) state that "the clearly established exceptions to the general positive correlation between longevity and size are those species which have a much higher value of K than would be expected from their L_∞," suggesting that K, rather than L_∞, is more closely realted to longevity. Again the present data offer no evidence to support this possibility. Whether or not a positive correlation exists between K and natural mortality needs further investigation, but, in view of the foregoing this is not to be expected. It is pointed out by Beverton and Holt (1959) that the association between high values of natural mortality and K may not hold for populations of the same species in closely adjacent waters, but this does not appear relevant here.

Thus the usual relations between temperature and growth are a decrease in maximum size with increase in temperature, but an increase in the rate at which this maximum size is attained. Taylor (1958) shows for cod from various areas, but mainly European, that a positive straight line correlation exists between the logarithms of values of K and mean annual surface temperature.

The fact that these relations tend to be reversed in the present data may mean that other factors, rather than temperature, exert the primary influence on growth. It is known, for example, (Fleming, 1960) that in this area the age and size at first maturity increase from north to south, and this would certainly tend to produce differences in growth in the direction as observed. Food relations and differences in feeding are not well known, but must be of importance. Further investigation along these and possibly other lines is required to reconcile the differences we have discussed in the temperature-growth relationship.

A relationship of the type found in the present data between latitude and L_∞ is described by Jones (1962), who gives L_∞ values for areas of fast and slow growth (southern and northern North Sea) as 58.1 cm and 48.3 cm respectively, though these differences are also related to depth.

In analysis of the present material the authors have found that the estimated values of L_∞ and K are very susceptible to small changes in the observed data. This has also been noted by Jones (1962), and Taylor (1962) shows that unrealistic values of L_∞ may be obtained by the usual method of estimation (regression of length at age *t+1* on length at age *t*). The observation by Jones (1962) applied particularly to data over a limited age range, though in the present material the authors

have found that significant changes in K and L_∞ could be brought about by the choice of the age range used to fit the equation. For this reason we have adopted Ricker's (1958) suggestion that the estimate of L_∞ derived as above be used as a trial value in the expression

$$\log (L_\infty - l_t) = \log L_\infty + Kt_o - Kt$$

and that the final L_∞ value be chosen as that which gives the straightest line for a plot of $\log (L_\infty - l_t)$ against t.

In view of the foregoing it is obvious that some caution must be exercised in deriving values of L_∞ and K to be used as representative of an area or a stock, particularly if the age range of the observed data is limited. Certainly some of the L_∞ values for cod (up to 200 cm) derived by Taylor (1958) from the limited age data of Saemundsson (1923) do not appear to have much biological meaning in relation to the maximum sizes found in the samples.

ACKNOWLEDGEMENT

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D-7

POSSIBLE INFLUENCE OF WATER TEMPERATURE
ON THE GROWTH OF THE WEST GREENLAND COD

By

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and

Paul M. Hansen[2]

ABSTRACT

From the 1920's to the beginning of the 1950's, the average length of cod of the same age decreased steadily. From about 1955 the average length increased. The variation of the length is compared with mean surface water temperature anomalies during the life of the cod year-class in question, and significant correlation coefficients are found for the age-groups V to IX. The possible influence of overpopulation on growth is discussed. It is found most probable that the variation in growth is mainly caused by temperature variation.

VARIATION OF LENGTH OF COD OF DIFFERENT AGE-GROUPS

Length measurements and age determinations of West Greenland cod were made nearly every year since 1924. Most of the material from the coastal area consists of samples taken from the Greenlanders' landings, but material from research vessels has also been included. The material from the offshore banks was obtained from research vessels. Only Danish material is used in this paper. The conditions in three different areas are discussed separately. The first area is the coastal area from Godthåb and northwards (*i.e.* north of approximately 62°30'N). The second area includes Frederikshåb and Julianehåb districts (*i.e.* the coastal area between Cape Farewell and 62°30'N), and the third area includes the West Greenland fishing banks from Dana Bank to Store Hellefiske Bank. From the length measurements the mean lengths of each of the age-groups V to IX were calculated for each year.

Variations in the length of age-groups V, VII and IX during the years 1924 – 62 are shown in Fig. 1 a and 1 b for the northern and the southern coastal area, respectively. Mean lengths have been decreasing since about 1932 in the northern area and since about 1936 in the southern area. They reached a minimum about 1954 and have since been increasing. Length curves for the southern area show greater fluctuations than those for the northern area. In the southern area there are probably two cod populations with different growth rates which probably are not evenly represented in the different samples.

Growth rate of cod varies considerably in the Greenlandic area. Mean length from the first half of the 1930's to the first half of the 1950's decreased from about 65 cm to about 50 cm for a five-year-old cod in the northern area. This corresponds to a decrease in weight from 2.5 kg to 1.2 kg. The mean length of a five-year-old cod in the northern area around 1930 was in fact about the same as the mean length of a seven-year-old cod around 1954.

VARIATION OF SURFACE TEMPERATURE ANOMALIES

For a comparison between growth rate and sea temperature, the temperature of the water layers in which the cod live should be used. However, sufficient subsurface temperature observations and information about the vertical distribution of the cod are not available. The only long-term temperature observations available are surface temperature observations collected by the Danish Meteorological Institute and presented by Smed (1959) as monthly mean temperature anomalies for each year and for selected areas. When averaged over a number of years the variation in the surface temperature anomalies for the area where the cod live, should represent fairly well the mean variation in

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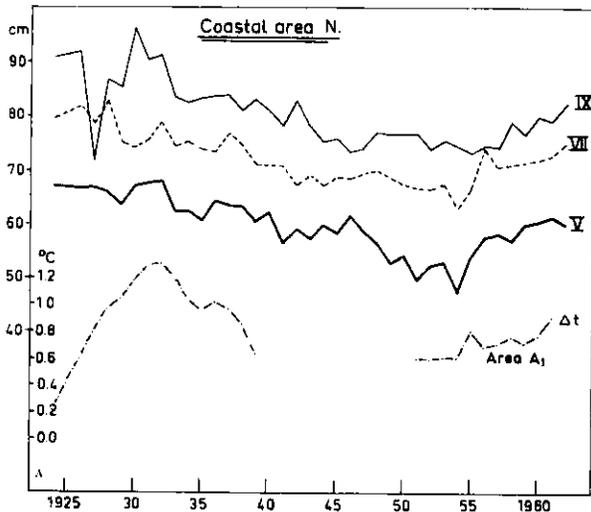[2] Greenland Fisheries Investigations, Charlottenlund, Denmark.

Fig. la. Variation in length of cod of age-groups V, VII and IX in the northern part of the West Greenland coastal area. Dotted lines mean surface temperature anomaly during the life time of age-group V.
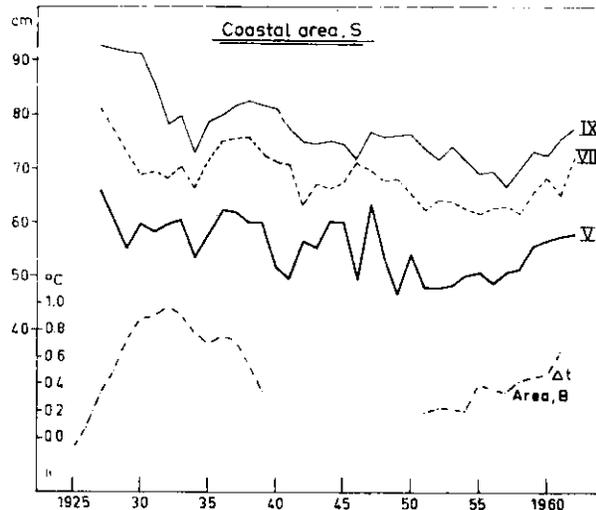
Fig. lb. Variation in length of cod of age-groups V, VII and IX in the northern part of the West Greenland coastal area. Curves are for the southern coastal area of West Greenland.

the layers where the cod live.

In the following account, the length of each age-group is compared with the mean surface temperature anomaly during the life time of the year-classes in question. For the northwestern area and for the bank area, the anomalies of Smed's area Al are used; for the southwestern area, those of Smed's area B (Fig. 5). In all years considered, temperature anomalies are available for the months April to September in area A_1 and for the months April to October for area B. Only material from these months is used below.

In the calculations of the mean temperature anomalies the anomalies of the single years have been weighted according to the fraction of the year the cod group in question has existed. As the cod is spawned in April the temperature anomaly for its first year of life is weighted by 0.75 and as the cod on the average is caught in July the temperature anomaly for its last year of life is weighted by 0.5 and only the mean anomaly for the months April to June is used. Thus, the formula used for calculating the mean temperature corresponding to a cod group of year-class a and age-group n is as follows for area A_1:

$(0.75 \cdot \Delta t_a$, Apr.-Sept.$^{+\Delta t}a+1$, Apr.-Sept.$^{+\cdots\cdot\Delta t}a+n-1$, Apr.-Sept.$^{+}$

$0.5 \cdot \Delta t_{a+n}$, Apr.-June$)$ ⸓ $(n+0.25)$, where Δt_a, Apr.-Sept. means the mean temperature anomaly for the months April to September in the year a. In the formula for area B, the period April-October replaces April-September in the above formula.

