SECTION

B

B-1

THE RELATIONSHIP BETWEEN THE DISTRIBUTION OF *SEBASTES* LARVAE, ZOOPLANKTON AND TEMPERATURE IN THE IRMINGER SEA

By

Jakob Magnússon[1] and Ingvar Hallgrímsson[1]

ABSTRACT

This contribution is based on material collected from the upper 50 m of the sea with Helgoland larvae nets and Icelandic High Speed Samplers at 178 stations during a cruise in May 1961 covering he Irminger Sea south to 60°N and east to 24°W.

Charts showing the station grid and the distribution and abundance of redfish larvae are pre-ented. *Sebastes* larvae were found in most of the oceanic region of the survey area. The main oncentrations were observed along the western slope of the Reykjanes Ridge in two main zones, one orresponding with the area bounded by the 1,000 and 2,000 m depth contours and the other mainly utside the area of the 2,000 m contour. Generally, the density zones and tongues ran in a south-orth direction.

Fairly large quantities of zooplankton were found. The volume distribution was also charac-erized by marked zones of high density extending into the area from south and east creating a very neven horizontal distribution of the zooplankton. This distribution is believed to be closely elated to the complex current system.

A chart showing the temperature distribution at a depth of 20 m is presented. A close connec-ion was established between the abundance of larval redfish and certain isotherms.

Although it was not possible to show a detailed correspondence between zooplankton abundance nd the isotherms at 20 m, it was evident that the isolines for the zooplankton volume mainly fol-owed the same general direction as the isotherms.

Generally, there was a good agreement between the abundance of redfish larvae and zooplankton ensity in the oceanic area. The larval abundance did not always coincide with high zooplankton olume. But in such cases a high percentage frequency of *Calanus finmarchicus* was found, this pecies being the most dominant one in the whole oceanic area (varying from 72% to 99% of the total ooplankton numbers). Thus, a good correlation existed between the abundance of larvae and *Calanus inmarchicus*. No such correlation was found with *Spiratella retroversa*. The percentage frequency f these two species is presented in charts. The results of this cruise have been compared with he results of cruises in 1962 and 1963. In 1961 and 1962, a great abundance of redfish larvae orresponded with a high standing stock of zooplankton. In 1963 there were relatively low numbers f larvae and the stock of zooplankton was low.

From these results, and assuming that year-class strength is determined during the larval hase, it is expected that the 1963 year class of redfish from this area will be a relatively poor ne.

University Research Institute, Skulagata 4, Reykjavik, Iceland.

CNAF SPEC. PUBL., NO. 6.

OTE: This contribution will be published *in extenso* in Rit Fiskideildar.

B-2

ON THE ANALYSIS OF VARIATION IN THE PLANKTON, THE ENVIRONMENT AND THE FISHERIES

By

J.M. Colebrook[1]

INTRODUCTION

One of the objectives of marine biology is the detection of relationships between the plankton, he hydrographic environment and the fisheries with a view to determining control mechanisms and stablishing prediction equations. Irrespective of the form of these relationships, the planktoloist's immediate problem is the same: how to measure and express the variations in the plankton in uch a way as to facilitate comparisons with variables obtained from hydrographical and fisheries tudies.

The purpose of this paper is to describe an approach to this problem based on the Continuous lankton Recorder survey of the North Sea and the North Atlantic. Plankton Recorders are towed by erchant ships and weather ships along a number of standard routes which are sampled (at a depth of 0 m) once in each month. The instrument has been described by Hardy (1939), the methods of analysis y Rae (1952) and Colebrook (1960) and the characteristics of the samples and the survey by Glover 1962). Fig. 1*a* shows the routes in operation in 1963 (supported by H.M. Treasury from the Developent Fund and by contract N62558-3612 between the Scottish Marine Biological Association and the nited States Department of the Navy, Office of Naval Research).

The survey of the western North Atlantic, including the ICNAF area, has been developed during he past two years and there is insufficient material from this area, as yet, for analyses of the ind described in this paper. These are based on the survey of the eastern North Atlantic and the orth Sea during the period 1948 to 1962. However, the intention here is to demonstrate possible ethods of analysing dats of this kind rather than to draw conclusions about any particular area.

The basic data consists of counts of species in samples at intervals of 20 nautical miles along he standard routes. On the average 150 samples have been collected in each month for the last 15 ears (up to 1962) and about 50 species occur regularly in the samples: this amounts to well over million observations. Each species shows geographical, seasonal and annual variations in abunance and clearly this situation is far too complicated to be compared, as it stands, with variations n hydrography and fisheries: it is necessary to simplify the situation in some way.

Glover (1957) and Glover *et al.*(1961) used year to year fluctuations in the abundance of zoolankton species as an estimate of annual variations in the plankton of the herring fishing grounds ff the east coast of Scotland. They found that the variations were related to water movements and o fluctuations in the success of the fishery. A more important result, in the present context, was hat groups of species were detected showing similar annual fluctuations of abundance. This sugests the possibility of deriving quantitative estimates, integrated by species, representing the nnual fluctuations in the abundance of the plankton as a whole. What would be required, in this ase, is a variable or a small number of variables giving the maximum discrimination between years nd including the variability of all the species in the plankton. Williamson (1961 and in press) erived such variables and used them to demonstrate quantitative relations between herring mortality nd distribution, hydrography and the fluctuations in abundance of the plankton. There is no reason hy the same principle should not apply to other aspects of plankton fluctuation such as seasonal nd geographical variations. This suggests the need for new methods of classifying the variations in he plankton as a whole. One possible system is that used in analysis of variance. The variability f the standing stock of the plankton as sampled by the Continuous Plankton Recorder can be repreented as a five dimensional variable, with standing stock as the variate, the other co-ordinates eing species, areas, months and years. The variability included in this system can be classified

---

Oceanographic Laboratory, Edinburgh, Scotland.

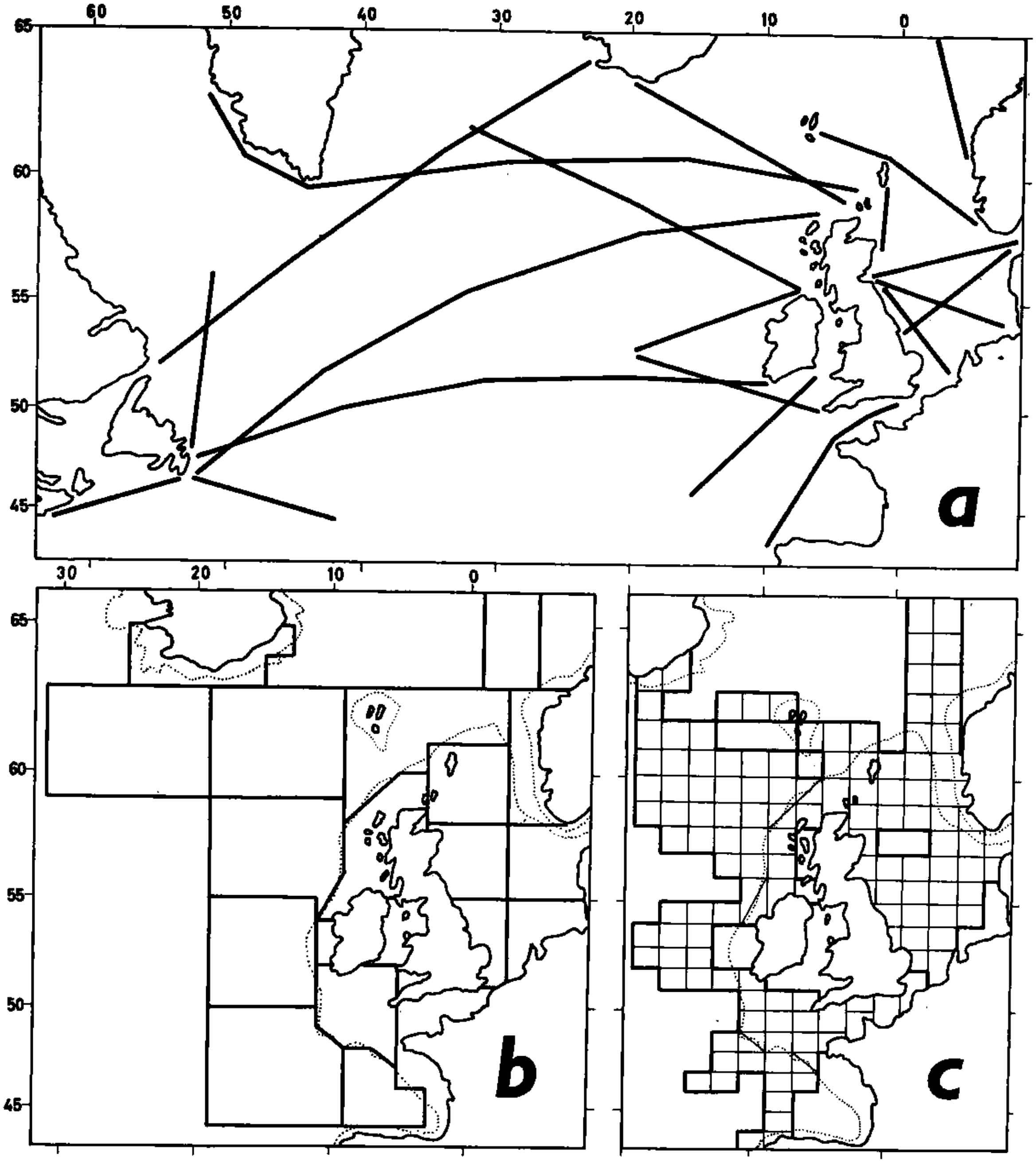


Fig. 1. (*a*) A chart showing the routes included in the Continuous Plankton Recorder survey in 1963.

(*b*) A chart showing the standard large area subdivision of the survey.

(*c*) A chart showing the subdivision of the Northeast Atlantic and the North Sea covering the area which has been sampled continuously since 1948. Each rectangle is 1° lat x 2° long: subdivided where necessary to give a boundary following the edge of the continental shelf.

s a four factor analysis of variance as shown in Table 1. Each source contains the variability easured along the included co-ordinates with the variability due to the other factors eliminated y averaging and also with the variability due to lower order sources involving the factors, if any, ubtracted. Thus, the source, species-areas, contains information about the geographical distri- utions of species with data for all years and months averaged and with the differences in abundance etween species and the variations in the overall abundance in the various areas eliminated.

The object of this classification is to divide the total variability of the standing stock of he plankton into a number of independent parts. Associated with each part is its degrees of free- om (the values shown in Table 1 are based on expressions of the data in the form described below). he sum of these degrees of freedom is the same as that of the original variable so this classifi- ation, as it stands, does not constitute any simplification of the system. In order to achieve he required simplification it is necessary to find out first of all whether any of the sources of ariation can be ignored. This can be done by carrying out the analysis of variance and expressing he variability included in each source as a proportion of the total. Any source which is small in elation to the others can be ignored without any great loss of information. For the remainder, it s necessary to find methods of representing the variation of each source, or of groups of sources ncluding the same factors, by means of a variable or variables with a smaller number of degrees of reedom.

TABLE 1. CLASSIFICATION OF VARIATION OF THE STANDING STOCK OF 22 SPECIES OF PLANKTON IN THE 17 STANDARD AREAS SHOWN IN FIG. 1*b* DURING THE PERIOD 1948-1962.

	Degrees of freedom
Species	21
Areas	16
Months	11
Years	14
Species - Areas	336
Species - Months	231
Species - Years	294
Areas - Months	176
Areas - Years	224
Months - Years	154
Species - Areas - Months	3696
Species - Areas - Years	4704
Species - Months - Years	3234
Areas - Months - Years	2464
Species - Areas - Month - Years	51744

The final object, therefore, is to represent a large proportion of the variability of the standing stock of the plankton by variables with relatively small total degrees of freedom. This objective has not yet been achieved in the analysis of the data from the Continuous Plankton Recorder survey but successful analyses have been done on several of the sources of variation. Some of these are described in the following sections of this paper; more detailed accounts of each analysis are being prepared for publication.

METHODS OF ANALYSIS

1. Presentation of Data.

The first problem in the representation of variability is the selection of suitable units and methods of presentation. This is a matter of compromise between the requirements of the analytical methods and the limitations of the original data. The calendar month and year have been used as the time units and a system of areas was selected dividing the survey into rectangles of 1° lat x 2° long (Fig. 1*c*). For many purposes a less detailed sub-division is convenient and a system of larger areas (Fig. 1*b*) was devised with the intention of dividing the survey into as small a number of areas as possible without introducing too great a loss of variability and also giving areas corresponding as closely as possible with those in general use for the presentation of fishery and hydrographic data. The variate, standing stock, is represented by the logarithmic transformation (in the form $y = \log [x + 1]$ of the original sample counts: all subsequent analyses are carried out using the transformed values.

Ideally the taxonomic unit should be a biologically self-contained population with its own characteristic parameters of reproduction, growth and mortality, which can be treated as being dynamically independent (Glover, 1961). In practice, the species is usually the smallest unit that can be identified and sometimes it is necessary to resort to larger taxonomic units or to groups of species to avoid spending an undue amount of time identifying the organisms. Judging from the results so far, it appears that most species represent ecologically homogeneous populations, within the context of the Recorder survey, but several cases of ecological differentiation within a species have been described by Colebrook and Robinson (1963).

Most of the analyses which have been carried out so far are based on data for the copepods and the gastropods *Clione* and *Spiratella*. The other major groups in the zooplankton are not identified to species during the routine counts and the phytoplankton has been omitted from most of the analyses because, up to 1958, the counting method that was used did not yield suitable data.

2. Classification and Analysis of Variance

Table 2 gives the results of an analysis of variance with the variability due to years excluded. The analysis was based on the monthly means of 22 species, averaged for the years 1948 to 1961 in the standard areas shown in Fig. 1*b*. The results are expressed as percentages of the total sum of squares and the degrees of freedom are given. It can be seen that by far the largest single source of variation is species with 43.4%; this merely reflects the fact that some species are more abundant than others and is of no particular interest in considering relationships with the environment. The second column in the table shows the percentage of the total sum of squares with species excluded. It is clear that the only source of variation that could be ignored with little loss of information is areas-months. In practice, however it was found convenient to include this source with species-areas months in a single analysis; similarly it was found convenient to include months with species-months and areas with species-areas.

TABLE 2. ANALYSIS OF VARIANCE FOR 22 SPECIES IN THE 17 STANDARD AREAS SHOWN IN FIG. 1*b* BASED ON LONG-TERM AVERAGES FOR THE PERIOD 1948-1962.

	% Sum of Squares		Degrees of Freedom
Species	43.4		21
Areas	5.2	9.2	16
Months	12.7	22.4	11
Species - Areas	11.8	20.8	336
Species - Months	13.5	23.8	231
Areas - Months	2.5	4.4	176
Species-Areas-Months	11.0	19.4	1344

3. The Variability due to Areas and Species-Areas.

The 2° x 1° rectangles (Fig. 1*c*) were used as the area units in this analysis and 22 species were included. The first step was to eliminate the variability involving the sources months and years by averaging; the resulting means were written as a two-dimensional matrix with each column referring to a rectangle and each row to a species. Each row of the matrix represented the mean geographical distribution of a species. Each row was expressed in standard measure, with a mean of zero and unit variance, by applying the transformation $t_{ij} = (m_{ij} - \overline{m}_i)/s_i$ to each row where $\overline{m}_i$ is the mean of the observations of species i and s_i is the standard deviation. This procedure is equivalent to subtracting the variability due to species in analysis of variance. The resulting standardized matrix contained only the variability due to areas and species-areas, *i.e.* the pattern of variation of the geographical distributions of the different species.