In this way the mean temperature anomalies for the age-groups V to IX were calculated for each year-class in the three areas in question. As an example, the mean temperature anomalies corresponding to age-group V have been plotted in Fig. la and lb.

CORRELATION BETWEEN LENGTH OF COD AND TEMPERATURE ANOMALIES

Figure 1 a and 1 b show that the mean temperature anomalies increased during the years from about 1924 to 1932 and then decreased. Unfortunately no temperature observations were made during the war, but in the post-war years there is a minimum around 1952 followed by an increase to 1961, the last year for which temperature observations are available.

The mean lengths of the cod and the variations in temperature thus show the same main features after 1932, but this was far from being the case in the 1920's.

The connection between temperature and average length of the single year-classes is further illustrated in Fig. 2a to 2e, 3a to 3e and 4a to 4e.   Here the average length of a certain age-group of each year-class is plotted against the mean temperature anomaly during the life time of the year-class in question. The figures show that the average lengths for most of the year-classes previous to year-class 1923 are higher than the average lengths of year-classes following year-class 1924.   Furthermore, the points of the year-classes between 1924 and 1956 group themselves around a straight line indicating increasing length with increasing temperature, but the year-classes previous to 1923 show no correlation with the temperature.

Because the numbers of cod in West Greenland waters increased rapidly in the first half of the 1920's and the lengths of the first year-classes which appeared in Greenland waters are nearly the same as those in the Icelandic cod stock, it seems reasonable to assume that the main part of the first year-classes which appeared at West Greenland had not grown up in these waters but had migrated from West Iceland waters to West Greenland as adult fish.   In 1924 cod were spawning in West Greenland waters as Vedel Tåning found cod larvae there.

It is, therefore, reasonable to assume that the year-classes following the 1924 year-class consist mainly of cod which grew up in Greenland waters, while the 1921, 1922 and 1923 year-classes probably are a mixture of cod which were spawned in Greenland waters and which have immigrated from Iceland, and year-classes previous to the 1921 year-class are mainly cod which have immigrated from Iceland.

The correlation coefficients r between average length and mean temperature anomalies and the corresponding regression coefficients b have been calculated for age-groups V to IX for the three areas considered using the material for all the year-classes after the 1924 year-class for which temperature anomalies are available.   The result as well as the number n of pairs of observations, and standard deviation, σ_b , on the regression coefficient are given in Table 1.

TABLE 1.   CORRELATION BETWEEN AVERAGE LENGTH OF COD AND MEAN TEMPERATURE ANOMALIES.

Age-group	Coastal area north				Coastal area south			West Greenland Banks			
	n	r	b (cm/C°)	σ_b	n	b (cm/C°)	σ_b	n	r	b (cm/C°)	σ_b
V	22	0.845	20.6	5.3	22	0.767	15.2	4.3	19	0.725	16.9	5.5
VI	20	0.788	15.9	4.6	19	0.679	13.5	4.7	19	0.710	15.2	5.0
VII	18	0.682	12.5	4.4	18	0.673	14.1	5.1	17	0.689	14.8	5.4
VIII	16	0.652	11.7	4.6	16	0.716	17.1	6.1	15	0.680	15.4	6.1
IX	14	0.818	15.4	5.2	14	0.784	18.7	6.6	13	0.790	16.5	6.1

All the correlation coefficients are significant within the 0.02 probability limit.   The regression coefficients show that the length of the cod increases by about 15 cm for an increase in temperature of one centigrade degree, and there are no significant differences in the regression coefficients of the different age-groups or from the different areas.

It is peculiar that the regression coefficients are not greater for the older age-groups than for the younger. Either the growth of cod is mainly influenced by the temperature during its first five years, or cod older than five years live mainly in water layers where the temperature variation does not follow the variation in surface temperature and therefore is not represented by the observations used in this paper.