A principal component analysis was applied to this matrix. The object of component analysis, as used here, is to select variables, which are linear functions of the geographical distributions of all the species included in the analysis, in such a way that the distributions may be represented by a smaller number of variables known as components. The first component is a representation of all the geographical distributions, selected so as to have the greatest possible variance. The second component is uncorrelated with the first and it has the greatest possible variance in relation

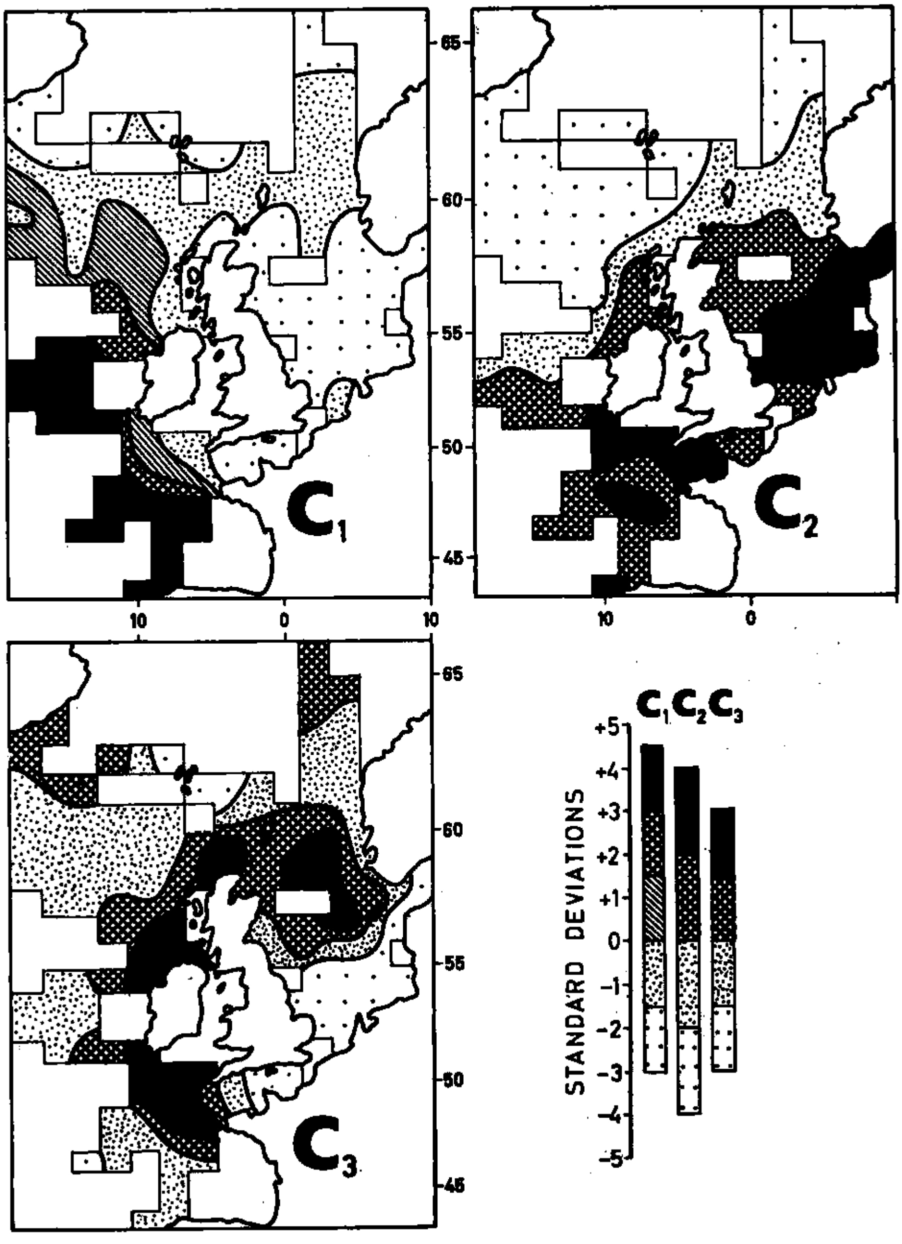


Fig. 2. Charts showing the distributions of the first three components (C_1, C_2 and C_3 of the geographical distributions of 22 zooplankton species. A key is given.

to the residual distributions after the removal of the variance associated with the first component, and so on. The details of the procedure are described by Kendall (1957). The components are row vectors with terms corresponding to the rectangles and the values may, therefore be plotted on charts and the distributions of the first three components are shown in Fig. 2. The sign of each component is arbitrary. The positive and negative forms of the first and second components and the positive form of the third component show sensible distributions which are easily related to those of individual species (Robinson, 1961; Colebrook *et al.* 1961; Vane, 1961).

The sum of the variances of these three components amounted to 65% of the total variance of the 22 species in the standardized data matrix. In the analysis of variance given in Table 2, the sources areas plus species-areas accounted for 30% of the total variability (excluding species) and had 352 degrees of freedom. The three components retain 65% of the 30% and have only 48 degrees of freedom. Clearly a considerable simplification in the representation of the variability has been achieved; the loss of information is, however, fairly high.

4. The Variability due to Months and Species-Months.

The mean seasonal variations in abundance of 18 species for the whole of the area shown in Fig. 1*b* were calculated by averaging by years and by standard large areas, thus eliminating the variability of those sources including years and areas. These seasonal variations were standardized (with zero mean and unit variance) eliminating the variability due to species. The resulting variables showed only the variability due to months and species-months, *i.e.* the pattern of variation of seasonal cycles of abundance of the different species.

The results of a correlation analysis of these variables are shown in Fig. 3*a* as a triangular matrix. The species are ranked along the principal diagonal of the matrix in such a way that as many as possible of the high positive correlations appear in the matrix as close as possible to the principal diagonal. This implies that species showing similar seasonal variations in abundance occur close together in the rank while species showing different variations occur further apart. The species in the matrix can be allocated to three overlapping groups each showing relatively high correlations within the group and lower values with the other groups. The means of the standardized seasonal variations of the species in each group were calculated and the resulting variables restandardized. They are shown in Fig. 3*b*; they account for about 86% of the total months and species-months variability. In the analysis of variance shown in Table 2 the sources months plus species-months accounted for 46.2% of the total variability and had 242 degrees of freedom. The seasonal variations shown in Fig. 3*b* retain 86% of the 46.2% and have only 33 degrees of freedom. Again a considerable simplification in the representation has been achieved and in this analysis the loss of variability is small.

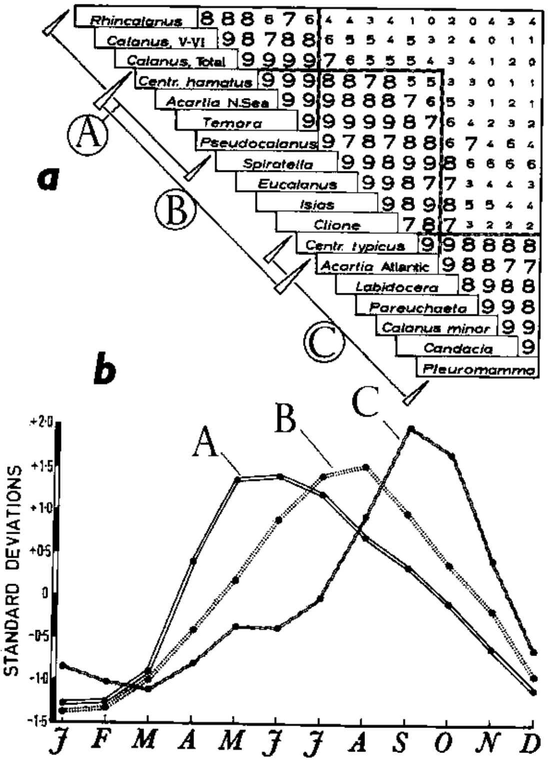


Fig. 3. (*a*) The correlation matrix of the mean seasonal cycles of 18 zooplankton species.
(*b*) Graphs of the standardised mean seasonal cycles of each of the groups of species shown in the matrix in *a*.

5. The Variability due to Months-Areas and Species-Months-Areas.

The variability included in these sources may be expressed as the geographical variation of the seasonal cycles of the different species. One of the main problems in finding methods of representing this variability is that many species do not occur throughout the area: in the analysis, the seasonal variations of 17 species in 17 standard areas (Fig. 1*b*) was included, but, because of the restricted distributions of many species, only 162 estimates of seasonal variation were available out of a possible total of 289. Because of this the more refined methods such as principal components analysis and correlation analysis could not be used, at least in the initial stages, and a relatively crude parametric representation of the variability was used and the loss of variability in the final representation cannot be estimated. Three parameters were used to represent the seasonal variations; mean abundance, timing (calculated by $T = \Sigma x_j \, j / \Sigma x_j$, where j is the number of the month, with January = 1, February = 2, etc., and x_j is the abundance in month j) and season duration (calculated by $L = \surd[\Sigma x_j \, (j - T)^2 / \Sigma x_j]$): two examples of the relationships between the parameters and seasonal variations are given in Fig. 4. Trials

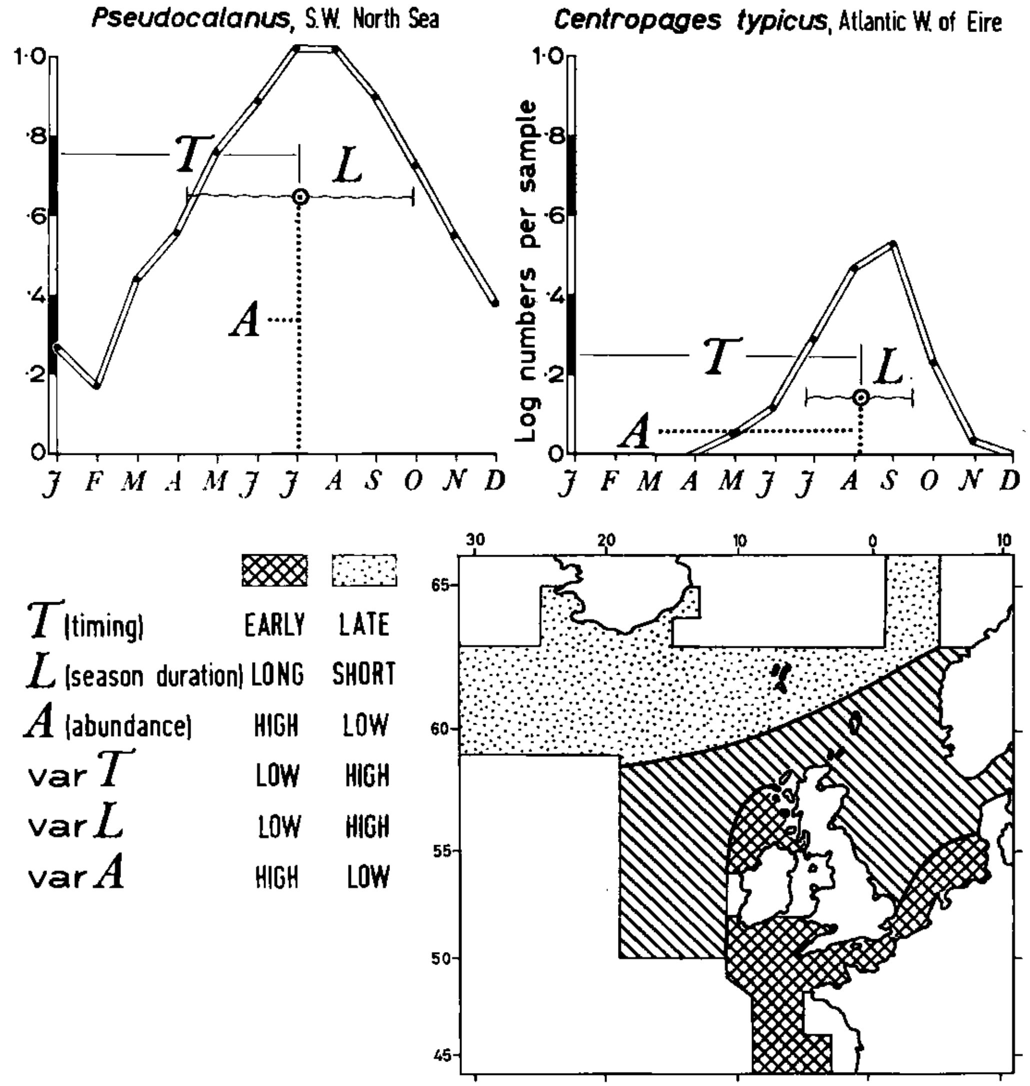


Fig. 4. The graphs show two examples of the values of the parameters *A*, *T* and *L* in relation to seasonal variations in abundance. The chart shows the distribution of the first component of the parameters and a key to the direction of variation of the parameters is given.

indicated that integration by species could be achieved by taking the mean and variance of these parameters. This was done for two groups of species. The first group contained only the common species for which nearly complete data were available; the few missing values were interpolated. The second group contained all the species included in the analysis and a system of weighting was devised to compensate to some extent for the missing values. At this stage a correlation analysis was carried out which showed that the two sets of estimates agreed quite well and that further integration of the parameters was possible. The first principal component of both sets of means and variances of the parameters was calculated and is shown in the chart in Fig. 4, together with a table indicating the direction of variation of the variables.

This chart is a representation of the variability in months-areas and species-months-areas, *i.e.* the geographical variation of the seasonal cycles of the different species; it has 16 degrees of freedom compared with a total of 1,451 in the original classification. The loss of variability is not known but is probably rather high.

6. The Variability due to Years and Species-Years.

In studying relationships with hydrography and fisheries, the annual variations in the plankton are, perhaps, the most interesting; they are, at the same time, the most difficult to interpret. For this reason only a preliminary study of the sources years and species-years has been carried out so far; the object being to assess the extent to which the fluctuations form coherent patterns.

Two series of correlation analyses have been carried out on data for the years 1948-1960, first on the annual fluctuations of the species in each of eight standard areas (Fig. 6) to find out whether there are any relationships between the annual fluctuation in abundance of different species, *i.e.* between-species within-area relationships; and second, on the annual fluctuations of each of 19 species in the different areas to find out whether some or all of the species showed geographical patterns of varying abundance, *i.e.* within-species between-area relationships. The correlation matrix for area *D5* is given in Fig. 5. This shows that there were clear relationships between the annual fluctuations of many of the species. In addition, there were marked similarities between the ranks of the species in the matrices for six out of the eight areas: the mean ranks of the species in the matrices were calculated and the results are given in Fig. 6*a*. This shows three clear groups of species. The order of the zooplankton species is very similar to the order in the correlation matrix of seasonal fluctuations (Fig. 3*a*) suggesting that species which occur at the same time of year tend to show similar annual fluctuations in abundance.

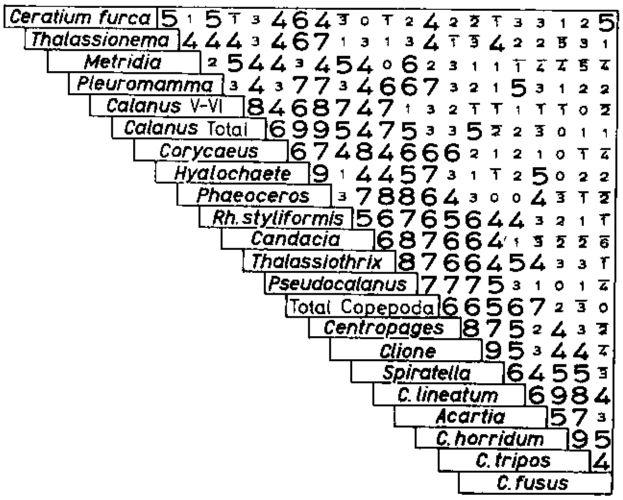


Fig. 5. The correlation matrix of the annual variations in abundance of 22 species or species groups in area *D5* (see Fig. 6).

Fig. 6*b* shows two within-species between-area matrices which have been selected to illustrate different patterns of fluctuation. The matrix for *Calanus finmarchicus*, stages V and VI, shows two groups of areas showing similar fluctuations of abundance within the groups but with differences between the groups (a more detailed analysis of the geographical fluctuations of *Calanus* has been carried out by Colebrook, 1963). The matrix for *Ceratium horridum* shows high positive correlations between all the areas. The implication is that this species fluctuates in abundance from year to year in a similar manner over the entire area: several other species show the same result. This is clearly of great interest considering the wide range of environmental conditions found in the area, varying from oceanic conditions over water more than 2,000 m deep in the Atlantic to fairly extreme neritic conditions in the southern North Sea.

7. The Variability due to Areas-Years and Species-Areas-Years.

The variability included in these sources represents annual fluctuations in the geographical distributions of species, and the obvious first stage in the analysis would be to carry out a principal component analysis based on estimates of the distribution of species in the individual years. However, because of year to year variations in the pattern of sampling and of gaps in the information about a number of species, it would be very difficult to obtain a truly comparable series for analysis

One of the stages in the principal component analysis of areas and species areas gives a series of variables, known as vectors, with terms referring to species. One variable is associated with

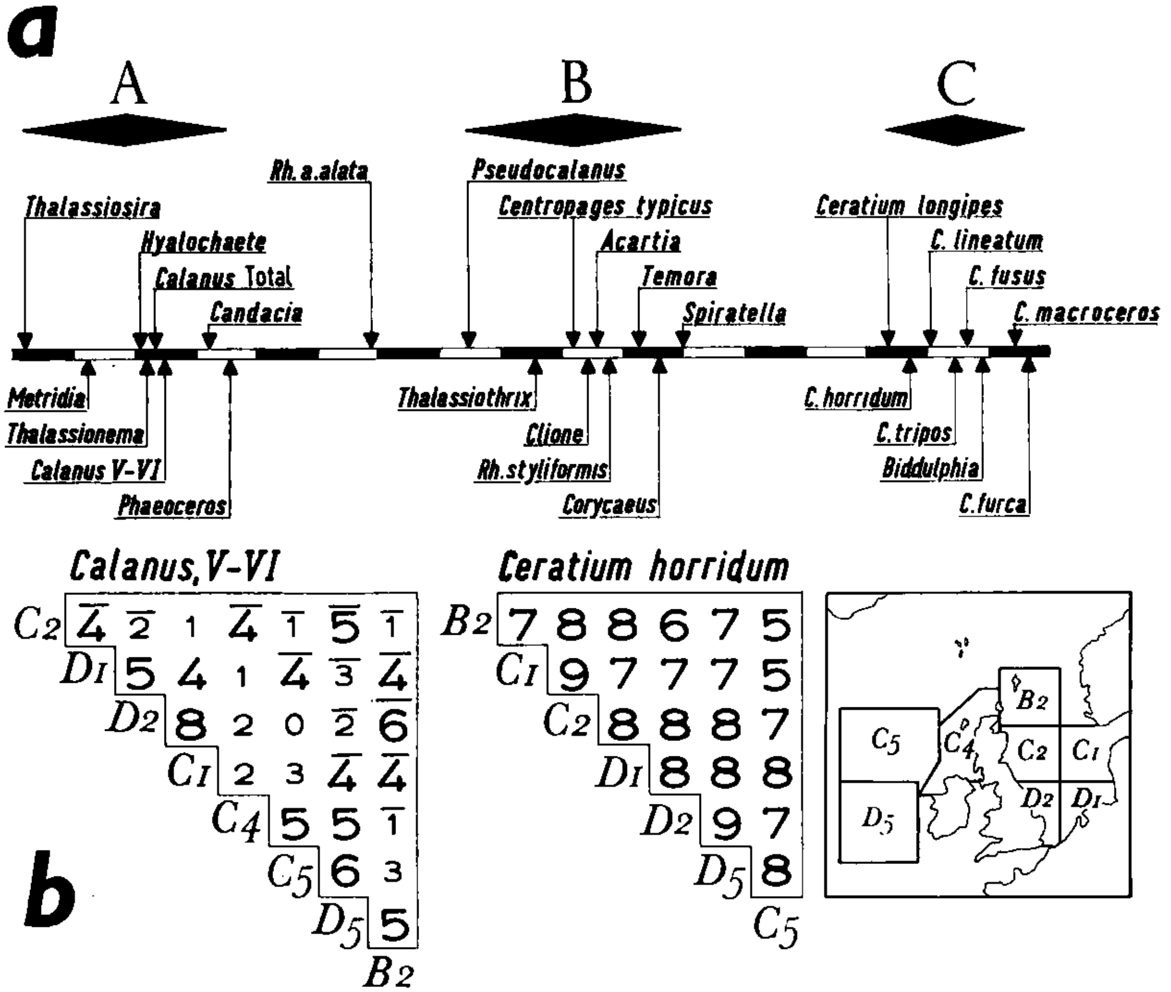


Fig. 6. (*a*) The mean ranks of the species in the correlation matrices of the annual fluctuations in abundance in each of the areas in the chart in *b*. The rank shows three clear groups of species indicated by the letters, A, B and C.

(*b*) Correlation matrices for the annual fluctuations in abundance of *Ceratium horridum* and *Calanus finmarchicus*, stages V-VI in the standard areas shown in the charts.

each component and is used in the derivation of the component. The vectors describe patterns of relationship between the species which are probably determined by variations between species in the response to environmental factors and there is no reason why these patterns should fluctuate from year to year to any great extent. And as a first approximation, these vectors, which were derived from the long-term mean distributions of the species, can be applied to the distributions of species in individual years to provide estimates of the components in individual years. This was done for the three components shown in Fig. 2 based on annual means for each species in the standard large areas (Fig. 1*b*).

The next problem is to find methods of extracting any systematic variation in the annual estimates of the components, and, as a first step the annual fluctuations of the variance of each component were calculated; they are shown in Fig. 7. Two features are immediately obvious. First, there is for each component a trend of increasing variance over the period from 1948 to 1962. A straight line was fitted to each variable using orthogonal polynomials and in each case the fit was significant, at the 1% level for C_1 and C_2 and at the 5% level for C_3.

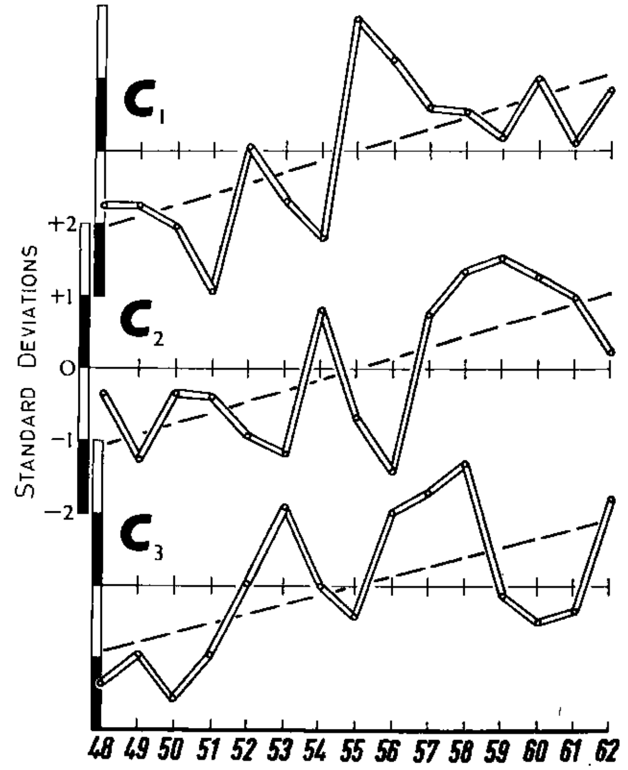


Fig. 7. Graphs showing the standardized annual fluctuations in the variance of annual estimates of the three components of geographical distribution shown in Fig. 2.

The second obvious feature was the relationship between the variance of C_3 in year n and C_2 in year $n + 1$. The correlation between the two variables in this manner was calculated and it was significant at the 1% level. To judge from these relationships the variables represent meaningful fluctuations in the geographical distribution of the plankton and they are in a form that can easily be compared with other estimates of annual variations.

APPLICATIONS OF THE ANALYSES

The analysis of the Continuous Plankton Recorder survey is just beginning to reach the stage where it is profitable to carry out extensive studies of relationships with hydrography or with fisheries; the examination of annual variation, however, is far from complete. It is probably desirable to complete these analyses because it seems likely that internal evidence from relationships between the different variables will be of assistance in reducing the inevitable trial and error element in the search for related environmental factors. A certain amount of work has been done, however, on the distribution components shown in Fig. 2 and Williamson (1961 and in press) using techniques similar to those described here, has studied relationships between the plankton of the north-western North Sea and the hydrography and herring fishery in the same area.

Williamson derived a series of six components describing the annual fluctuations in abundance of 23 species or species groups in the plankton. The first component was correlated with an estimate of the annual fluctuations in the vertical mixing of the water in the spring. The second component was not related to any of the hydrographic or herring parameters that were tested. The third component was correlated with the mean temperature anomaly for March, April and May. The fourth component was correlated with a rank estimate of the strength of inflow of water from the Atlantic into the North Sea and also with a measure of the northerliness of southerliness of the herring stock. The fifth plankton component was correlated with the apparent mortality of the herring and the sixty component was not related to any of the hydrographic or herring parameters.

It must be stressed that these comparisons represent a very incomplete analysis of the situation; the information that was available about the hydrography, the herring fishery and the plankton did not permit a complete study of the variability. However, one feature in relation to the fishery is capable of a reasonable interpretation. In the vector associated with Williamson's fourth component of the plankton the two most abundant species, *Calanus finmarchicus* and *Spiratella retroversa*, both showed large values with the same sign. The correlation with the position of the herring stock was such that when these two species were common the stock was more southerly, when they were scarce the stock moved northwards. Further, the abundance of these zooplankton species may be related to the strength of inflow of Atlantic and coastal water into the northern North Sea.

Colebrook (in preparation) has described some possible relationships between hydrography and the components of plankton distributions shown in Fig. 2. Data for surface salinity and temperature were studied and Fig. 8*a* shows a matrix of correlations between the components and a number of temperature and salinity functions. The first component was correlated with the distribution of salinity ($\hat{S}$) and the distribution of temperature in the winter months (T_w). The second component was correlated with the distribution of temperature during the summer months (T_s) and also with the

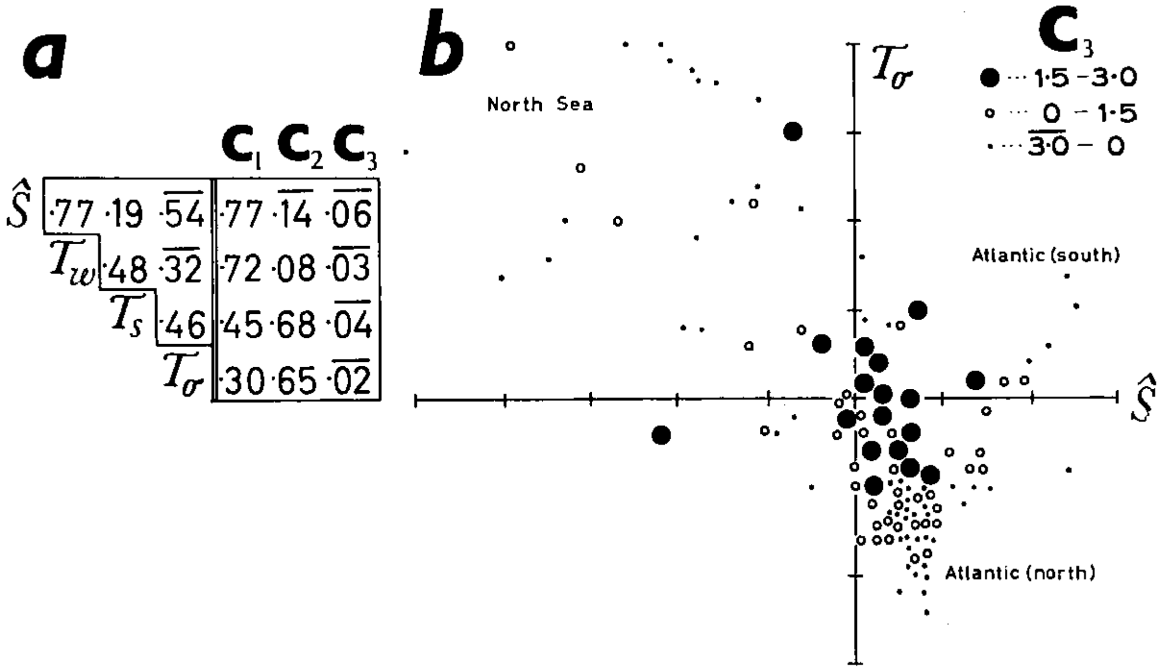


Fig. 8 (*a*) The matrix of correlations between the first three components of geographical distribution, C_1 C_2 and C_3 (see Fig. 2) and the distributions of surface salinity ($\hat{S}$), winter temperature (T_w), summer temperature (T_s) and the standard deviation of the seasonal variations of temperature (T_o).

(*b*) A scatter diagram of salinity ($\hat{S}$) against the standard deviation of temperature (T_o). At each point the value of C_3 (Fig. 2) is shown by a symbol. A key to the symbols is given.

range of temperature (T_σ). The third component was not directly related to any of the temperature and salinity functions but Fig. 8*b* shows a form of T.S. diagram with the values of the third component superimposed; the high positive values of the component tend to fall in the centre of the plot. It seems likely that the first component was related to salinity, the second component to a complex function of temperature involving vertical stability and summer temperature and the third component might be related to the distribution of mixed oceanic and coastal water.

CONCLUDING REMARKS

It is obvious that the methods of analysis that have been described can result in considerable simplification in the representation of the variability of the standing stock of the plankton. Moreover, it seems that in some cases more has been achieved than the derivation of convenient mathematical artefacts. The three distribution components shown in Fig. 2 would appear to have identifiable separate existences and to be genuine "components" related to specific environmental factors. In other cases the final variables may be no more than convenient representations with no identifiable reality; probable examples are the three seasonal variations shown in Fig. 3*b*; there is little doubt, however, that these variables will be useful in investigating the factors which determine the variations in the timing of plankton organisms.

Plankton, hydrography and the pelagic stages of fish can be considered as subdivisions of a single ecosystem. It is obviously necessary to study this system as a whole in order to determine the interactions within the organisms and between the organisms and the abiotic environment. The methods of analysis that I have described in relation to the plankton could also be applied to hydrographical and fisheries data and they offer at least a partial solution to the problems of analysing the complex patterns of variation within the system and of studying the interactions and relationships between its various parts.

REFERENCES

COLEBROOK, J.M. 1960. Continuous Plankton Records: methods of analysis, *Bull. Mar. Ecol.*, 5: 51-64.

1963. Continuous Plankton Records: annual variations in the abundance of *Calanus finmarchicus*, 1948-1959. *Bull. Mar. Ecol.*, 6: 17-30.

COLEBROOK, J.M., D.E. JOHN, and W.W. BROWN, 1961. Continuous Plankton Records, 1948-1956: contributions towards a plankton atlas of the north-eastern Atlantic and the North Sea. Part II: Copepoda. *Bull. Mar. Ecol.*, 5: 90-97.

COLEBROOK, J.M. and G.A. ROBINSON, 1963. Ecological differentiation in the plankton of the waters around the British Isles. *Systematics Assoc. Publ.*, No. 5: 157-169.

GLOVER, R.S. 1957. An ecological survey of the drift-net herring fishery off the north-east coast of Scotland. Part II: the planktonic environment of the herring. *Bull. Mar. Ecol.*, 5: 1-43.

1961. Biogeographical boundaries: the shapes of distributions. *Int. Oceanogr. Congr.*, 1959: 201-208.

1962. The Continuous Plankton Recorder. *Rapp. Cons. Explor. Mer*, 153: 8-15.

GLOVER, R.S., G.A. COOPER, and D.C.T. FORSYTH, 1961. An ecological survey of a Scottish herring fishery. Part III: geographical and ecological groups in the plankton. *Bull. Mar. Ecol.*, 5: 195-205.

HARDY, A.C. 1939. Ecological investigations with the continuous plankton recorder: object, plan and methods. *Hull. Bull. Mar. Ecol.*, 1: 1-57.

KENDALL, M.G. 1957. A course in multivariate analysis. London. Charles Griffin & Co. Ltd. 185 p.

RAE, K.M. 1952. Continuous Plankton Records: explanation and methods, 1946-1948. *Hull. Bull. Mar. Ecol.*, 3: 135-155.

ROBINSON, G.A. 1961. Continuous Plankton Records, 1948-1956: contributions towards a plankton atlas of the north-eastern Atlantic and the North Sea. Part I: phytoplankton. *Bull. Mar. Ecol.*, 5: 81-89.

VANE, F.R. 1961. Continuous Plankton Records, 1948-1956: contributions towards a plankton atlas of the north-eastern Atlantic and the North Sea. Part III Gastropoda. *Bull. Mar. Ecol.*, 5: 98-101.

WILLIAMSON, M.H., 1961. An ecological survey of a Scottish herring fishery. Part IV: changes in the plankton during the period 1949-1959. *Bull. Mar. Ecol.*, 5: 207-229.

In press. The relation of plankton to some parameters of the herring population of the north-western North Sea. *Rapp. Cons. Explor. Mer*.

B-3

A PRELIMINARY STUDY OF *SEBASTES* LARVAE IN RELATION TO THE PLANKTONIC ENVIRONMENT OF THE IRMINGER SEA

By

V. Bainbridge[1]

ABSTRACT

The diet of young *Sebastes* from the Irminger Sea was investigated using material collected during the Continuous Plankton Recorder Survey. Individuals smaller than 10 mm were found to be feeding principally on *Calanus* eggs, *Spiratella* larvae being virtually the only other organisms eaten. *Calanus finmarchicus* is the dominant copepod in the Irminger Sea where it constitutes over 70% of the total numbers of zooplankton organisms present in Recorder samples. The extrusion of *Sebastes* larvae occurs during April and May which coincides with the main spawning period of *Calanus*. During May, when maximum numbers of both young *Sebastes* and spawning *Calanus* occur, a positive correlation exists between the spatial distribution of the numbers of fish larvae and the numbers of *Calanus* stages V and VI.

This might be accounted for if the survival of young *Sebastes* was largely dependent on the availability of food, *i.e.* the numbers of *Calanus* eggs, but direct evidence is lacking and other factors may be involved.