The regression lines of cod lengths on mean surface temperature anomaly for the year-classes following the 1924 year-class, as well as the regression equations, are shown in Fig. 2a to 4e.
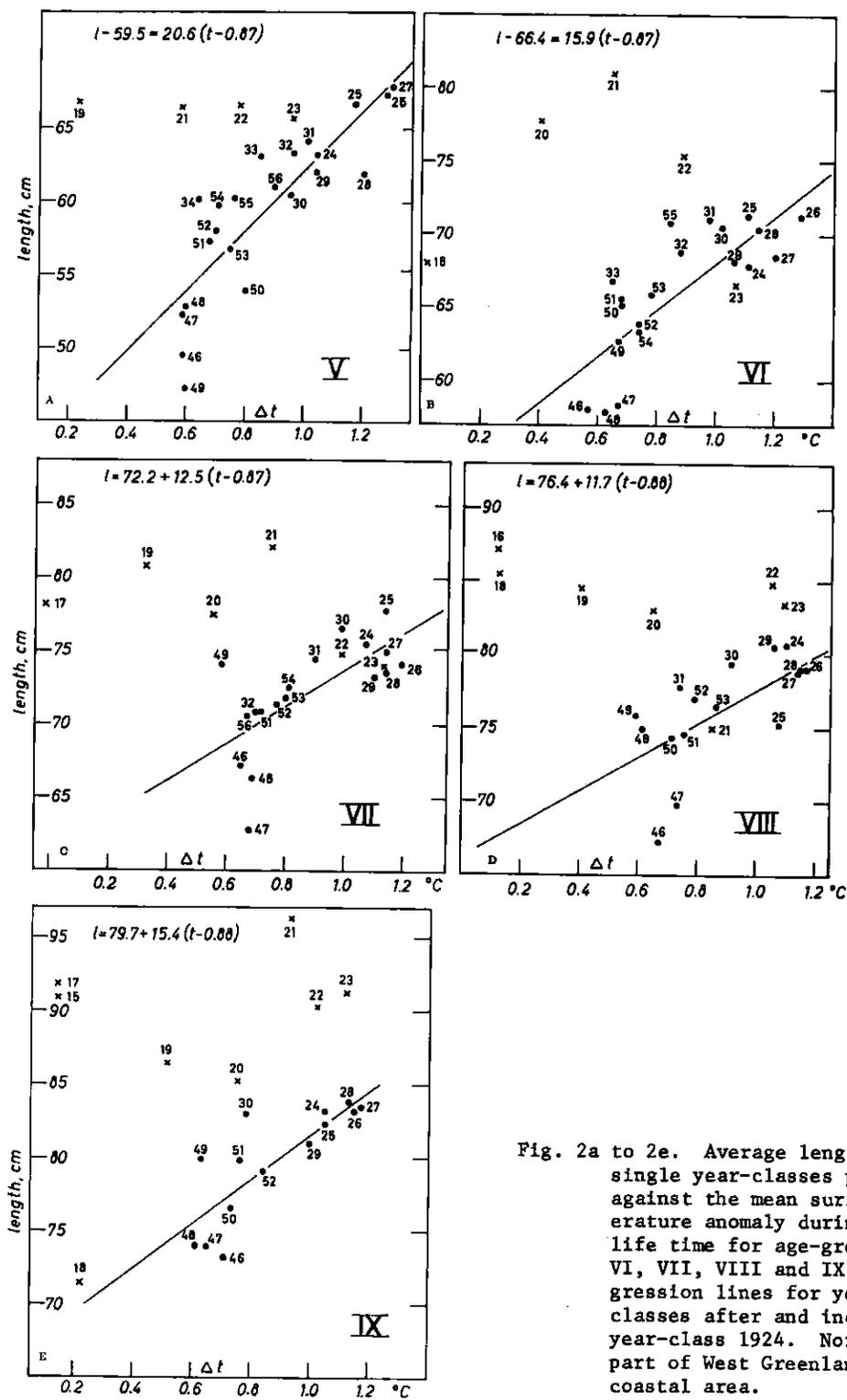
Fig. 2a to 2e. Average length of the single year-classes plotted against the mean surface temperature anomaly during their life time for age-groups V, VI, VII, VIII and IX. Regression lines for year-classes after and including year-class 1924. Northern part of West Greenland coastal area.
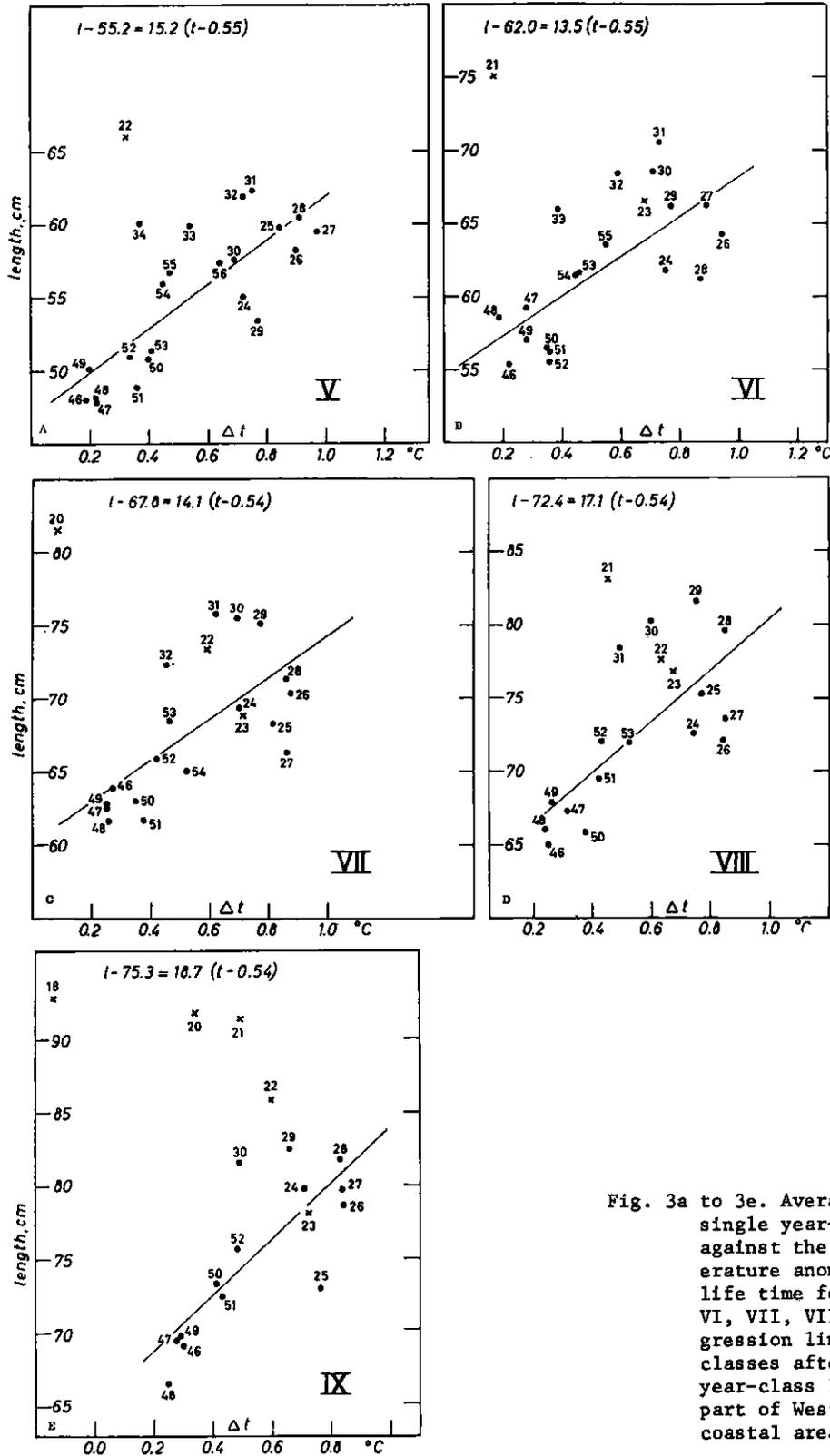
Fig. 3a to 3e. Average length of the single year-classes plotted against the mean surface temperature anomaly during their life time for age-groups V, VI, VII, VIII and IX. Regression lines for year-classes after and including year-class 1924. Southern part of West Greenland coastal area.
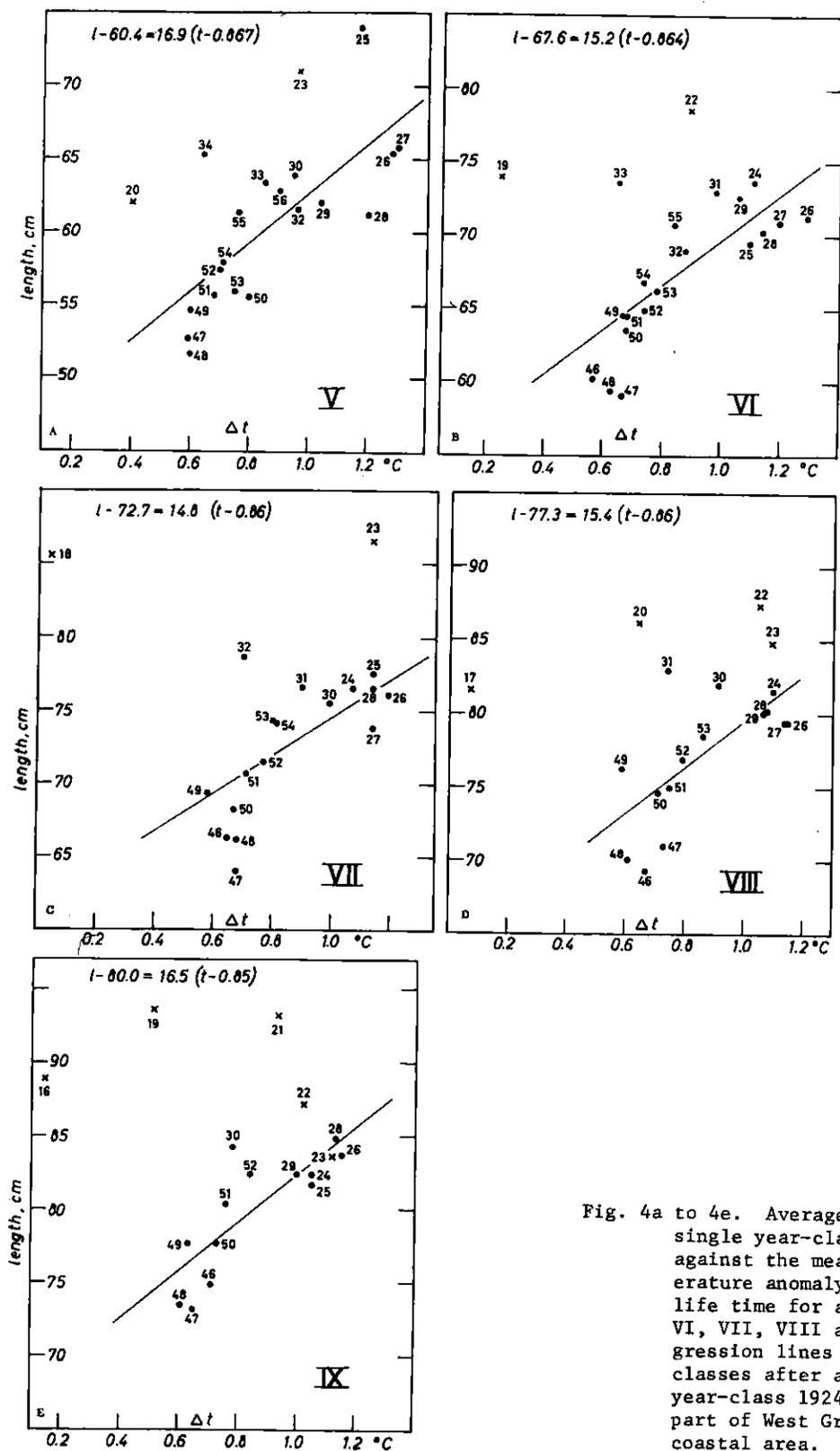
Fig. 4a to 4e. Average length of the single year-classes plotted against the mean surface temperature anomaly during their life time for age-groups V, VI, VII, VIII and IX. Regression lines for year-classes after and including year-class 1924. Western part of West Greenland coastal area.
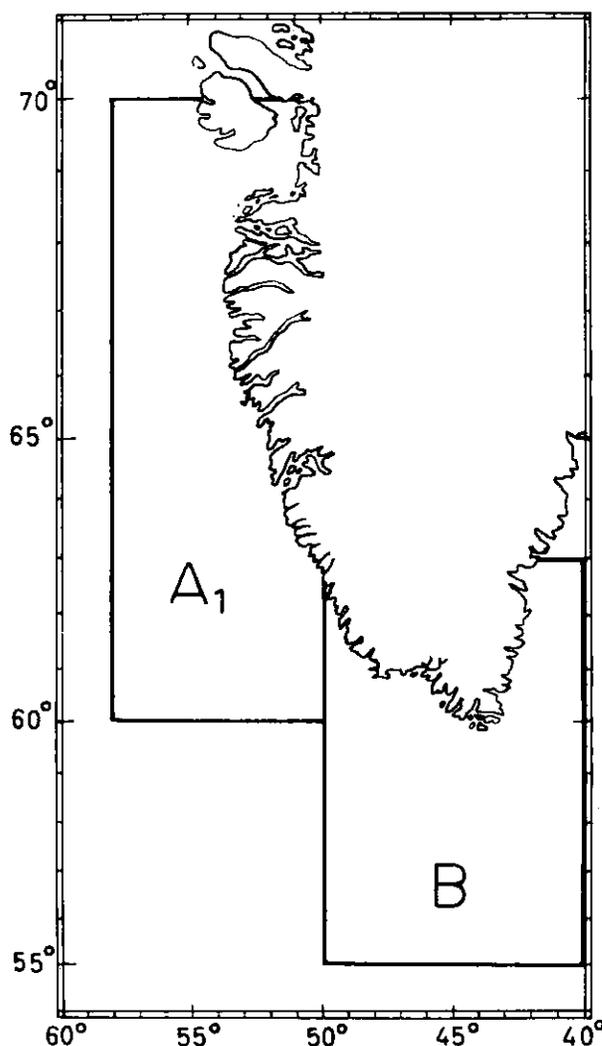
Fig. 5. Location of areas A₁ and B.