INTRODUCTION

The distribution of young *Sebastes* in relation to the planktonic environment was discussed by several contributors to the ICES/ICNAF Redfish Symposium of 1959[2]. Dietrich, *et al* (1961) described the results of a series of cruises in the Irminger Sea during 1955 and 1958. Highest numbers of *Sebastes* larvae were found in the area of the Reykjanes Ridge, a distribution which appeared to be associated with high turbidity, due mainly to zooplankton and detritus. A correlation with high numbers of the trachymedusan *Aglantha digitalis* during May and June was also noted. Hansen and Anderson (1961) investigated the distribution of *Sebastes* larvae from 1947 to 1958 at 21 standard plankton stations on a transect worked regularly along 62°N lat from the Faroes to East Greenland. They suggested that the considerable annual fluctuations in numbers of larvae present might be related to the food available at the time of extrusion. Einarsson (1960) considered relationships between *Sebastes* fry and zooplankton in Icelandic waters and adjacent seas. He made some preliminary observations on the food of the young fish at two stations and noted a preference for food organisms of about 150µ in diameter. *Spiratella* larvae, together with copepod and other crustacean eggs, were found to be the main items in the dietary of specimens less than 25 mm in length. Larger food organisms, such as the copepodite stages of copepods, were found in the stomachs of young *Sebastes* greater than 25 mm in length.

An attempt is now being made to extend these environmental studies using material from the Continuous Plankton Recorder Survey and a preliminary report is presented in this contribution. The work includes some observations on the food of young *Sebastes* in relation to the planktonic environment which may help towards an interpretation of their distribution and fluctuations in abundance. Charts illustrating the distributions of these larvae are given by Henderson (this symposium) who also discusses the problem of their specific identity.

Recent accounts of the Plankton Recorder and of the scope and methods of the survey operated from the Oceanographic Laboratory, Edinburgh, are given by Colebrook, *et al* (1961) and Glover (1962). The Recorder, which is towed by merchant ships and Ocean Weather Ships, takes a continuous sample of plankton at a depth of 10 m. The plankton is collected on silk with a mesh-aperature of 230–250µ.

THE DIET OF YOUNG *SEBASTES*

A detailed study has been made of the food of young *Sebastes* from the Irminger Sea during May, the month in which largest numbers were usually taken by the Recorder. Alternate "10 mile" samples collected during May of the years 1959 to 1962 within the standard sub-areas B6, B7 and C7 shown on Fig. 1 have been examined and an analysis made of the gut contents of all undamaged larvae. A total of 193 *Sebastes* ranging in length from 6 to 10 mm were dissected and the results are given in Table 1.

---

[1] Oceanographic Laboratory, Edinburgh

[2] Spec. Publ. int. Comm. Northw. Atlant. Fish., No. 3, 1961.

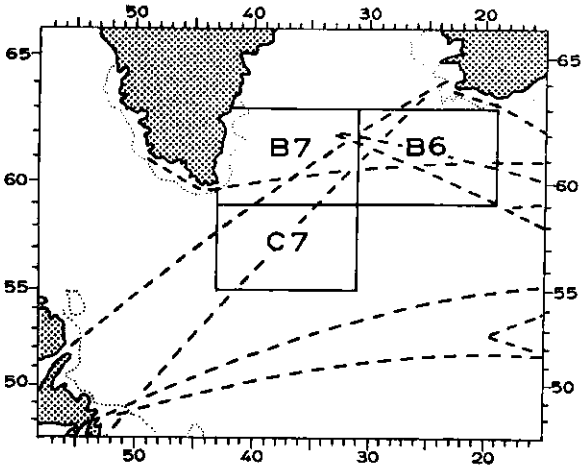


Fig. 1. Area used for the study of *Sebastes-Calanus* relationships. It comprises 3 of the standard sub-areas (B6, B7 and C7) of the Plankton Recorder survey (Glover, 1962). Recorder routes are shown as broken lines.

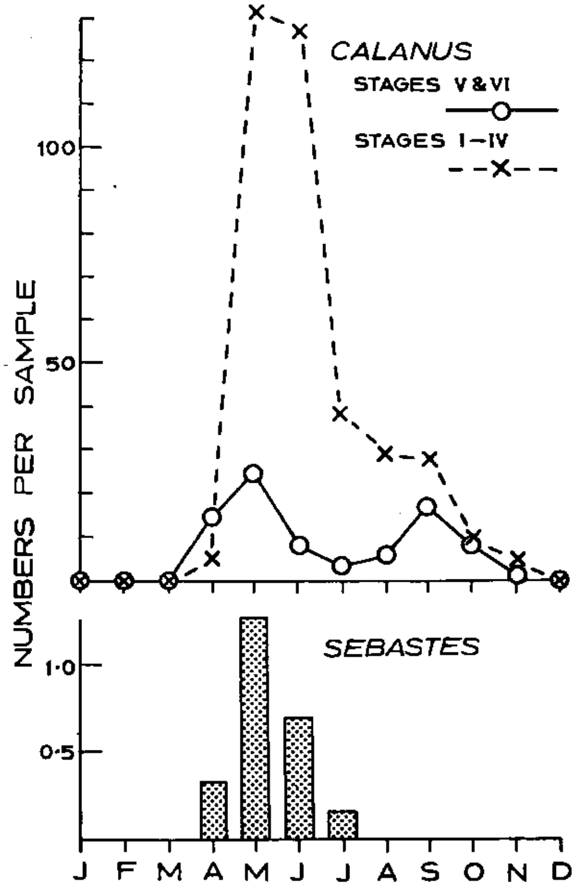
The young fish were feeding on *Calanus* eggs (140-160μ diameter) and *Spiratella* larvae (shells 100-150μ across), the only other organisms present being two specimens of the diatom *Coscinodiscus* sp. (100μ diameter). Numbers of *Calanus* eggs in the guts showed a marked diurnal variation; during the period between midday and sunset there was an average of 8.3 eggs per gut compared with an average of 1.6 between midnight and sunrise. The eggs were at various stages of digestion and numerous egg membranes were also present. This extremely restricted diet should be considered in relation to the composition of the zooplankton in the Irminger Sea. Table 2 gives the average numbers per "10 mile" sample (equivalent to $3m^3$ of water filtered) of the various species and groups within the sub-areas B6, B7 and C7 during May. There was an overwhelming predominance of the various stages of *Calanus finmarchicus* while the small copepods and Cladocera, which are important members of the plankton of coastal waters as well as many oceanic areas covered by the Recorder survey, were very poorly represented. Apart from

TABLE 1. THE GUT CONTENTS OF YOUNG *SEBASTES* LESS THAN 10 MM IN LENGTH FROM RECORDER SAMPLES TAKEN DURING THE MONTH OF MAY.

	1959	1960	1961	1962	May of all four years
Percentage containing food	73%	-	68%	75%	72%
Number of larvae examined	45	2	65	83	195
Total *Calanus* eggs	136	4	384	510	1034
Total *Spiratella* larvae	2	5	130	218	355
Other organisms (*Coscinodiscus* sp.)	-	-	1	1	2

TABLE 2. THE COMPOSITION OF THE PLANKTON TO A DEPTH OF 10m DURING MAY: MEAN NUMBERS PER "10 MILE" SAMPLE (EQUIVALENT TO $3m^3$ OF WATER FILTERED) WITHIN THE SUB-AREAS B6, B7 AND C7.

	1959	1960	1961	1962	May of all four years
Total *Calanus* (all stages)	101	65	127	325	154
Calanus stages V and VI	22	7	43	47	30
Copepoda other than *Calanus*	28	20	4	28	20
Spiratella (mainly *S. retroversa*)	15	10	8	21	13
Euphausiids (mainly *Thysanoessa longicaudata*)	2	1	5	10	4
Larvacea	2	10	7	1	5
Other zooplankton	1	<1	<1	<1	<1
No. of samples	68	38	90	83	279



ig. 2. Seasonal fluctuations in the numbers of *Calanus* and young *Sebastes* at a depth of 10 m in the Irminger Sea. Average numbers per sample have been calculated using all data collected from 1957 to 1962 within the three standard sub-areas shown in Fig. 1.

Calanus, the commonest copepods were *Oithona* spp. and *Euchaeta Norvegica*, two genera in which the eggs are carried in ovisacs. Of the other groups, only the gastropods *Spiratella* spp. and the euphausiid *Thysanoessa longicaudata* were present in appreciable numbers. It has not been possible to trace a reference to the egg size of *T. longicaudata* but both *T. inermis* and *T. raschii*, two species in which the early furcilias are of similar size to *T. longicaudata*, are known to have egg diameters exceeding 400μ (Einarsson, 1945), much larger than the selected particle size suggested by Einarsson (1960).

The monotonous diet of *Sebastes* larvae during the early weeks after extrusion must therefore be at least partly due to the limited choice of food organisms available, the early stages of *Calanus* and *Spiratella* being the only abundant organisms to fall within a suitable size range.

The apparent absence of nauplii in the diet is noteworthy but I have found some in the gut contents of early *Sebastes* larvae from stramin net samples taken off the east coast of Greenland during the Danish NORWESTLANT cruises. *Calanus* nauplii are present mainly in the top 50 m (Marshall and Orr, 1955), and were, in fact, frequently present in Recorder samples from the Irminger Sea during May, but like the eggs, they are too small to be samples quantitatively by silk with a mesh-aperture of 230-250μ. It is possible therefore that, in addition to size, other factors such as mobility may also play a part in determining the relative vulnerability of prey. It may be relevant that the *Spiratella* larvae present in the gut contents were veligers with cilia as the only organs of locomotion. *S. retroversa*, the common species in the Irminger Sea, does not develop swimming 'wings' until the shell measures about 300μ across (Lebour, 1932).

Although this paper is concerned primarily with *Sebastes* larvae during the first weeks after xtrusion it should be mentioned here that larvae of 15 mm or more in length which occur in the ecorder samples during June and July have a more varied diet including the calyptopsis and furcilia tages of euphausiids as well as the copepodites and adults of *Calanus*.

THE SEASONAL DISTRIBUTION OF YOUNG *SEBASTES* AND *CALANUS*.

Calanus eggs are clearly the principal food item of redfish larvae during the first weeks after xtrusion so it is interesting to consider the seasonal distribution of the young fish in relation o the breeding of *Calanus*. Figure 2 shows the average monthly distributions of *Calanus* and young *ebastes* in the Irminger Sea estimated from data collected over the period 1958 to 1962. *Calanus* tages V and VI, which were virtually absent at the 10 m level during the winter months, showed a ig increase from March to April reaching a maximum in May, while highest numbers of copepodite tages I-IV were found during May and June.

These observations may be interpreted by a consideration of the findings of Østvedt (1955) who tudied the vertical distribution of *Calanus finmarchicus* at Weather Ship M in the Norwegian Sea. e found that the overwintering stock of *Calanus* consisted chiefly of stages IV and V with the maority of the population below a depth of 600 m and that an ascent to the surface occurred during

April to May. Moulting from stage V to stage VI occurred both during or after the migration and was immediately followed by the spring spawning. Henderson (1961) found that newly extruded *Sebastes* were present in Recorder samples from early April to the end of May. From Fig. 2 it can be deduced that it is during these two months that highest numbers of spawning *Calanus* are present in the surface layers. During May both maximum numbers of *Calanus* V and VI and young *Sebastes* were present.

THE SPATIAL DISTRIBUTION OF YOUNG *SEBASTES* AND *CALANUS*

During the analysis of Recorder samples it was noted that during May samples with high numbers of young *Sebastes* were frequently those with high numbers of *Calanus* stages V and VI. In Table 3, the samples have been divided into two groups, those with more and those with less than 50 *Calanus* stages V and VI. The higher average numbers of redfish larvae were found in samples with more than 50 *Calanus* V and VI in every year except 1958 when, as in 1960, only a few samples contained young *Sebastes*. The young fish were too scarce to allow a similar comparison for April while, during June, distributions are likely to be confused by the effects of dispersal.

TABLE 3. AVERAGE NUMBERS OF YOUNG *SEBASTES* PER POSITIVE RECORDER SAMPLE IN MAY, GROUPED ACCORDING TO WHETHER THERE WERE MANY OR FEW *CALANUS* STAGES V AND VI IN THE SAMPLES. THE NUMBERS OF SAMPLES ARE GIVEN IN PARENTHESES.

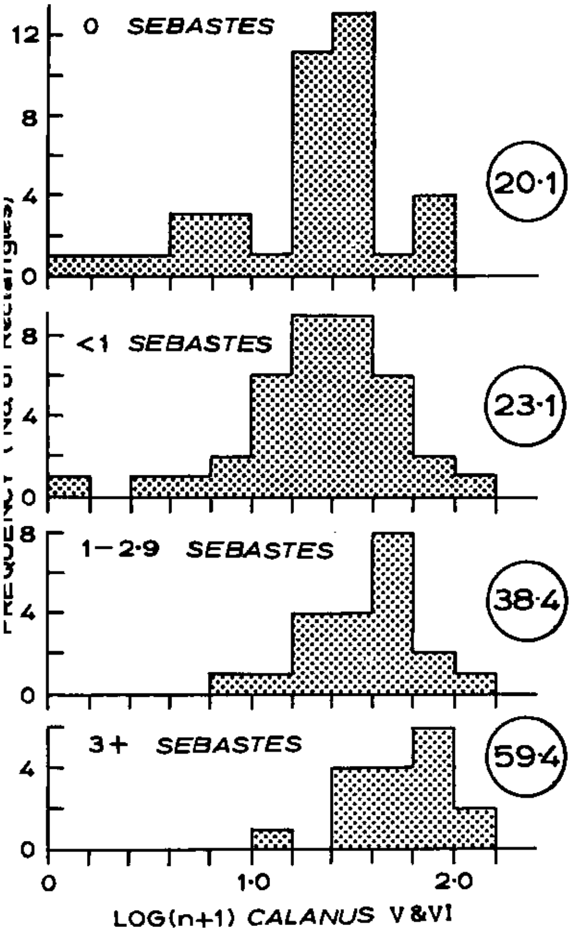
Year	Samples with 50 *Calanus* V & VI		Samples with 50 *Calanus* V & VI	
1957	2.3	(13)	1.9	(17)
1958	1.5	(2)	1.5	(2)
1959	4.7	(8)	2.3	(17)
1960	3.0	(1)	1.0	(2)
1961	5.4	(25)	3.1	(28)
1962	4.9	(17)	3.7	(27)
All years combined	4.5	(64)	2.9	(85)

The two variables can also be compared in each of the standard statistical rectangles used to present the results of the Recorder survey (*e.g.* Colebrook, *et al.*, 1961). These are the small rectangles, 1° lat 2° long, illustrated by Henderson (this symposium). Figure 3 shows the frequency of occurrence of sampled rectangles in relation to the logarithm of the mean number of *Calanus* stages V and VI per sample. The histograms are arranged in four groups according to the mean number of young *Sebastes* per sample (0,<1, 1-2.9,3+). All the rectangles sampled each May from 1957 to 1962 over the area of the Irminger Sea (*i.e.* sub-areas B6, B7 and C7) have been included. The frequency distributions show that there was a clear tendency, during the month of May over the six years, for high numbers of *Sebastes* young to be associated with high numbers of *Calanus* V and VI. An analysis of variance has shown that there is a significant difference between the groups of rectangles with 0 and <1 young *Sebastes* and the group with 3+ *Sebastes* ($P < 0.001$). The difference between the groups with 0 and <1 and the group with 1-2.9 young *Sebastes* is significant at a lower level ($P < 0.05$). The analysis of variance does not take into account the possible effects of interaction between adjacent rectangles.

The correlation raises a number of questions since the combination of data from several years conceals the effects of annual and spatial fluctuations. However, the relationship is not merely due to highest numbers of *Sebastes* larvae being extruded in exactly the same area of the Irminger Sea each year which happens also to be an area of high *Calanus* production. If, for example, the six year mean number per sample of *Sebastes* larvae and *Calanus* V and VI during May in each rectangle is calculated, no correlation between the two variables is evident.

Diurnal variations are difficult to assess but would appear to have little, if any, effect on the relationship. During May less than one-third of all samples are taken at night in this sea area and the day/night ratio of the average numbers of *Calanus* V and VI per sample was only 1:1.3.

There would seem to be two possible explanations of the apparent positive relationship between young *Sebastes* and *Calanus*. The main concentrations of adult 'spawning' redfish in the Irminger Sea



ig. 3. Histograms showing the frequency of occurrence of sampled rectangles during May in relation to the logarithm (n+1) of the mean number of *Calanus* stages V and VI per sample. The data are grouped according to the mean number of young *Sebastes* per sample. All rectangles sampled each May from 1957 to 1962 within the three standard subareas of Fig. 1 have been included. The mean numbers of *Calanus* per sample for the four groups of histograms are shown in circles.

may be directly or indirectly related to the standing stock of *Calanus* V and VI during May. Alternatively, the survival of young might be related to the numbers of *Calanus* stages V and VI present and, since the food of *Sebastes* during the first weeks after extrusion consists mainly of *Calanus* eggs, this latter hypothesis merits further investigation.

CONCLUDING REMARKS

Sebastes constitutes about 90% of the total stock of young fish in the Irminger Sea (Einarsson, 1960, Henderson, 1961) and 'spawning' may take place in almost the entire region although the intensity of extrusion is variable (Magnusson, 1962). The monotonous nature of the surface zooplankton in this vast sea area, with the great numerical predominance of *Calanus*, and the remarkable uniformity of the diet of *Sebastes* young, mainly *Calanus* eggs, have been established. It is possible therefore, as Einarsson (1960) has suggested, that the ecological relationships between young *Sebastes* and the other plankton organisms may be more easily elucidated than the undoubtedly complex relationships between the fish larvae and plankton of coastal waters.

Further work is in progress and it is hoped to determine whether or not annual variations in the numbers of young *Sebastes* are related to the timing and intensity of the spring spawning of *Calanus*.

ACKNOWLEDGEMENTS

I wish to thank Dr G.T.D. Henderson for allowing me to use his data on the distribution of young *Sebastes*. This work was assisted by a grant from H.M. Treasury through the Development Fund and by Contract N62558-2834 between the Office of Naval Research, Department of the United States Navy, and the Scottish Marine Biological Association.

REFERENCES

COLEBROOK, J.M., R.S. GLOVER and G.A. ROBINSON. 1961. Continuous Plankton Records: Contributions towards a Plankton Atlas of the north-eastern Atlantic and the North Sea: General Introduction. *Bull. Mar. Ecol.*, 5 (42): 67-80.

DIETRICH, G., H. AURICH, and A. KOTTHAUS. 1961. On the relationships between distribution of redfish and redfish larvae and the hydrographical conditions in the Irminger Sea. *Rapp. Cons. Explor. Mer.*, 150: 124-139.

EINARSSON, H. 1945. Euphausiacea, 1. Northern Atlantic Species. *Dana Rep.*, (27): 1-191.

1960. The fry of *Sebastes* in Icelandic waters and adjacent seas. *Rit Fiskid.*, 2(7): 3-64.

GLOVER, R.S. 1962. The Continuous Plankton Recorder. *Rapp. Cons. Explor. Mer.*, 153: 8-15.

HANSEN, V.K. and K.P. ANDERSEN. 1961. Recent Danish investigations on the distribution of the larvae of *Sebastes marinus* in the North Atlantic. *Rapp. Cons. Explor. Mer.*, 150: 201-215.

HENDERSON, G.T.D. 1961. Continuous Plankton Records: The distribution of young *Sebastes marinus* (L). *Bull. Mar. Ecol.*, 5 (46): 173-193.

1964. Redfish larvae in the North Atlantic. *This symposium Contribution No. B-4.*

LEBOUR, M.V. 1932. *Limacina retroversa* in Plymouth Waters. *J. Mar. biol. Ass. U.K.*, 18: 123-130.

MAGNUSSON, J. 1962. Redfish larvae in the Irminger Sea in May 1961. ICES. C.M. 1962, (90): 1-5, illus.

MARSHALL, S.M. and A.P. ORR. 1955. Biology of a marine copepod. *Calanus finmarchicus* (Gunn.). Edinburgh. Oliver and Boyd Ltd. vii + 188p.

ØSTVEDT, O.J. 1955. Zooplankton investigations from Weather Ship M in the Norwegian Sea. *Hvalråd. Skr.*, (40): 1-93.

B-4

REDFISH LARVAE IN THE NORTH ATLANTIC

By

G.T.D. Henderson[1]

ABSTRACT

The distribution of young stages of *Sebastes* in the North Atlantic between Iceland and Newfoundland in the months of April and July is described and illustrated. The results suggest the possibility that the young stages may be found in four more or less separate localities. The younger appear to be more abundant in some restricted parts of the temperature range, at the surface and at 200 m, within which they have been found. The specific identity of these young stages is discussed in relation to the catches of adult *mentella-type* at Ocean Weather Station Alfa.

INTRODUCTION

During the course of the regular survey of the North Sea and North Atlantic with Continuous Plankton on the Recorders, the young stages of the redfish (*Sebastes*) were encountered during the months of April and July in certain areas of the North Atlantic. The preliminary account of their distribution has been given by Henderson (1961, *a, b*).

Although the sampling is limited to the single depth of 10 m and the individual samples are small (representing the plankton in only 3 m^3 for each 10 nautical miles of tow) the repetition of sampling at regular intervals makes it possible to study annual and seasonal changes in distribution and abundance over a very wide area.

The first account of the distributions of these young *Sebastes* (Henderson, 1961 *a, b*) was based on the material available up to 1960. Since then the scope of the Recorder survey has been widened by the extension of existing routes and the introduction of additional ones; our knowledge of the distribution, therefore, is now much more detailed than that shown in the earlier report, and the charts in Fig. 1 are provided for convenient reference. This work was assisted by a grant from H.M. Treasury through the Development Fund and by Contract N62558-2834 between the Office of Naval Research, United States Department of Navy and the Scottish Marine Biological Association.

DISTRIBUTION OF THE YOUNG STAGES

The results of the Recorder sampling are expressed as the mean numbers of *Sebastes*, per 10 m^3 sampled, in statistical rectangles measuring 1° of lat x 2° of long.

The average distributions of the young stages of *Sebastes* are shown in Fig. 1; each of the charts for the months April to July is based on the combination of all Recorder sampling, in those months, from 1955 to April 1963. Kotthaus (this symposium) discusses the distribution of young *Sebastes* in the Atlantic from April to June 1961, and suggests that there are three main areas of abundance. He defines these and believes that they were discernible in the charts shown in the earlier account of the Recorder work (Henderson, 1961 *b*, Fig. 3) but is not certain of the separation south of Iceland which might be due to the combination of data. Because the charts in Fig. 1 represent combined results from a number of years, and because of the limitations imposed by the geographical distribution of the available sampling, the Recorder data are not yet considered adequate to demonstrate these separations with certainty. For the purposes of this paper, however, it is convenient to divide the distributions into four groups (a,b,c and d) which are similar to those of Kotthaus, although it seems possible that one of his areas may be divisible into two, (a) over the Reykjanes Ridge and south of Iceland and (b) south to southeast of Greenland.

In April the young were found in small to moderate numbers (mean length 7.3 mm). They appeared

---

[1] Oceanographic Laboratory, Edinburgh, Scotland.

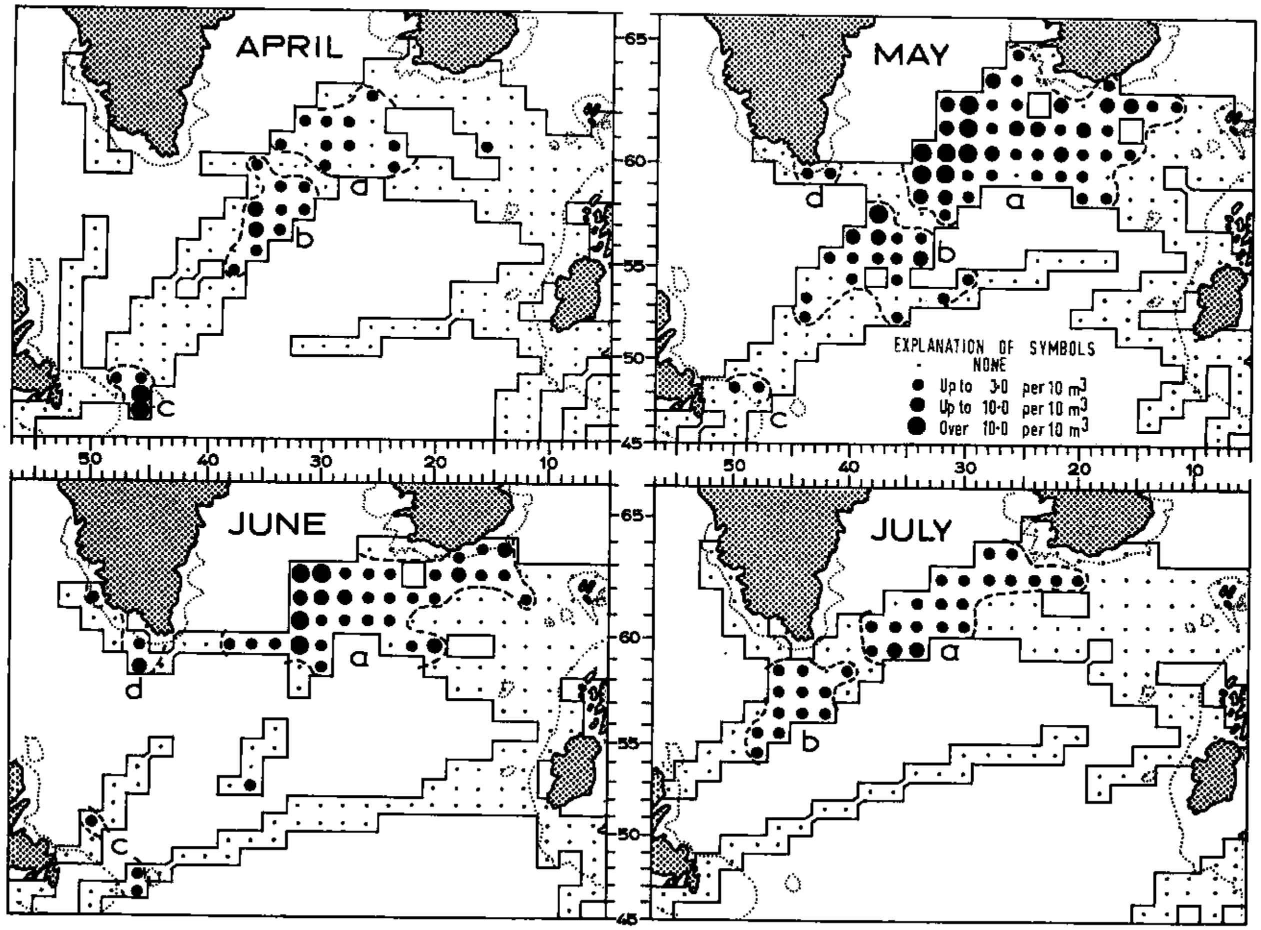


Fig. 1. Charts showing the average distribution of young stages of *Sebastes* (excluding *S. viviparus*) in the months April to July. The charts are composite ones, including all the information from 1955 to April 1963. The symbols indicate the mean numbers per 10 m^3 for all sampling in each statistical rectangle 1° of latitude by 2° of longitude. The broken lines and lower case letters a to d on the charts indicate the localities discussed in the text.

to be present in three more or less separated localities; (a) on both sides of the Reykjanes Ridge and south of Iceland, but mainly to the north of lat 59° N, with the larger numbers between 60° and 62° N lat; (b) in an area southeast of Cape Farewell (Greenland) over the mid-Atlantic Ridge between the lat of 54° and 59° N; and (c) between the northeast edge of the Newfoundland Banks and Flemish Cap. In May (mean length 8.1 mm) the pattern was generally similar but the distributions over the Reykjanes Ridge and southeast of Greenland (a and b above) have expanded in area and greatly in abundance while that near Flemish Cap (c) has diminished. There is a suggestion of a possible fourth concentration of young (d), close to the southern tip of Greenland.

In June populations of young redfish (mean length 11.4 mm) were present in three of the localities described above (a, c and d). The numbers were generally lower than those found in May, and included only a few recently extruded individuals. In July (mean size 20.0 mm) relatively small numbers of young were taken, more or less within the localities defined above as a and b. However, in June and July the limits of separate concentrations may be more difficult to define due to drift and dispersal of the now more active young stages.

The separation of these oceanic stocks of young *Sebastes* into different localities, outlined above, must be considered as tentative as it is dependent on the sampling available since 1955. Regular sampling west of 35°W. long has only been available over the last one to three years; there have been some unfortunate gaps in June; and in July one of the routes alters when the ships change to the Belle Isle track and so traverses an area south of Cape Farewell not sampled in the preceding months. It has not, therefore, been possible to establish any connection between the localities b and d which might be considered likely from an inspection of the May and July charts in Fig. 1.

HYDROGRAPHIC ASSOCIATIONS

Tåning (1949) suggested that the 'spawning' (or extrusion of young) of the large redfish (*Sebastes*) required temperatures of between 3° and 8.5°C in depths of about 300-500 m, with salinities of from 34.8 to 35.3 °/oo. Einarsson (1960 pp. 16-20) discussed the temperature requirements in relation to fluctuations observed in the numbers of young stages, and suggested the possibility of a narrower temperature range, from 4° to 6°C, at a deeper 'spawning' level of 500-800 m. He considered that this hypothesis resulted in better agreement with the distributions of young stages. Kotthaus (this symposium) expresses support for Einarsson's suggestion, pointing out that so far no 'spawning' redfish has been caught in fishing trials of any kind down to a depth of 450 m (see also below - section on adults), and that hydrographic conditions favouring this hypothesis may be found over quite large areas along the Mid-Atlantic and Reykjanes Ridges.

The Continuous Plankton Recorder survey does not provide contemporaneous observations of temperature or salinity, so that direct comparisons between the Recorder catches of young *Sebastes* and the immediate hydrographic environment cannot be made. Several attempts have been made to compare the mean numbers of young in our statistical rectangles for the individual months in various years with contemporary data for surface temperature, but so far without satisfactory results because there were too few occasions on which *Sebastes* and temperature data were available for the same rectangles, and very little temperature data for greater depths.

In the earlier account (Henderson 1961 *a*, p. 188), it was noted that the long term mean surface salinities based on observations extending over more than 50 years (Krauss 1958), were within the limits postulated by Tåning (1949) - 34.8 to 35.3 o/oo - in all areas where young were taken except for the patch off the Newfoundland Banks, where the salinity was about 34.0 o/oo. The additional material obtained since then confirms this observation, and adds only the fact that the catches close around Cape Farewell were also taken where the surface salinity was about 34.0 o/oo.

1. Associations with Surface Temperature.

Henderson (1961*a*, p. 187) noted "....some correspondence between the distribution and the surface temperatures". The additional sampling since 1960 has provided many more observations, and a detailed examination of this correspondence has been attempted. The long term mean surface temperatures for the months April to June, based on observations extending over more than 50 years (Krauss, 1958) are compared with the mean abundance of *Sebastes*, and the results are shown as histograms in Fig. 2 A.

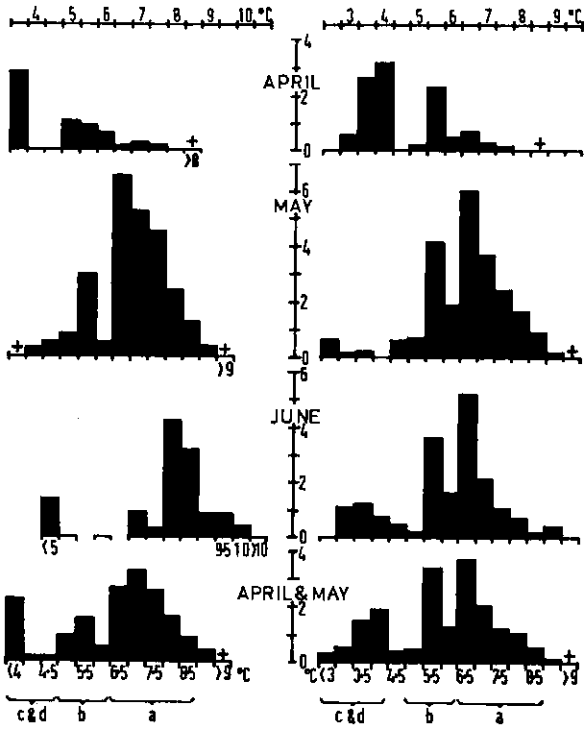
In April the mean surface temperatures over the area sampled ranged from <3°C up to >8°C, and the majority of the young *Sebastes* were found within the range of 5.0° to 7.5°C. The largest mean numbers of *Sebastes* per unit volume occurred in temperatures of from 5° to 6°C with one exception at <4°C, which is composed entirely of the catches off Flemish Cap. In May, with a mean temperature range of from <4°C to >9°C the catches occurred over the whole temperature range, but the largest numbers, exceeding 2.0 per 10 m^3, were found at 5.5°C and from 6.5° to 8°C. This is the month of greatest abundance of young stages. In June, with a mean temperature range of from <5° to >10°C the majority of the young stages occurred in temperatures between 7° and 10°C, maximum mean numbers occurring at 8° and 8.5°C. The single exception, at <5°C, represents the catches close to the southern tip of Greenland.