The fact that there is a significant cor-
relation between the length of cod and the varia-
tion of sea temperature does not prove that the
variation in length is caused by the variation
in temperature. It only shows that the variations
of cod lengths and of temperature have the same
main features over a certain number of years.

Of factors other than sea temperature which
could have influenced the growth rate of the cod,
overpopulation is probably the most likely. The
cod population could have increased in number
from almost nothing about 1920 to a maximum in
the early 1950's when the average lengths were
a minimum. Owing to the strong development of
the fishery on the West Greenland banks in the
1950's, the density of the population could de-
crease again with a consequent increase in growth
rate.

Data on landings and effort show, however,
that this overpopulation hypothesis is hardly
correct. Hansen *et al.(this symposium)* found,
from tagging experiments, that the fishing ef-
fort of the Greenlanders was 3.3 times greater
in 1946-58 than in 1924-39. The average annual
catch by the Greenlanders was 19,900 tons in
1924-39. The ratio between catches and the
ratio between efforts are thus nearly the same
in the two periods and consequently the average
size of the cod population seems to have been
roughly the same in the two periods.

The period 1924-39 represents the period
when the growth rate was at its maximum and the
period 1946-58, when the growth rate was at a
minimum. Therefore, the decrease in average
length from the beginning of the 1930's to the
beginning of the 1950's can hardly be explained
as an effect of overpopulation.

The increase in length of the latest year-
classes, 1954 and 1955, seems in the correlation
diagram to be somewhat greater than could be expected from the increase in temperature. The increase
in growth rate found in the latest years may be a combined effect of rise in temperature and de-
creased density by fishing.

It seems improbable that a different degree of overpopulation is the main cause of the long
term variations in the growth rate of the West Greenland cod. The authors are inclined to believe
that these variations are mainly an effect of temperature variations. The effect of the temperature
may be direct by affecting the activity of the cod, or indirect by affecting the abundance of food
animals.

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D-8

RELATIONSHIP BETWEEN THE GROWTH RATE AND POPULATION
DENSITY OF HADDOCK IN THE BARENTS SEA

By

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ABSTRACT

This contribution deals with the relationship between the rate of growth of haddock of individual year-classes, their abundance and the total abundance of haddock stock.

The Polar Research Institute (PINRO) has undertaken studies of growth rates (weight and length) of haddock of various sizes and age-groups, as well as of the individual year-classes, with the purpose of making more exact forecasts of the replenishment of the commercial stock.

The growth rate of haddock is influenced by many factors, including the abundance and availability of food, and the temperature conditions of the sea. Population density is also one of the factors determining the growth rate of the haddock. The present contribution deals with the relationship between the average length and weight, and the abundance of stock and of individual year-classes of haddock. The average length and weight of haddock of the same age vary from year to year. (Tables 1 and 2). In 1952, the average weight of 2- and 3-year-old specimens and the average length of 3-year-old individuals were somewhat below the long-term average estimated for 11 years. For the other age-groups, the average length and weight were found to be above the long-term average. In 1953 and 1954, the average weight and length observed in haddock under 5 years of age were below, but in older specimens, above or equal to the long-term average. From 1955 to 1958, the average weight and length of almost all age-groups were below the long-term average. In 1959, the average weight was somewhat greater, and specimens from 2 to 6 years old showed positive deviations. The rate of increase in length, however, remained slow and positive deviations were observed only in specimens from 1 to 3 years old. The average length of haddock of the other age-groups was below the long-term average. In 1960, the average weight and length were at the level of the long-term standard and in 1961-62 considerably above them. In these years, 3- to 8-year old haddock had especially high average weight and length.

Comparison of the rates of increase of weight and length growth with the relative abundance of the stock of haddock in the southern part of the Barents Sea for various years (Tables 1-3, Fig. 1) reveals that in the years when the stock of haddock was very abundant the rates of increase of weight and length growth were low, while in the years with a reduced or average abundance of the stock the rates were considerably higher. In 1952 and 1953, when small- and medium-size haddock of the 1950 and 1948 year-classes were very numerous, the rate of their growth was low. In the years characterized by a very abundant stock of haddock (1954 - 57) the rate of growth of all age-groups was declining; in the following years, characterized by a reduced and average abundance of the stock, the rate of growth was gradually rising, reaching a peak in 1961 and 1962.

An analysis of the rates of growth of various year-classes of haddock makes this relationship still more evident. Figure 1 shows deviations in growth of length and weight of the 1945 - 59 year-classes from the long-term average rate calculated for the period of 1945 - 62. The figure shows that the 1945 - 48 year-classes give mainly positive deviations of the growth rates whereas the 1949 - 53 year-classes are characterized by negative deviations. The lowest rate of growth is observed in the 1950 and 1949 year-classes. The rate of growth of the 1954 and 1955 year-classes is close to the long-term average for the first 6 years of their life, then it rises abruptly. The 1956 - 59 year-classes show high growth rates and positive deviations.

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TABLE 1. AVERAGE WEIGHT (KG) OF VARIOUS AGE-GROUPS OF HADDOCK IN THE SOUTHERN PART ,OF THE BARENTS SEA: NUMBER OF SPECIMENS IN PARENTHESIS

Age Group	Year					
	1952	1953	1954	1955	1956	1957
I	– (-)	0.09 (9)	0.18 (7)	– (-)	0.12 (3)	0.11 (65)
II	0.22 (130)	0.17 (187)	0.22 (5)	0.20 (1)	0.34 (103)	0.20 (19)
III	0.42 (36)	0.33 (1,225)	0.42 (75)	0.37 (2)	0.40 (537)	0.40 (108)
IV	0.74 (982)	0.53 (88)	0.62 (1,672)	0.50 (72)	0.55 (139)	0.60 (1,009)
V	1.13 (43)	1.01 (368)	1.05 (26)	0.77 (1,253)	0.76 (274)	0.79 (180)
VI	1.74 (26)	1.45 (30)	1.59 (263)	1.09 (43)	1.03 (2,250)	1.12 (243)
VII	2.18 (10)	1.92 (14)	1.67 (4)	1.98 (23)	1.58 (27)	1.32 (1,372)
VIII	2.97 (6)	3.20 (2)	2.47 (4)	– (-)	1.85 (15)	1.85 (23)
IX	3.12 (11)	– (-)	3.62 (2)	– (-)	– (-)	2.61 (17)
X	4.05 (2)	2.50 (1)	– (-)	– (-)	– (-)	– (-)
XI	4.90 (1)	3.95 (4)	– (-)	– (-)	4.75 (2)	– (-)

TABLE 1 (CONTINUED)

Age Group	Year						Average annual increment
	1958	1959	1960	1961	1962	1952–62	
I	0.08 (18)	0.10 (54)	0.09 (127)	0.09 (14)	0.17 (2)	0.11	0.11
II	0.24 (232)	0.31 (513)	0.25 (102)	0.30 (197)	0.26 (230)	0.25	0.14
III	0.39 (128)	0.59 (3,562)	0.57 (1,588)	0.65 (482)	0.56 (1,645)	0.46	0.21
IV	0.70 (317)	0.75 (545)	0.80 (2,361)	1.02 (1,442)	0.88 (936)	0.70	0.24
V	0.90 (1,436)	1.05 (415)	0.96 (224)	1.38 (1,171)	1.34 (1,403)	1.01	0.31
VI	1.21 (149)	1.43 (911)	1.49 (37)	1.76 (59)	1.84 (748)	1.43	0.42
VII	1.71 (173)	1.81 (66)	1.90 (36)	2.51 (16)	2.33 (45)	1.90	0.47
VIII	2.00 (504)	2.33 (67)	2.43 (8)	2.81 (34)	3.14 (22)	2.50	0.60
IX	2.91 (9)	2.77 (138)	3.39 (5)	3.93 (3)	3.26 (41)	3.20	0.70
X	3.85 (2)	3.49 (7)	3.40 (7)	3.71 (4)	3.15 (3)	3.45	0.25
XI	3.70 (1)	– (-)	– (-)	4.41 (15)	3.94 (7)	4.27	0.82

Comparison of rates of growth with the abundance of the various year-classes indicates that the rate of growth of each individual year-class is not closely related to its abundance.