It is thought possible (Henderson, 1961*a*, p. 188) that the temperature requirements of the larger stages found in June and July (less than 20% are under 10 mm in length) may be less critical than are required for the earlier stages found in April and May (less than 10% are over 10 mm in length). The April and May results are shown combined in the final histogram where the largest mean numbers of young *Sebastes* are found at <4°, at 5° and 5.5° and between 6.5° and 8°C. The subscript to this histogram indicates the localities (p.309) within which the majority of the catches contributing to the individual histograms were taken.

2. Associations with Temperature at 200 Metres.

If the 'spawning' of redfish in the oceanic areas of the north Atlantic takes place only where temperatures of between 3° and 8.5°C are found in depths of 300 - 500 m (Tåning, 1949) or within the narrower range of from 4° to 6°C at 500 to 800 m (Einarsson, 1960), it would appear that a comparison of the abundance of young (at the levels at which they are sampled) with temperatures below the surface might provide clearer results than when the surface temperatures were used. It has recently been possible to make some comparisons of this kind with the mean annual temperatures at 200 m presented by Schroeder (1963). The results are shown as histograms in Fig. 2B. The three months April, May and June are plotted separately, and April and May results are combined in the final histogram to emphasise the importance of the period of extrusion. The temperatures were available as annual means only, so that any relationship with seasonal changes in temperature is obscured (although Schroeder says that "....over most of the North Atlantic temperature conditions are remarkably stable".) Catches of young *Sebastes* were taken over the whole temperature range of from <3° to >9°C. There is, however, some separation into groupings of larger mean numbers of young stages between 3° and 4°C and from 5.5° to 8°C. The subscript to the final histogram indicates the localities (p.309) within which the majority of the catches making up the individual histograms were taken.

ABUNDANCE OF THE YOUNG STAGES



A Surface Temperature B Temperature at 200 Metres

Fig. 2. Histograms showing the relationship between the mean abundance of young *Sebastes* and: A, the long term mean surface temperatures for the months April to June: B, the mean annual temperature at 200 metres depth. The scale of *Sebastes* represents the mean number per 10 m^3 found at each 0.5°C interval. The subscripts to the combined April and May histograms for both A and B indicate the localities within which the majority of the observations were contained.

In each year the average abundance of young *Sebastes* in April and May has been assessed for a standard area south and southwest of Iceland, where the sampling has generally been fairly uniform. Quite large fluctuations from year to year have been noted and possible relationships between these and other variables in the environment have been examined, so far with little success. It was noted, however, that the poorest year for young *Sebastes*, 1958, was that in which the surface temperature anomalies published by Smed (1957-1962) reached high values. The annual fluctuations in numbers of young *Sebastes*, expressed as standard deviations from the mean, are compared, in Fig. 3, with the mean surface temperature anomalies up to 1961 for March, April and May for Smed's large area F, which most nearly corresponds with the standard area from which the *Sebastes* figures are derived. The coincidence of the three highest positive temperature anomalies in this area with the three lowest points on the *Sebastes* curve seems worthy of note. However, the period of years covered is rather short, and it is as yet by no means certain how much significance there may be in associations with surface temperatures, so that this may be of coincidental significance only. Nevertheless, it is considered that these comparisons should be continued over a further period of years, and in greater detail over a wider area as results become available, to assess their possible value.

IDENTITY OF THE YOUNG STAGES

The adults of the large redfish, *Sebastes marinus* (L.) are separated into *marinus*- and *mentella*- types. Both are ovo-viviparous and the larvae have been distinguished from those of *S. viviparus* (Kr.) (Tåning 1949,1961), and from each other (Templeman and Sandeman, 1959) by the absence or presence of isolated melanophores ventrally at the root of the

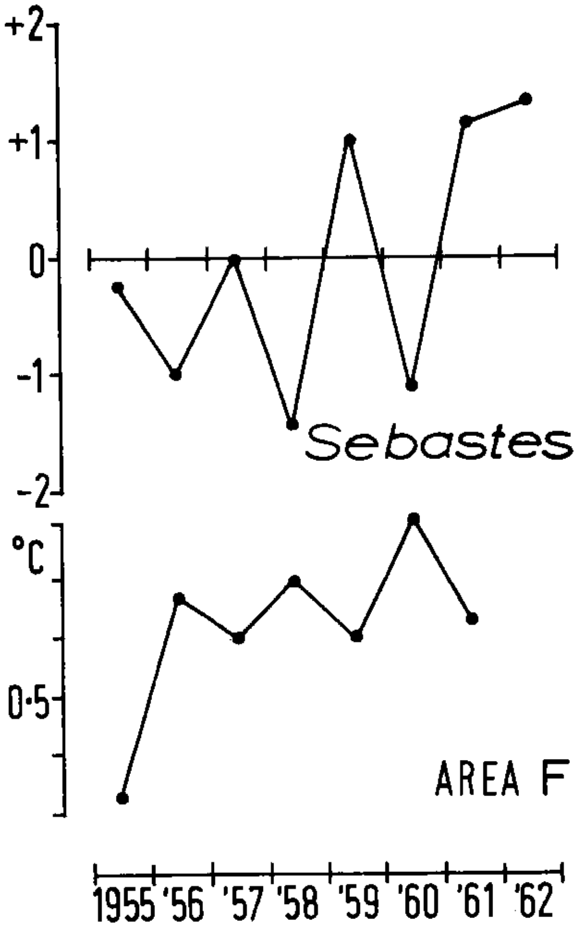


Fig. 3. Graphs showing the relation between the annual fluctuations in abundance of young *Sebastes* (based on the sampling in a standard rectangle south and southwest of Iceland in April and May and expressed as standard deviation from the mean for the years 1955 to 1962) and the surface temperature anomalies for March, April and May combined for the large Area F, for which Smed (1957-1962) has published data.

primordial caudal fin. All the young stages taken in the oceanic areas by the Recorder survey have been without sub-caudal melanophores and have been considered to be the *marinus*-type. Doubts as to the reliability of this identification are growing, however, (for example, Graham, 1962, p. 148) and it is evident that much more directly related information about parents and young is required. It is known that the only adults caught at Ocean Weather Station 'A' (see next section) are *mentella*- type, and pre-extrusion and 'left over' larvae from these have all been without the sub-caudal melanophores which should have been present in this type (Templeman & Sandeman, 1959). It will probably be some time before sufficient material is available to determine whether or not young stages from different parts of the oceanic area exhibit any characteristics which can be used to distinguish them.

IDENTITY OF THE ADULT STOCK

In late May and June 1961, the crew of the Dutch weather ship *Cumulus* caught redfish by angling at Ocean Weather Station 'A' (lat 62° N, long 33°W). This station is situated over the western slope of the Reykjanes Ridge, in an area where young *Sebastes* have usually been abundant in April and May, and a series of fishing trials was carried out from April to September 1962, with the help of British and Dutch weather ships occupying this station. These trials have been resumed, with the added help of Norwegian and French weather ships, to cover the whole of 1963. The trials were designed to sample down to 400 m, the main objectives being: (a) to catch 'spawning' redfish and, (b) to obtain as much information as possible about the adult stock from specimens preserved in formalin and returned to the laboratory. At the time of writing these fishing trials have been carried out in 1962 or 1963 (or in both years) from January to December and specimens have been obtained in each of these months except most of April and the first part of May. Although these trials are not yet completed some observed facts about the adults caught may be stated.

1. All the 172 specimens received in the laboratory so far were taken at depths of 100-250 m, the majority between 150 and 200 m.
2. All these specimens agree with the published criteria for the *mentella*-type. No *marinus*-type adults have been taken.
3. It is thought that the gap in the sequence of catches in April and early May is more likely to be due to 'spawning' activity than the absence of fish because large numbers of larvae are found at this time. The fish may be at a deeper level at this time or may be disinclined to take the hooks.
4. Some of the specimens taken in March had well developed larvae in the ovaries, and in many of the 'spent' fish caught from mid-May to mid-July some larvae had been retained. None of

these larvae so far examined exhibited the sub-caudal melanophores which might have been expected for *mentella-* type parents (Templeman and Sandeman, 1959).

5. The existence of a resident population of *mentella-* type redfish in the area around Ocean Weather Station 'A' must, it seems, now be considered a probability. These observations are, however, limited to the vicinity of Station 'A', but it may be possible to relate the findings to the larval population in the Reykjanes Ridge area. Much more information will be required before wider application becomes practicable.

SUMMARY

1. The distribution of the young stages of the redfish (*Sebastes*) in the north Atlantic, as sampled by the Continuous Plankton Recorder survey at 10 m depth, is described and illustrated for the months April to July. The possibility that this oceanic population may be found in four more or less separated localities is indicated, but precise definition of these localities is hindered by the limitations of the sampling.

2. Comparisons have been made between the mean catches of young *Sebastes* and (1) monthly mean surface temperatures, (2) annual mean temperatures at 200 m depth. The young stages are caught over most of temperature ranges encountered, but in April and May they appear to be rather more abundant in limited parts of the temperature range. There is a measure of correspondence here with the localities in which they appear to occur more or less separately.

3. The coincidence of the exceptionally poor year for young *Sebastes*, 1958, with high or maximum surface temperature anomalies in certain relevant areas in the Atlantic is noted, but some reservations exist about the significance of this.

4. The identity of the young stages is discussed and the current doubts as to the validity of the specific characteristics which have been used for some time are stated.

5. The identity of that part of the adult stock which has been sampled by fishing trials at Ocean Weather Station 'A' is found to be the *mentella-* type. The stock appears to be represented in the area for a large part of the year. Larvae taken from ripening and spent ovaries were found to be without the pigment characteristics which would have been expected for *mentella-* type.

REFERENCES

EINARSSON, HERMANN. 1960. The Fry of *Sebastes* in Icelandic waters and adjacent seas. *Rit Fiskid.* , 2 (7): 1-67.

GRAHAM, HERBERT, W. 1962. United States Research Report, 1961. *Int. Comm. Northw. Atlant. Fish. Redbook, 1962*, Part II: 143-157.

HENDERSON, G.T.D. 1961*a*. Continuous Plankton Records: The distribution of young *Sebastes marinus* (L). *Bull. Mar. Ecol.* 5: 173-193.

1961*b*. Continuous Plankton Records: The distribution of young *Sebastes marinus* (L). *Annu. Proc. int. Comm. Northw. Atlant. Fish*, 11: 103-110.

KOTTHAUS, ADOLF. 1964. The breeding and larval distribution of redfish in relation to water temperature. *This symposium, Contribution No. B-17.*

KRAUSS, WOLFGANG. 1958. Temperatur, Salzgehalt und Dichte an der Oberfläche des Atlantischen Ozeans. *Wiss. Ergebn. dtsch. atlant. Exped. "Meteor"*, Bd. V., 251-410.

SCHROEDER, ELIZABETH, H. 1963. North Atlantic Temperatures at a Depth of 200 Meters. *Serial Atlas of the Marine Environment* Folio 2. Published by the American Geographical Society.

SMED, JENS. 1957-1962. Monthly Anomalies of the Surface Temperature in Areas of the Northern North Atlantic. *Ann. biol. Copenhague*, 13: 10-11, 14: 12-14, 15: 14-15, 16: 22-23, and 17: 21-23.

In press. Monthly Anomalies of the Surface Temperature in Areas of the Northern North Atlantic in 1961. *Dansk, Nautisk Meteorol. Aarbo.*

TÅNING, Å.V. 1949. On the breeding places and abundance of the redfish (*Sebastes*) in the north Atlantic. *J. Cons. int. Explor. Mer.*, 16: 85-95.

TÅNING, Å.V. (the late) Introd. E. BERTELSEN. 1961. Larval and Postlarval Stages of *Sebastes* Species and *Helicolenus dactylopterus*. *Rapp. Cons. Explor. Mer*, 150: 234-240.

TEMPLEMAN, W. and E.J. SANDEMAN. 1959. Variations in caudal pigmentation in late state pre-extrusion larvae from *marinus*- and *mentella*-type female redfish from the Newfoundland area. *J. Fish Res. Bd. Canada* 16: 763-789.

B-5

THE DISTRIBUTION AND BEHAVIOUR OF PELAGIC AND EARLY DEMERSAL STAGES OF HADDOCK IN RELATION TO SAMPLING TECHNIQUES

By

John B. Colton, Jr.[1]

CONTENTS

---

[1] U.S. Department of the Interior, Fish and Wildlife Service, Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, Massachusetts, USA.

ABSTRACT

Data is presented on the vertical distribution and diurnal variation in the catch of haddock eggs, larvae, and pelagic juveniles, and on the diurnal variation in the catch of the early demersal stages of haddock in the Gulf of Maine.

Haddock eggs were concentrated in the surface layers and there was a decrease in their abundance with an increase in depth. Haddock larvae and pelagic juveniles were concentrated within a limited depth stratum, the depth limits of which were defined by the thermocline. There were no significant diurnal differences in the catch or in depth distribution of larval and juvenile haddock during surveys in which high-speed samplers having a high ratio of effective filtering area to sampling aperture were used.

The otter trawl catch of young-of-the-year and one-year-old haddock was greater during the night while the catch of 2+ year haddock was greater during the day. The diurnal variation in the catch of 2+ year haddock is due to a change in availability resulting from a movement off the bottom during the night, while the diurnal variation in the catch of young-of-the-year and one-year-old haddock appears to be due to an increase in avoidance or escape through the trawl meshes during the day.

Suggestions are made regarding sampling techniques which take cognizance of these distribution and behaviour patterns.

INTRODUCTION

Fishery biologists have been spared for the most part the heavy pressure for predictions that has long beset the meteorologist. A most important goal and primary obligation of fishery biologists, however, is to prepare predictions of value to the industry regarding the relative abundance of fish, the years when fish will be abundant and the areas where fish will concentrate. But what is more significant, the proof of our understanding of what is happening in the sea is the ability to specify what will happen next. In order to assess the seasonal and yearly fluctuations in distribution and abundance of fish and to make predictions regarding future availability and size of stock, it is essential that we conduct census surveys of these populations before they enter the commercial fishery. Although sampling is the heart of such studies, a more thorough examination of sampling techniques and of distribution and behaviour patterns is needed before reliable estimates and predictions of abundance and distribution can be made.

The problems involved are complex, for populations of fish are not static and are not distributed randomly in either time or space. The vertical and horizontal distribution of fishes varies with the stage of development, season of the year and time of day. In addition, many species of fish are able to avoid or escape from standard collecting gear, and this ability also varies with the stage of development and time of day. It is the purpose of this paper to present data on the vertical distribution of haddock eggs, on the vertical distribution and diurnal variation in the catch of larvae, pelagic juveniles and early demersal stages of haddock in the Gulf of Maine - Georges Bank area. Sampling techniques are suggested which take cognizance of these distribution and behaviour patterns and which are possibly applicable to other species of fish.

VERTICAL DISTRIBUTION OF HADDOCK EGGS

There have been three surveys in the Gulf of Maine - Georges Bank area in which quantitative samples were obtained in a suitable form for analysis of the vertical distribution of haddock eggs. The first series of observations was made during March, April, May and June, 1931 and April, 1932, in connection with a study of the distribution and survival of haddock eggs and larvae on Georges Bank (Walford, 1950). Sampling consisted of 30-min oblique tows with 1-m nets at a towing speed of 1.5 knots. In depths less than 100 m two nets were used, and in depths of 100 m or more three nets were used. The approximate depth ranges of the three strata sampled were 0 m to 55 m, 55 m to 110 m and 115 m to 170 m.

In Table 1 the average abundance and percentage of haddock eggs by depth strata are tabulated for stations where two nets were used in series (78 stations) and for stations where three nets were used in series (36 stations). These values were determined from Walford's Tables 4 and 5, p. 64-65. His values of eggs per minute have been converted to eggs per cubic metre.

TABLE 1.—THE AVERAGE ABUNDANCE AND PERCENTAGE OF HADDOCK EGGS BY DEPTH STRATA, MARCH - JUNE, 1931 AND APRIL 1932

	Depth strata	No. of eggs per cubic metre	Percent
2 strata	0 m - 55 m	0.258	70
stations	55 m - 110 m	0.111	30
3 strata	0 m - 55 m	0.034	87
stations	55 m - 110 m	0.002	5
	115 m - 170 m	0.003	8

Although there was considerable variation in the relative abundance of eggs in the three depth strata between individual stations, in only 5 of the 78 stations where tows were made at two levels were more eggs taken in the second stratum than in the upper stratum. In only 2 of the 36 stations where tows were made at three levels were more eggs taken in the deepest stratum than in the upper two strata. Eggs were found throughout the water column at most stations, but by far the majority of eggs were in the upper 55 m of the water column and in shallower water areas.