In the following account, individual year-classes of haddock are defined as (1) poor; (2) medium; (3) rich; and (4) strong.

According to the results of the estimation of young fish (Baranenkova, 1957; Baranenkova and Baranova, 1962), the 1950 year-class of haddock is strong, the 1948, 1953, 1956 and 1959 year-classes are rich, the 1951 and 1957 year-classes are medium, and the rest are poor. The year-classes varying in abundance show both positive and negative deviations from the average rate of growth. The lowest rate of growth was observed for the strong 1950 year-class and for the poor 1949 year-class during almost the entire period of their life. Three of the rich year-classes (1948, 1956 and 1959) showed positive deviations, and the fourth one (1953) negative deviations. Of the two medium year-classes, one (1951) showed negative, and the other (1957) positive deviations. Of the poor year-classes, 1945 - 47 and 1958 are characterized by high, 1949 and 1952 by low, and 1954 and 1955 by medium growth rates.

A close correlation is, however, observed between the rate of growth of individual year-classes and the abundance of the entire stock of haddock. In the years with an abundant stock of haddock, a drop in the rates of growth of individuals of all year-classes was observed. On the other hand, when the stock of haddock was not abundant, all year-classes displayed a high growth rate. The existence of this relationship has already been mentioned by the author (Sonina, 1961).

TABLE 2. AVERAGE LENGTH (CM) OF VARIOUS AGE GROUPS OF HADDOCK IN THE SOUTHERN PART OF
THE BARENTS SEA: NUMBER OF SPECIMENS IN PARENTHESIS

Age Group	Year					
	1952	1953	1954	1955	1956	1957
I	–	16.9 (9)	22.5 (37)	– (–)	21.4 (3)	22.9 (65)
II	29.2 (130)	25.4 (190)	26.4 (12)	25.1 (17)	32. (103)	26.5 (19)
III	34.5 (36)	33.0 (1,365)	33.6 (81)	30.8 (20)	34.5 (537)	34.6 (108)
IV	42.3 (982)	38.1 (109)	40.0 (2,247)	36.6 (156)	38.3 (139)	40.5 (1,009)
V	48.0 (44)	48.6 (601)	46.6 (32)	43.0 (2,424)	43.4 (274)	44.2 (180)
VI	55.3 (26)	54.4 (37)	52.7 (259)	47.7 (69)	48.0 (2,250)	49.2 (243)
VII	62.5 (10)	57.4 (17)	58.0 (2)	58.0 (38)	55.2 (27)	52.4 (1,372)
VIII	68.9 (6)	66.4 (3)	68.0 (2)	73.0 (1)	58.7 (15)	58.0 (23)
IX	69.4 (11)	– (–)	68.0 (2)	73.0 (1)	– (–)	66.0 (17)
X	75.5 (2)	68.0 (1)	– (–)	73.0 (1)	– (–)	– (–)
XI	78.0 (1)	75.5 (4)	– (–)	– (–)	80.5 (2)	– (–)

TABLE 2 (CONTINUED)

Age Group	Year						Average annual increment
	1958	1959	1960	1961	1962	1952–62	
I	20.8 (18)	21.7 (57)	20.6 (127)	19.5 (14)	20.5 (2)	20.8	20.8
II	29.6 (238)	30.0 (573)	28.4 (102)	29.4 (197)	28.4 (230)	28.2	7.4
III	34.5 (130)	37.1 (3,688)	37.8 (1,592)	38.5 (482)	37.0 (1,645)	35.1	6.9
IV	40.9 (336)	40.5 (570)	42.3 (2,367)	45.5 (1,442)	43.9 (936)	40.8	5.7
V	45.2 (1,603)	45.9 (424)	45.4 (226)	51.0 (1,171)	51.0 (1,403)	46.4	5.6
VI	49.3 (171)	51.1 (920)	51.4 (38)	55.7 (59)	57.5 (748)	52.0	5.6
VII	56.0 (178)	56.0 (67)	57.7 (44)	63.0 (16)	62.4 (45)	58.0	6.0
VIII	58.8 (533)	61.5 (67)	62.6 (11)	65.9 (35)	68.7 (22)	64.6	6.6
IX	67.6 (11)	64.7 (138)	68.9 (12)	73.0 (3)	70.3 (41)	69.0	4.4
X	75.5 (2)	69.4 (7)	70.7 (19)	14.5 (7)	73.0 (3)	73.1	4.1
XI	73.0 (1)	– (–)	78.0 (1)	76.1 (28)	75.2 (7)	76.8	3.7

The 1945-48 year-classes, characterized by positive deviations, were growing up when the stock of haddock in the southern part of the Barents Sea was not abundant. This is shown by the rather poor average catches of haddock in 1949-53 (Table 3) as well as by the number of haddock of different sizes caught per hour's trawling (Fig. 2).   Figure 2 also shows the state of the stocks from 1945-62. The left side of the figure presents the numbers of haddock of different sizes in catches obtained per hour of trawling in 1945-62; the right side represents deviations from the long-term average. The figure shows that the period 1949-51 is characterized by a scarcity of fish of almost all sizes (except the small-sized fish in 1950) when compared with the long-term average. Haddock of the 1949-53 year-classes were growing up when the stock was abundant. Individuals of the 1954-55 year-classes during their early life were growing up,first,when the stock was abundant and, later, when the stock was reduced.

In 1958-62, when the abundance of the stock of haddock in the southern part of the Barents Sea became reduced, the rate of increase in weight and length observed in haddock of the 1956-59 year-classes increased and exceeded the average for the whole period of haddock life.

In haddock of the 1948 year-class a considerable drop in the rate of increase in weight and length was observed at the age of eight and nine years, *i.e.*, in 1956-57 when the stock of medium- and large-size haddock was more abundant than ever in the period under review. On the other hand, the rate of growth of the 1949-55 year-classes reached and exceeded the average in the period of
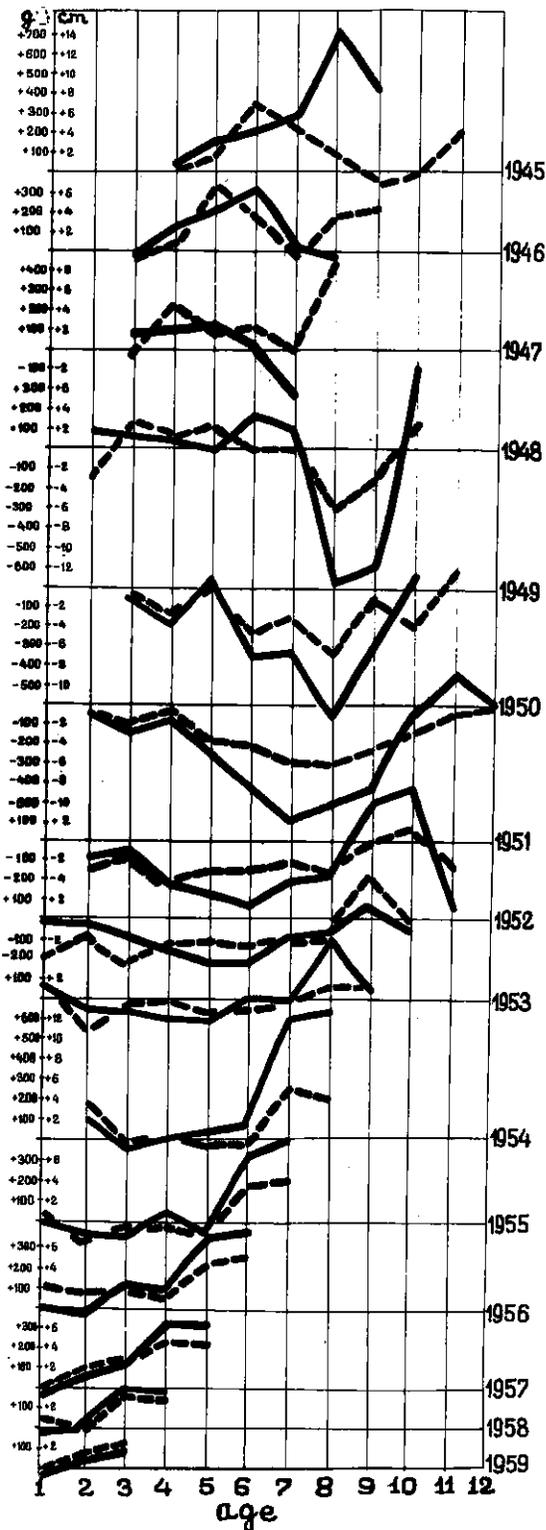
Fig. 1. Deviations in weight (———) and
length (— — —) of 1945-59 year-
classes of haddock from the long-
term averages for 1945-62. Weight
(g). Length (cm).

TABLE 3. AVERAGE CATCHES OF HADDOCK PER HOUR
OF TRAWLING (CENTNERS)
(1 CENTNER = 100 KG).

Year	1949	1950	1951	1952	1953	1954
Average catch per hour	0.5	0.8	0.6	1.0	1.1	1.6

Year	1955	1956	1957	1958	1959	1960
Average catch per hour	2.3	3.0	2.0	0.9	0.9	1.3

Year	1961	1962	1949-62
Average catch per hour	1.4	1.5	1.4

1958-62, $i.e.$, in the years characterized by a
reduced abundance of the stock of haddock in the
southern part of the Barents Sea.

It is, therefore, obvious that the growth
rate of haddock of various year-classes depends
on the abundance of the stock as a whole in the
given years. When the stock is not abundant
haddock grow fast and, on the other hand, an
increase in the abundance of the stock results
in a drop in the rate of growth of all year-
classes living in the southern part of the Bar-
ents Sea at that time.

The growth rate of haddock, therefore, can
be used to a certain degree as. an indication of
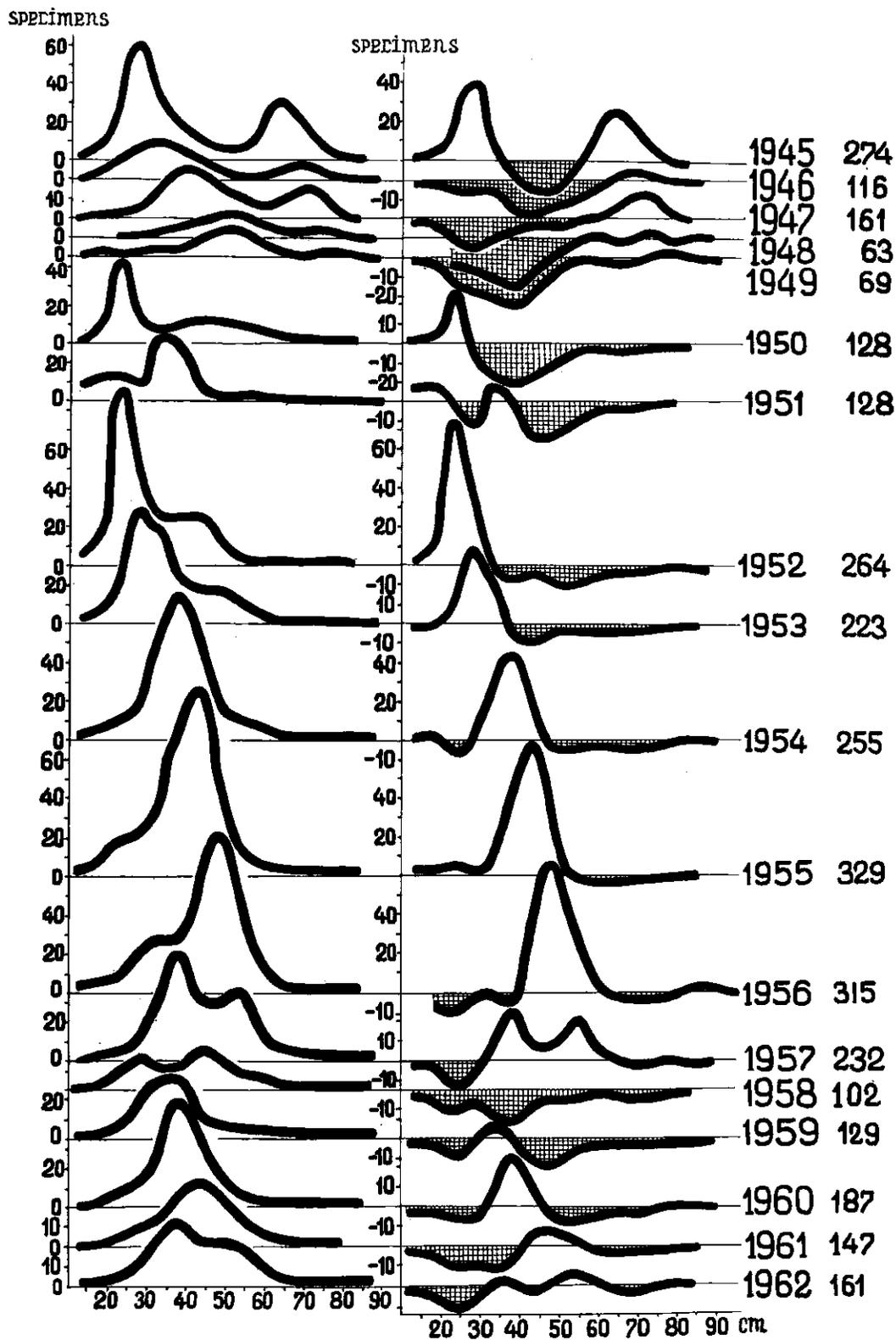the abundance of the haddock stock.

Fig. 2. Number of haddock of different sizes caught per hour's trawling (left) and
their deviations from the long-term average (right), for the period 1945-
1962. Figures on the right indicate average annual catches per hour of
trawling (no. of specimens).

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BARANENKOVA, A.S., and Z.P. BARANOVA. 1962. Quantitative indices of the results of estimation of cod and haddock young in the Barents Sea in winter 1961-1962. *Scientific Bulletin of PINRO*, No. 4(22). p.5, Fig. 2, Table 7. Murmansk.

SONINA, M.A. 1961. Growth rate of haddock in the Barents Sea. *Scientific Bulletin of PINRO*, No. 2-3 (16-17). p.3, Fig. 2, Table 3. Murmansk.

D-9

CHANGES IN THE GROWTH RATE OF THE BARENTS SEA COD AS AFFECTED
BY ENVIRONMENTAL FACTORS

By

T.F. Dementyeva[1] and E.M. Mankevich[2]

ABSTRACT

   The growth rate of the cod in the Barents Sea continued to increase during the period from
the end of the 1930's to the middle of the 1950's. It is suggested that this phenomenon was due to
an increasing metabolic rate which was, in turn, caused by increased warming of the waters of the
North Atlantic during the period. Such conclusions are based on analogic data on the growth in
length of various fish species living in different environmental conditions and living on different
food items over the same years and periods of life. Increase in growth rate is related to early
maturity and mortality in cod.

   Changes in the age of maturity of fish are known to be closely related to their growth rate as
determined by the specific character of these fish. Vasnetsov (1934) demonstrated that maturation
of fish was related to their length and not to their age.[3] This was later confirmed by Alm, 1959;
Nümann, 1959; Monastyrski, 1952; Dementyeva, 1952; Tokareva, 1964, and others.

   The relationship between growth and maturity is used to estimate future yields and, in par-
ticular, to calculate the amount of recruitment to the commercial stock (Monastyrski, 1952;
Dementyeva, 1952 and others). Early maturation results in a shortening of the life-span of fish
and, consequently, in a faster rate of exploitation of a given year-class by the fishery
(Dementyeva, 1963; Tokareva, 1964).

   It is, therefore, important to detect and explain changes in growth rate in order to determine
the population dynamics of the fish and to make fishery forecasts.

   This paper deals with the growth changes of the Barents Sea cod. Assumptions are made as to
the causes and results of such changes on the basis of some long-term data.

   Data include average lengths of the age-groups of cod in the catches made in 1934-37 (Maslov,
1944) and in 1946-60 (Mankevich, 1960).

   Figure 1 presents the results of the analysis of the average lengths. Specimens four to nine
years of age were used for comparison as they made up the most abundant age-groups in the Southern
Barents Sea.

   The data reveal, first, that, throughout the period, the average length of age groups, in
general, increased gradually to 1937 and from the mid-1940's to 1958; second, that, along with this
general increase in average length, some years had simultaneous increases in body length, while
others had decreases; and, third, that growth of the younger age-groups varied more than that of
the older age-groups.

   It is quite evident that the rate of growth of fish and the factors affecting this rate should
be estimated from the growth values obtained by means of back calculations. A comparison of the
average sizes of fish by age-groups reveals only the general trend of the growth changes. Never-
theless, this trend is so pronounced (Fig. 1) that we may concentrate our attention on the changes

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[3] We do not consider here the problem of under-sized fish attaining maturity as a result of
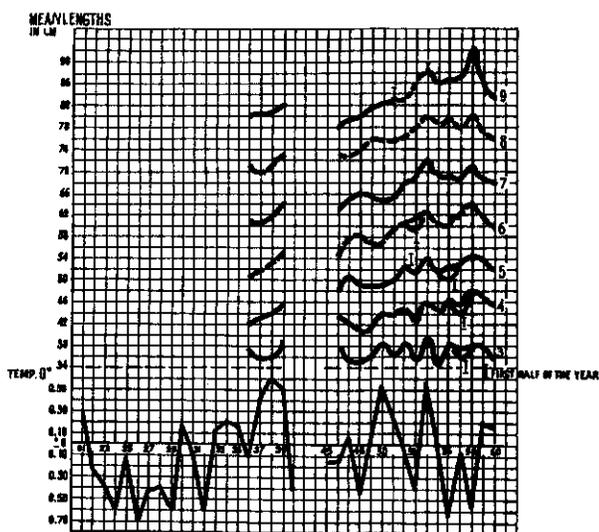   accelerated development.