The second series of data was collected on Georges Bank in the springs of 1940 and 1941 in connection with studies of the distribution of *Sagitta elegans* (Clarke, *et al.*, 1943). The tabulations of fish eggs and larvae collected during these cruises have been placed at our disposal by Dr Clarke. Briefly, the zooplankton was collected by means of quantitative oblique hauls with Clarke-Bumpus Samplers (Clarke and Bumpus, 1950) arranged vertically to divide the total depth of water into two or three strata. The samplers were equipped with No. 2 silk nets and hauls were made at a speed of approximately 2 knots. The depth strata to be sampled were designated as follows:

Stratum	Water depth less than 75 m	Water depth more than 75 m
Shallow	0 m to 25 m	0 m to 25 m
Second Depth	25 m to bottom	25 m to half distance to bottom (or half distance to 200 m)
Deep	- - - - - - -	Remaining distance to bottom (or to 200 m).

The average depths actually sampled were as follows: "Shallow",- 0 m to 22 m, "Second Depth", - 22 m to 56 m, and "Deep", - 66 m to 104 m.

For each station the number of eggs per cubic metre was calculated for each stratum, and the total number of eggs under each square metre of sea surface was determined by multiplying the number per cubic metre for each stratum by its thickness and then adding the products. The average number of eggs per cubic metre for the whole water column at each station was obtained by dividing the number of eggs under each square metre by the total depth of water sampled at each station.

The abundance of haddock eggs in each depth stratum is presented in Table 2. The data are shown for individual cruises and also include the seasonal average and percentage at each depth.

TABLE 2.—THE ABUNDANCE (NUMBER PER CUBIC METRE) AND PERCENTAGE OF HADDOCK EGGS BY DEPTH STRATA AT TWO AND THREE LEVEL STATIONS, THROUGH - JUNE, 1940 AND 1941

	1940							
	Atlantis Cruise No:	95	96	97	98	100	Avg	Percent
	Date:	21 March 2 April	17-27 April	9-16 May	1-8 June	19-27 June		
2 level stations	shallow 0 m - 22 m	1.12	1.98	2.04	0.12	0.01	1.05	57
	second depth 22 m - 56 m	1.03	1.46	1.42	0.08	0	0.80	43
3 level stations	shallow 0 m - 22 m	1.92	2.47	2.46	0.11	0.01	1.39	47
	second depth 22 m - 56 m	1.42	2.16	1.19	0.07	0	0.96	33
	deep 66 m - 104 m	0.45	1.69	0.74	0.03	0	0.58	20

	1941						
	Atlantis Cruise No:	112	113	114	116	Avg	Percent
	Date:	21 March 2 April	15-23 April	7-14 May	28 May 4 June		
2 level stations	shallow 0 m - 22 m	3.00	2.90	1.91	0.26	2.02	61
	second depth 22 m - 56 m	0.96	1.66	2.41	0.16	1.30	39
3 level stations	shallow 0 m - 22 m	4.11	2.53	1.54	0.25	2.11	58
	second depth 22 m - 56 m	1.00	0.88	1.99	0.13	1.00	27
	deep 66 m - 104 m	0.77	0.64	0.75	0.06	0.56	15

In both 1940 and 1941 the average abundance of haddock eggs decreased with depth. The relative abundance in the three depth strata varied considerably between cruises, but with the exception of Cruise 114 in May 1941, when eggs were slightly more abundant in the second depth stratum in both two and three level stations, eggs were more abundant in the upper stratum during all months. The average depth range of the upper two strata (0 m to 56 m) sampled during the 1940-41 cruises coincides with the depth range of the upper stratum sampled during the 1931-32 cruises (0 m to 55 m) and confirms the finding that haddock eggs are more abundant in the upper 50 m of the water column. In addition, it is seen that haddock eggs are most abundant in the upper 20 m of the water column.

The third series of data was collected during the Continuous Plankton Recorder surveys of the Gulf of Maine - Georges Bank area during March, April and May, 1953 and February, March, April and May 1955 and 1956. These surveys were designed to locate spawning areas and to study the effects of associated environmental factors upon the survival of haddock eggs and larvae. During these cruises Recorders were towed at a speed of 10 knots, one just below the surface and one at 10 m. The average abundance (catch per cubic metre) and percentage of early stage eggs (from fertilization to the approach of the germinal ring to the equatorial position), late stage eggs (from the equatorial position of the germinal ring to hatching), and total eggs at the surface and 10 m during 1953, 1955 and 1956 are presented in Table 3.

TABLE 3.—THE ABUNDANCE AND PERCENTAGE OF HADDOCK EGGS AT THE SURFACE AND 10 m DURING 1953, 1955 AND 1956

		Early stage eggs		Late stage eggs		Total eggs	
		No. / m^3	%	No. / m^3	%	No. / m^3	%
1953	Surface	0.024	89	0.079	88	0.103	88
	10 m	0.003	11	0.011	12	0.014	12
1955	Surface	0.088	77	0.053	79	0.141	78
	10 m	0.026	23	0.014	21	0.039	22
1956	Surface	0.097	56	0.102	61	0.198	58
	10 m	0.076	44	0.065	39	0.141	42

Although the proportion of eggs at the surface and at 10 m varied between years and between cruises within a given year, the proportion of early stage and late stage eggs at the surface and at 10 m was similar within each year, during all years both early and late stage eggs were most abundant at the surface. There were only two cruises in which haddock eggs were taken in greater numbers at 10 m than at the surface. In February 1963, 68% of the late stage eggs and in March 1963, 63% of the early stage eggs were found at 10 m.

The corroborative evidence from the three series of surveys demonstrates that although haddock eggs are present throughout the whole water column, eggs in all stages of development are concentrated in the surface layers, and there is a decrease in abundance with an increase in depth. To my knowledge there have been no detailed studies made of the vertical distribution of haddock or other gadoid eggs in other areas, but the observations of Sette (1950), Silliman (1943) and Kramer (1960) which showed that the eggs of the Atlantic mackerel (*Scomber scombrus*), Pacific sardine (*Sardinops caerulea*) and Pacific mackerel (*Pneumatophorous diego*) were concentrated in the upper 20 m of the water column and above the thermocline, and of Farris (1961) who found jack mackerel (*Trachurus symmetricus*) confined to the upper 40 m of the water column, indicate that vertical segregation occurs in the eggs of many species and in many areas.

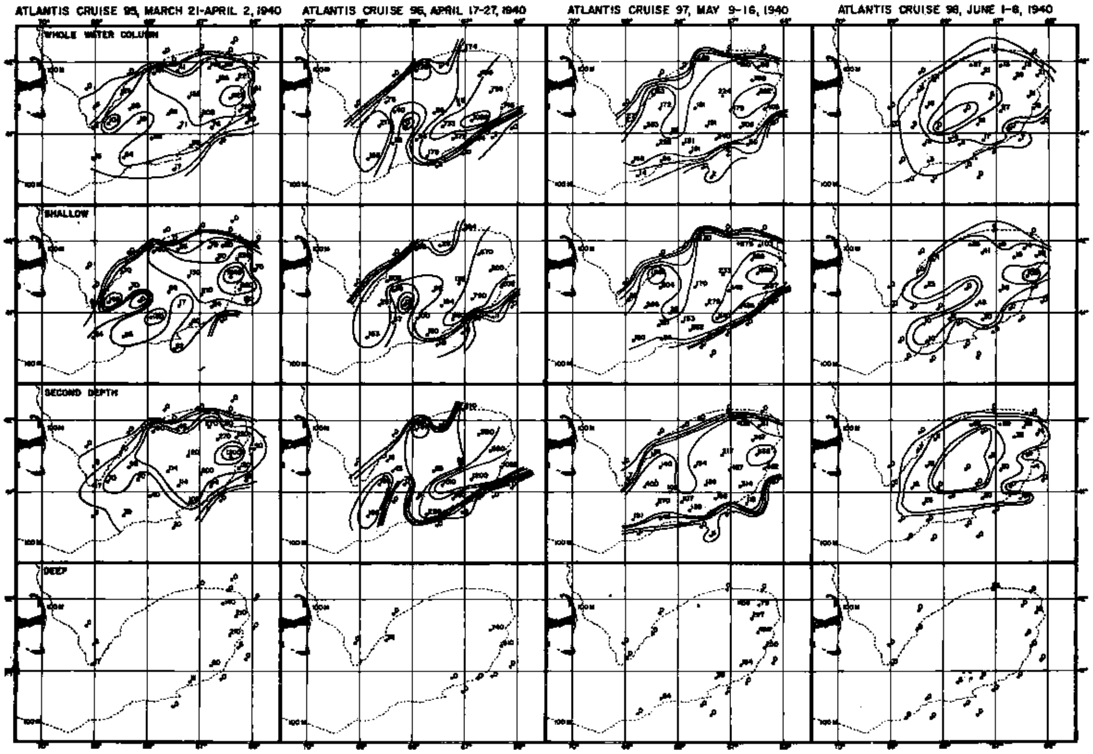


Fig. 1. Distribution of haddock eggs by depth strata, March-June 1960. Values are the number of eggs per 100 cubic metres.

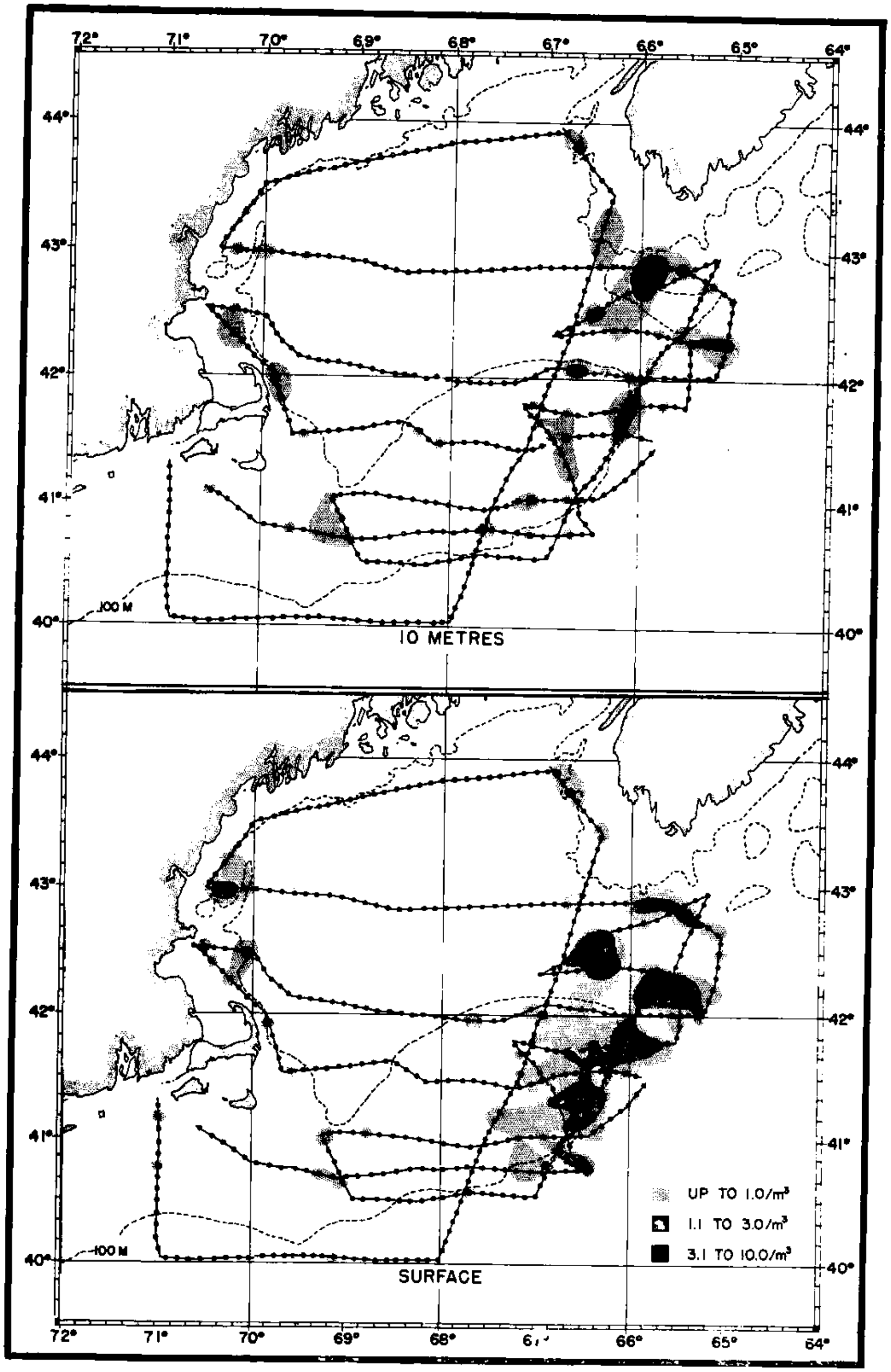


Fig. 2. Distribution of haddock eggs at the surface and 10 m, April 1956.

If, as seems likely, the vertical distribution of haddock eggs does not vary appreciably in time or space, it would be possible to obtain a reliable estimate of the relative abundance of haddock eggs between years from samples within the upper 20 m of the water column. Furthermore, if the relative abundance between stations in the depth stratum of maximum abundance was similar to that based on a sample of the whole water column, the horizontal distribution and thus the time and location of spawning could be determined from sampling a limited depth stratum. To test the feasibility of such an approach a comparison is made in Fig. 1 of the distribution of haddock eggs as determined from a sample of the whole water column and of the 0 - 22 m, 22 - 56 m, and 66 - 104 m depth strata during March, April, May and June, 1940.

In all cruises the relative abundance of eggs between stations in the shallow and second depth stratum was generally similar. The distribution of eggs in the shallow depth stratum was most representative of the distribution as determined from a sample of the whole water column.

One distinct advantage of confining sampling to a restricted depth zone is that once the depth and depth range of this stratum of maximum abundance is established for a particular species of egg a more rapid and thorough coverage of an area can be accomplished. This is not only desirable in studies of the timing of spawning, but because of the patchiness of the distribution of eggs it is also essential to obtain a maximum number of samples in order to delineate spawning locations accurately. A good illustration of the irregularity in the horizontal distribution of haddock eggs is afforded by the data collected during the Continuous Plankton Recorder surveys. The distribution of haddock eggs at the surface and 10 m during April 1956 is shown in Fig. 2.

VERTICAL DISTRIBUTION AND BEHAVIOUR OF HADDOCK LARVAE AND PELAGIC JUVENILES

1. Vertical Distribution

There have been four surveys made in the Gulf of Maine - Georges Bank area in which quantitative samples were obtained in a form suitable for an analysis of the vertical distribution of larval and juvenile haddock. The first series of data was collected during the *Atlantis* cruises to Georges Bank during the springs of 1940 and 1941. The majority of haddock collected during these cruises were prolarvae and early postlarvae (average length - 4.7 mm and size range - 3.1 mm to 10.0 mm). The average number of larvae per cubic metre in the individual depth stratum for stations where tows were made at two levels and for stations where tows were made at three levels for individual cruises and the yearly average number per cubic metre and percentage of haddock larvae in individual depth stratum for 2 and 3 level stations are presented in Table 4.

The relative abundance of larvae in the three depth strata varied considerably between cruises. In both 1940 and 1941 and on individual cruises in which appreciable numbers of larvae were caught, the average abundance of larval haddock was greatest in the shallow stratum at both two and three level stations. At three level stations, the average abundance in the second and deep stratum was similar in 1940, but greater in the second stratum than in the deep stratum in 1941.

Decidedly fewer larval haddock than haddock eggs were collected during the Continuous Plankton Recorder surveys of the Gulf of Maine - Georges Bank area in the springs of 1953, 1955 and 1956 (average number of eggs per cubic metre - 0.106, average number of larvae per cubic metre - 0.018). The average length of the larvae collected at the surface and 10 m during these surveys was 9.2 mm and the range in length 3.1 mm to 40.0 mm. The average length of larvae caught at the surface (10.0 mm) was greater than the average length of larvae caught at 10 m (8.5 mm). The average abundance and percentage of larval haddock at the surface and 10 m for individual years and for the 3 years combined are presented in Table 5.

In 1953 and in 1956 larval haddock were more abundant at 10 m than at the surface, while in 1955 they were slightly more abundant at the surface. The percentage of larvae at 10 m was greatest in 1956, the only year in which appreciable numbers of larvae were caught. Although the 1940 - 41 data indicated that both haddock eggs and larvae were most abundant in the upper 20 m of the water column, the Continuous Plankton Recorder survey data indicated that, unlike haddock eggs, which showed a steady decrease in abundance with depth, the depth at which larval haddock are most abundant is well below the surface.