Fig. 1. Mean length of the age groups of the Barents Sea cod by years and the water temperature anomalies on the Kola meridian.
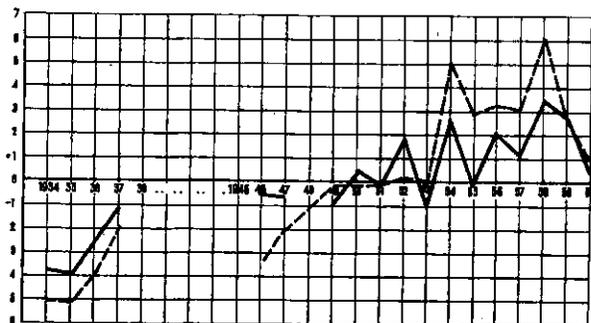

Fig. 2. Mean lengths of the older (——) and younger (— — —) age-groups shown as deviations from the long-term average for the period 1934-60.

that occur inside the population, despite the deficiency of data.

These changes are of greater importance than the general trend when the growth changes of cod have to be defined. For this purpose the annual deviations in growth rate from the long-term average were computed for the older and for the younger age-groups separately on account of the greater variability of the younger age-groups (Fig. 2). The mean lengths of the age-groups before 1952-53 were below the long-term average whereas those after 1952-53 were above. The growth of the younger specimens show the greatest deviations.

Maslov (1944) has pointed out that"the data obtained in 1937 revealed higher mean lengths for all age-groups of cod as compared to previous years. The reason for the increase in the mean length is yet to be ascertained". Earlier Rollefsen (1938) pointed out that fish of the same mean age were about 9 cm longer in 1936 than in 1932. The author suggested that the increase in the growth rate evidently was caused by changes in the hydro-meteorological conditions and that changes in the stock composition of cod results from the great sensitiveness of fish to environmental factors.

The following causes may be responsible for the above mentioned growth changes of the Barents Sea cod: 1) intensified growth in connection with poor yield[4] from year-classes; 2) changes in quantity and/or quality of food organisms; and 3) changes in metabolic activity and in availability and digestibility of food caused by fluctuations in the thermal regime.

Let us first consider the last of these three factors. It is, in our opinion, the most important because the simultaneous increase of growth of all the age-groups as shown in Fig. 1 forms a basis for the assumption that the cause of this increase may be the same for all the age-groups, i.e. metabolic changes may be caused by the general warming of the water. Figure 1 presents the variations of the mean temperature anomalies on the Kola meridian as deviations from the long-term temperature average. These data enable us to judge the changes in the hydrological conditions of the Northeast Atlantic. Comparison of these data with the increase of the growth rate of cod reveals that the best growth was observed mainly in the warmer years (1937, 1947, 1954, and 1957).

Analysis of the curve of temperature anomalies (Fig. 1) shows that the deviations during the period, 1922-32, were mainly negative, whereas after 1934 they were positive with the exception of those in the early 1940's and in the late 1950's. Thus 1945-55 is a period of warm years coinciding with the general increase in the growth rate of cod (Fig. 2). The low temperatures in 1939-42 and in the late 1950's resulted in lower values of fish length. The decrease in the growth of cod during 1939-46 is further confirmed by Rollefsen (1953) and from data on the mean length of "skrei" provided by G. Saetersdal (personal communication).

The dependence of the growth changes of cod on temperature is shown in Fig. 3 and 4. Figure 3 shows the fluctuations of the mean lengths of the three main age-groups, IV, V and VI, compared

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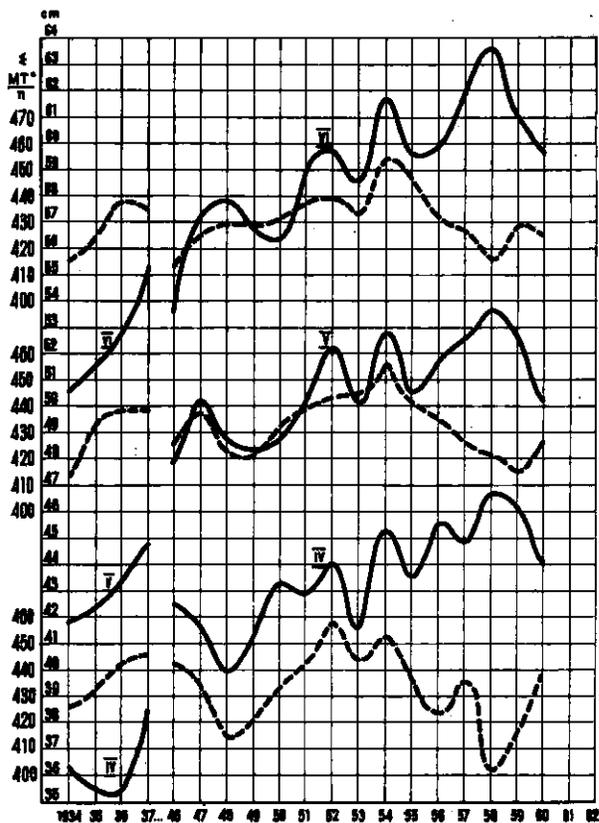[4] the lower density of the stock caused by heavy fisheries

Fig. 3. Fluctuations of the mean lengths of
cod (————) and the heat content of
waters (— —·—) during feeding per-
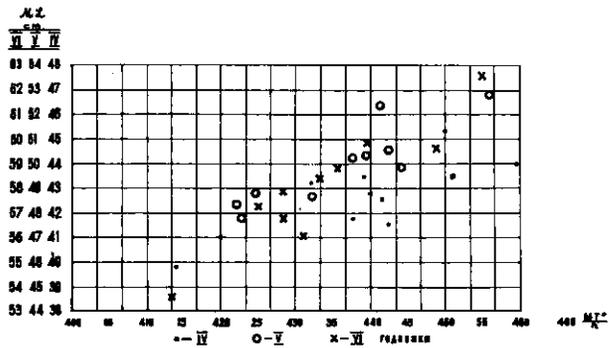iods throughout the life of speci-
mens.

Fig. 4. Correlation between the mean lengths
of the age groups of cod and the total
average temperatures during feeding
periods in 1946-56.

with the total average temperatures during the
feeding period of the cod in the years, 1934-37
and 1946-62. To 1955-56 the trend in the heat
content of the waters follows closely the trend
in growth rate. With the onset of the cooler
period, after 1955-56, the sizes of cod con-
tinued high to 1958 then decreased. Several
reasons account for the large size of cod in
1958: first, the growth of these fish during
their early years of life had taken place under
higher temperatures; second, the sharp decline
in numbers of cod during these years increased
the growth rate; a fact which will be commen-
ted upon below. In Fig. 4 the mean lengths and temperature data for the period 1946-56 are plotted
on the correlation grid. The correlation factor was found to be 0.71.

The variations in the growth rate of fish in relation to water temperature during the peak of
the feeding period combined with the length of this period have been discussed by many authors.
Nikolaev (1954) illustrates this by referring to studies (also experimental) on particular species
of fish. Nikolski (1961) emphasizes the existence for each species of an optimum temperature which
is the most suitable for metabolism and provides the fastest growth. One may assume that cod, like
many other fish, grow faster in warmer than in colder years. In warmer years the feeding period is
extended, the search for food is intensified, the digestion is improved so that food organisms are
consumed in greater quantities which in turn causes an increase in the growth rate.

In their summary work on fishery hydrography, Hela and Laevastu (1961) formulate this problem
as follows: "The rate of feeding, metabolism and growth is related not only to the availability
of food, but also directly to water temperature. The feeding activity usually drops with the de-
viations from the optimum temperatures. The cod was found to cease feeding if the temperature went
below 1°C. The growth is directly related to the intensity of metabolism, i.e. to the speed with
which the food substances are transformed into the living matter. Hence the optimum growth corres-
ponds to the optimum temperature and the intensity of metabolism of a given species depends to a con-
siderable degree on the temperature". Taylor (1958) points to the susceptibility of cod to temp-
erature fluctuations. He shows a linear relation between surface water temperature and the growth
rate of certain North Atlantic populations of cod and warns against possible errors in evaluating
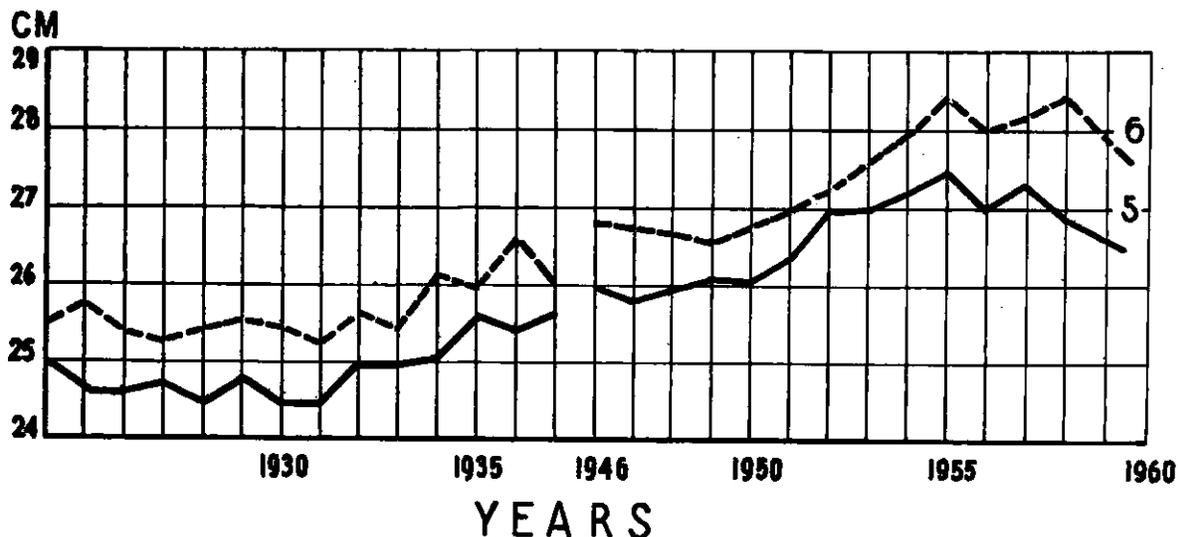the significance and effect of the fishery.

Fig. 5. Changes in the mean lengths of herring in 1932-59 (after Cushing, 1961).

The observed relation between growth rate of cod and temperature conditions was further supported by the fact that during the same years North Sea herring have also increased their growth rate. Cushing (1962) noted that herring have increased their growth rate since 1951. Figure 5, borrowed from his work, shows that the trend and the rate of increase of the mean length of herring are similar to those of the Barents Sea cod. Since 1958 both species have slowed down their rate of growth which is probably related to the onset of the colder period. Ancellin (1960) also showed that for 7 to 8 years, to 1955, the sizes of fish of one and the same age have considerably increased. However, in 1955-59 sizes decreased to normal as seen from the following table:

The mean length of herring by age groups

(after Ancellin)

Age	Years of catch		
	1945	1955	1959
3	22.56	26.41	23.0
4	22.47	26.12	25.17
5	25.73	27..42	26.82
6	26.59	28.13	27.76

The similarity in the growth changes in different North Atlantic species both in respect of food and fishing mortality suggest that the main cause of these changes is the intensity of metabolic processes, probably connected with changes in the general hydrological conditions of the North Atlantic waters including the habitat of the species under consideration.

This indicates the close relation between the processes in the physical medium and their influence on the productivity of the sea. This was discussed by Izhevski (1961) who also pointed out on page 19, the common nature of the water dynamics not only of each of the North Atlantic seas but also of all north European seas collectively.

Changes in the hydrological regime also affect the availability and accessibility of the food organisms themselves, plankton in particular, which, in turn, results in changes in the growth rate

of plankton-eaters in certain years (Burd, 1962). Izhevski develops this idea pointing out that the growth rate of fish exclusively depends on the availability of the food, which is more abundant in the warmer years.

Unfortunately, we have no information on the year-to-year abundance of food organisms and we cannot follow this relationship with respect to cod on a long-term basis. We can, however, refer to sporadic data available in literature on the feeding of cod.

The feeding habits of the Barents Sea cod were studied by Zatsepin and Petrova (1939) and later by Grinkevich (1957). The authors conclude that annual changes in the feeding habits of cod follow the seasonal pattern, but are influenced by the biological peculiarities and the changes in the abundance of food organisms.

For example, in warm years, cod begin feeding on euphausiids as their main food item, earlier than in the cold years when the spawning of euphausiids is delayed and the euphausiids reach the near-bottom layers later than usual. In cold years, the habitat of the cod coincides closer with that of their food item – Polar cod (*Boreogadus saida*). During these colder years, capelin became the most sifnificant cod food item because their northeast migration is slower and they, therefore, remain in the area of cod fisheries much longer.

The feeding of cod on herring also depends on the availability of red *Calanus*. Intense production of the latter in June-July accounts for the high fat content of herring and facilitates the formation of their near-bottom concentrations, thus providing better feeding conditions for cod.

These data enable us to conclude that even in years with different hydrological conditions cod can be satisfactorily supplied with food. Thus changes in the growth rate of cod, though being to a certain degree related to the availability and accessibility of food (Mankevich, 1960), are much more dependent on the metabolic intensity of the consumers.

In warm years the production of plankton organisms serving as food for herring, increases. However, this is not the case with such cod food items as capelin, polar cod, bottom crustaceans, etc. whose abundance is affected by conditions for reproduction in the previous year or years.

In a number of cases the growth rate of fish is influenced by the density of the population, especially when there is a sharp increase of cod produced by rich year-classes. Under such circumstances the growth rate of fish becomes slower even with a fairly good food supply. Also, the growth rate becomes faster when the stock is thinned out by fisheries and when the stock is composed of a number of poor year-classes.

The intensified rate of growth of the Barents Sea cod was observed both in 1950-55 when the rich 1950 year-class was dominant and in the years 1957-58 when there was a sharp decline in abundance of fish. In the latter years (Fig. 3) the decline of the density factor may have played a considerable role along with the increased heat content of the water, in causing the greater growth of cod.

Saetersdal and Cadima (1960) concluded that body length tended to decrease with increasing density of the "skrei" population. However, if their data are analysed from the point of view of the time of sampling (excluding samples made in 1925-30), it will be seen that the lowest lengths were observed in samples from 1931-37 and the highest lengths in samples from 1940-47, *i.e.* the changes in the body length of the "skrei" fit into the pattern shown in Fig. 2. We suggest that the changes observed in this particular case are due more to environmental factors than to insufficient amounts of food during the growth period of the rich year-classes.

GROWTH RATE AND MATURITY

As mentioned in the beginning of this paper, there is a direct relationship between growth rate and age of maturity. This relationship can be used to calculate the composition of the stock under formation and the fishing mortality. Mean lengths of cod in each age-group have been shown to vary as much as 11 to 15 cm over the years (Fig. 1). This greatly influences the rate of maturity of cod.

It must be noted that during the period under consideration, there was an intensive development of the trawl fishery. This has resulted in a lower mean age of the stock as evident from the following table of data taken from the ICES Working Group on the Arctic cod (1959), from Rollefsen (1953) and from Saetersdal (1959):

Relation of fishing intensity to the rate of exploitation
of cod generations by fisheries:

Years	Hours of trawling (in thousands) in the Southern Barents Sea	Prevailing age	
		in the Barents Sea stock	in the "skrei" stock (acc. to Norwegian data)
1932–38		6–7–8	
1945–50	75–131	6–7	10–11
1950–55	162–267	4–5–6	9–10
1955–59	186–333	4–5–6	8–9

These data show that mean age of the commercial stock decreases with the growing fishing intensity and that regulation measures are required. It may be supposed, however, that the decrease in mean age of the stock is not only caused by the development of fisheries; but may also be caused, to a certain degree, by the earlier maturation of cod due to more rapid growth, especially in the early 1950's, when the fishery had not yet reached full intensity.

Saetersdal suggests that, in addition to the influence of fishing, changes in the age af maturity of the Arctic cod caused the decrease in mean age of the spawning stock of cod in Norwegian waters. He notes, however, that investigators lacked opportunities to distinguish changes from those inflicted by the fisheries.

Still earlier Rollefsen (1938) indicated that the early age of maturity may conceivably result from increased growth rate of cod. He believed that even if there was no direct causal connection, the same circumstance which conditioned the faster growth rate may have also influenced the course of sexual maturation. "Furthermore," says G. Rollefsen, "the earlier age of maturity and the increased mortality in the mature stock should be looked upon as the cause responsible for the reduction of the average age of the stock". We support this author's opinion, and believe that the above data serve to clarify, to some extent, the causes which are responsible for the changes in the composition of the stock of cod, though these causes do not fully determine the actual ranges of the changes. It appears from our observations that these causes were valid not only for the Barents Sea but also for the whole North Atlantic area, including the North Sea.

SUMMARY

The above data on cod provide the basis for the following recommendation:

When analysing the changes in the composition of the total and the commercial stocks of a fish, it is necessary to determine all the causes inflicting these changes, including the changes in the maturity rate in relation to the growth rate. Changes in the age at maturity may be caused by the feeding conditions and intensified by the influence of the hydrological factors (thermal regime affecting the intensity of the metabolic exchange resulting in the consumption of food organisms in greater amounts than usual). The rate of exploitation of the year-classes which, in its turn, sometimes is intensified by extensive fisheries, increases with early maturation.

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