During May 1958, a cruise was undertaken with the objective of getting more detailed information

TABLE 4.—THE ABUNDANCE (NUMBER PER CUBIC METRE) AND PERCENTAGE OF HADDOCK LARVAE BY DEPTH STRATA AT TWO AND THREE LEVEL STATIONS, APRIL - JUNE, 1940 AND 1941

1940

	Atlantis Cruise No:	96	97	98	Avg	Percent
	Date:	17-27 April	9-16 May	1-8 June		
2 level stations	shallow 0 m - 22 m	0.01	0.27	0.38	0.17	75
	second depth 22 m - 56 m	0.03	0.04	0.14	0.06	25
3 level stations	shallow 0 m - 22 m	0	0.05	0.23	0.08	46
	second depth 22 m - 56 m	0.02	0.02	0.13	0.05	27
	deep 66 m - 104 m	0	0.01	0.15	0.05	27

1941

	Atlantis Cruise No:	113	114	115	Avg	Percent
	Date:	15-23 April	7-14 May	28 May 4 June		
2 level stations	shallow 0 m - 22 m	0	0.13	0.48	0.21	54
	second depth 22 m - 56 m	0.01	0.17	0.34	0.18	46
3 level stations	shallow 0 m - 22 m	0	0.03	0.42	0.15	62
	second depth 22 m - 56 m	0	0.02	0.21	0.08	32
	deep 66 m - 104 m	0	0.03	0.01	0.02	6

TABLE 5.—THE ABUNDANCE AND PERCENTAGE OF LARVAL HADDOCK AT THE SURFACE AND 10 M DURING 1953, 1955 AND 1956

	1953		1955		1956		Avg	
	No./m^3	%	No./m^3	%	No./m^3	%	No./m^3	%
Surface	.005	42	.007	54	.017	31	.007	39
10 m	.007	58	.006	46	.063	69	.011	61

on the depth distribution of postlarval haddock, employing multi-depth sampling techniques. Modified Hardy Plankton Samplers (Miller, 1961) were used and sampling took place at three stations in the Georges Bank area. Each station was occupied for 2 consecutive days. Thirty-minute horizontal tows at a speed of 7 knota were taken every 2 hours at depths of 1, 10, 20, 30, 40, 50 and 75 m. The average length of haddock larvae caught during this cruise was 9.0 mm and the range in length, 4.0 to 21.0 mm. A detailed analysis of these data has been made by Miller *et al* (1963). The abundance, percentage, and mean length of larval haddock caught at each depth at the three stations are listed in Table 6.

Although there was a variation in the depth of maximum abundance of larvae between stations and between size groups of larvae, at all stations over 80% of the larvae occurred between the 10-m and 40-m levels. The average "larval-depth" (determined by multiplying the number of larvae by the

TABLE 6.—THE ABUNDANCE, PERCENTAGE, AND MEAN LENGTH OF HADDOCK LARVAE BY DEPTH, MAY 1958

	Station I			Station II			Station III		
Depth	No./m^3	%	Mean length	No./m^3	%	Mean length	No./m^3	%	Mean length
Surface	0.046	4.2	10.4mm	0.050	9.2	11.8mm	0.017	2.7	10.6mm
10 m	0.267	24.3	8.6mm	0.221	40.8	12.0mm	0.114	18.1	9.0mm
20 m	0.218	19.8	7.2mm	0.135	25.0	12.0mm	0.386	38.6	8.8mm
30 m	0.277	25.1	6.6mm	0.082	15.1	11.2mm	0.202	31.9	9.5mm
40 m	0.187	17.0	6.7mm						
50 m	0.106	9.6	6.8mm	0.040	7.4	10.9mm	0.055	8.7	9.6mm
75 m				0.013	2.5	11.7mm			

depth sampled, summing the weighted samples and dividing by the total larvae at all depths) was 25 m at Station I, 20 m at Station II, and 24 m at Station III. Larval haddock less than 8 mm in length were dispersed over a greater depth range than the larger larvae. The average larval depth for larvae smaller than 8 mm was 27 m. The data showed that over 80% of the haddock larvae in the 8 - 21 mm size range were concentrated within the depth range of the thermocline which occupied about 25% of the entire water column sampled.

Data on the vertical distribution of juvenile haddock were obtained on four cruises to the Gulf of Maine during the periods 25 July - 2 August and 5 - 11 September, 1957 and 28 July - 1 August and 9 - 16 September, 1958 (*Albatross III* Cruises 99, 102, 116 and 117) in connection with a study of the vertical distribution of redfish (Kelly and Barker, 1961). The sampling gear used was a 10-ft Isaacs-Kidd midwater trawl modified to operate as an opening and closing net. Consecutive 1-hour tows were made at a speed of 4.5 knots at depths of 10,20,30,40,60,80,100 and 110 m. A total of 366 haddock were caught in 1957 (average length - 92.6 mm, size range - 32 mm to 124 mm) and a total of 4,261 haddock were caught in 1958 (average length - 90.4 mm, size range - 27 mm to 121 mm). In Table 7 the number of tows, catch per tow and percentage of juvenile haddock by depth for the 1957, 1958 and total cruises are tabulated.

TABLE 7.—NUMBER OF TOWS AND ABUNDANCE AND PERCENTAGE OF JUVENILE HADDOCK BY DEPTH, JULY - SEPTEMBER, 1957 AND 1958

	Albatross III Cruises 99&102 July - September 1957			*Albatross III* Cruises 116&117 July - September 1958			Total Cruises		
Depth	No. of tows	Catch per tow	%	No. of tows	Catch per tow	%	No. of tows	Catch per tow	%
10 m	23	1.3	9.6	14	85.9	21.2	37	33.3	22.3
20 m	35	7.1	52.2	15	118.1	29.2	50	40.4	27.1
30 m	20	2.3	16.8	11	59.3	14.7	31	22.5	15.1
40 m	21	0.8	5.9	10	44.3	11.0	31	14.8	9.9
60 m	7	1.3	9.6	4	48.3	11.9	11	18.3	12.3
80 m	6	0.8	5.9	4	48.5	12.0	10	19.9	13.3
100 m	8	0	0				8	0	0
110 m	4	0	0				4	0	0

In both 1957 and 1958 the greatest abundance of juvenile haddock occurred at 20 m, although the proportion of fish at this depth was greater in 1957 than in 1958. No juvenile haddock were found below 80 m. During all four cruises the thermocline extended from approximately 10 to 50 m (Kelly and Barker, 1961, Fig. 2, p. 227), and it was in this zone of rapid temperature change that the greatest numbers of juvenile haddock were caught. The average depth of juvenile haddock depth was 28 m in 1957 and 33 m in 1958. The average depth of juvenile haddock from July to September was greater than that of larval haddock in May as was the average depth of the thermocline. In 1957, 85% and in 1958, 76% of the juvenile haddock were found within the depth range of the thermocline. These percentages agree closely with those obtained in May 1958 for postlarval haddock.

In Fig. 3 the percentage of 10-mm length groups of juvenile haddock at each depth are plotted for the periods July - August, 1957 and 1958 (*Albatross III* Cruises 99 and 116) and September, 1957 and 1958 (*Albatross III* Cruises 102 and 117). The average length of juvenile haddock caught during July - August was 84 mm and during September was 99 mm. The average depths during all cruises for the eight length groups in order of increasing size were 31, 28, 32, 32, 33, 39, 37 and 30 m. With the exception of haddock larger than 79 mm in July - August, all length groups were concentrated between 10 and 40 m during both periods. During the July - August period the greatest percentage of juvenile haddock 80 mm and larger was at the 80 m level. Although appreciable numbers of haddock were caught in only one of the 10 tows made at this depth, the data for both periods indicate that there is an increase in the average depth and depth range with an increase in length. Further sampling incorporating high-speed simultaneous tows is needed to validate these data.

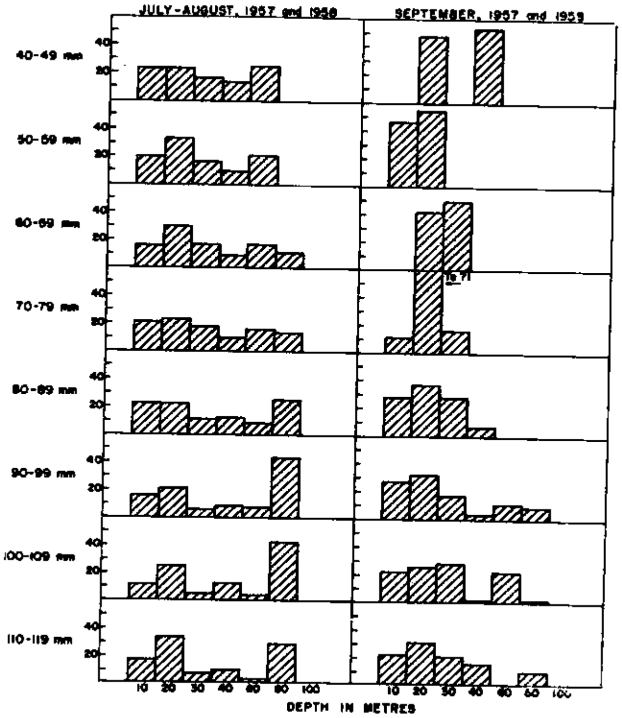


Fig. 3. The relative abundance in percent of 10 mm length groups of haddock by depth, July - August, 1957 and 1958 and September 1957 and 1958.

Vertical segregation has been observed for other species of larval and juvenile fish by many investigators (Russell, 1928; Silliman, 1943; Wiborg, 1948; and 1960; Sette, 1950; Ahlstrom, 1954, and 1959; Bridger, 1958; Kramer, 1960; Colton *et al.*, 1961; and Farris, 1961). The four series of observations in the Gulf of Maine - Georges Bank area demonstrate that prolarval, postlarval and juvenile haddock up to approximately 120 mm in length also tend to be concentrated within a narrow depth range. Over 90% of the prolarval and postlarval haddock (4.0 - 21.0 mm) occurred in the upper 40 m of the water column and over 80% of the postlarval haddock (8.0 - 21.0 mm) were concentrated within the thermocline. Although haddock larvae smaller than 8 mm were dispersed over a greater depth range than larvae larger than 8 mm, their average larval depth was only slightly greater. Wiborg (1960) found that in waters off the coast of Norway smaller cod larvae were also dispersed over a greater depth range and that there was an increase in depth stratification with an increase in length.

Over 75% of haddock up to 124 mm in length occurred between the 10- and 40-m levels, so that it appears that it would be possible to obtain a reliable estimate of the relative abundance of larval and juvenile haddock within a given area, between years, from a sample within a limited depth stratum. The depth range of maximum abundance of larval and juvenile haddock coincided with the depth range of the thermocline. The depth limits of the thermocline are readily definable and do not vary markedly with location in an area such as Georges Bank. These facts suggest that it would be possible to determine the horizontal distribution of these fish from a sample within this restricted depth zone.

2. Behaviour

There are two aspects of the behaviour of larval and juvenile fish, namely diurnal migration and escapement, that must be considered in any sampling program. Diurnal migrations, at least for many species of larval and juvenile fish, are not as extensive as once assumed (Johansen, 1925; Russell, 1928; and Sette, 1950), as it has been demonstrated that variations in the day and night catch are due in large part to the ability of many species to avoid slow-moving collecting nets (Silliman, 1943; Ahlstrom, 1954; Bridger, 1956 and 1958; and Colton and Marak, 1962). This ability to avoid capture increases with the size of the fish and the amount of light, with a resulting decrease in the catch and average size of fish caught in the surface layers during the day and an increase during the night. Bridger (1958) and Southward (1962) in experiments made with the Gulf III high-speed sampler have shown that a reduction in the shock wave that precedes the net and an increase in filtration efficiency are as important as high speed in preventing evasion by fast moving animals.

The data used in this report corroborate these findings. For example, the average size and range in size of haddock and cod larvae taken with the Continuous Plankton Recorder were considerably greater than the average size and range in size of haddock and cod larvae collected with 1-m nets on the same cruises or with Clarke-Bumpus Samplers during similar seasons (Colton and Marak, 1962). In addition, there was no consistent diurnal difference in the average number of larval haddock caught in the upper 10 m of the water column with the Continuous Plankton Recorder (54% in the day and 46% at night), while with both the metre net and Clarke-Bumpus Sampler many more larval haddock were caught during the night. More juvenile haddock were caught during the night at all depths except 80 m with the Isaacs-Kidd midwater trawl during 1957 and 1958. The average catch per tow of juvenile haddock for all depths during the day was 17.5 and during the night was 36.5. The night/day ratio in the catch tended to decrease with depth and increase with the length of fish. There was no significant difference at any depth in the abundance, average size/and size range of larval haddock, caught with the modified Hardy Plankton Samplers during the vertical distribution studies in May, 1958 (Miller *et al.*, 1963).

During both surveys in which there were no significant differences in day and night catch of haddock, high-speed samplers having a high ratio of effective filtering area to sampling aperture were used. The Continuous Plankton Recorder has a filtering ratio of 32 to 1 and the modified Hardy Plankton Sampler has a filtering ratio of 18 to 1. Both these ratios are much larger than those of the ordinary tow nets and thus assure a more rapid movement of water through the mouth of the gear.

There was no evidence of any diurnal change in the depth distribution of larval haddock in May 1958. The average larval depth at the three stations was 24 m during the day and 22 m during the night. The average depth of juvenile haddock caught with the Isaacs-Kidd trawl in 1957 and 1958, however, did show diurnal variation, being at 40 m during the day and at 30 m during the night. Considering that no juvenile haddock were found below 80 m during the day or night, that over twice as many juvenile haddock were caught during the night than during the day, and that the night/day ratio in the catch tended to decrease with depth, it would appear that this diurnal variation in depth distribution is an artifact resulting from increased daylight avoidance. In addition, simultaneous tows were not made with the Isaacs-Kidd trawl so that there was considerable variation in time and location between sampling depths. In neither series of data was there any evidence of a night-time migration of larvae or juveniles from depths below the maximum depth sampled. Such stability in the depth distribution of larval and juvenile fish has been observed in other species as well (Ahlstrom, 1959 and Farris, 1961).

VERTICAL DISTRIBUTION AND BEHAVIOUR OF EARLY DEMERSAL STAGES OF HADDOCK

Census surveys of the groundfish populations in the Gulf of Maine - Georges Bank area were made in September 1955 (*Albatross III* cruises 65 and 66), November 1956 (*Albatross III* cruises 81 and 82), and October 1958 (*Albatross III* cruises 118, 119, and 120). One of the objectives of these surveys was to estimate the abundance of young-of-the-year haddock for predictions of year class strength. The survey gear was a standard otter trawl having a 1.3 cm mesh cotton liner in the cod end and upper belly. The towing speed was 2.5 knots, and all tows were 1/2 hour long from hook-up to haul-back.

An analysis of these data showed that the abundance of young-of-the-year and 1-year-old haddock fluctuated in the same way, both being high in all areas in 1955 and 1958 and low in 1956. This tendency towards a greater abundance of haddock in certain years was also manifest to a lesser degree in the survey catches of older haddock. For example, the catch per tow of haddock of all ages was greater in 1958 than in 1956. One consequence of this fluctuation in fishing efficiency between years is that estimates of year class strength are dependent upon what age fish are chosen to represent the year class and in what year the sampling was done. From these data the 1956 year class would appear much stronger on a basis of the abundance of 2-year-old haddock in 1958 than of the abundance of young-of-the-year haddock in 1956.

The gear, method of tow and area of coverage were similar during all survey cruises, so that it does not appear that the variation in fishing efficiency between years could be due to any differences in fishing technique. However, commercial vessels tend to catch more haddock during the day than during the night and this variation in the day and night catch is greatest in deeper water. If during the survey cruises, there had been a marked variation in the proportion of day and night tows, this could, conceivably, be the cause of the variation between years in fishing efficiency. To determine if such was in fact the case, a tabulation was made in Table 8 of the number of day and night tows and of the catch per tow of young-of-the-year, 1-year-old, and 2+ year haddock during the day and night for the three survey cruises. Young-of-the-year and 1-year-old haddock are tabulated separately, for it was for these ages that the most marked yearly variation in abundance were observed. The reason for the difference in the number of tows tabulated for young-of-the-year haddock and in the number of tows tabulated for 1-year-old and 2+ year haddock in 1955 and 1956 is that at some stations only young-of-the-year haddock were counted or young-of-the-year haddock were lost due to a tear in the fine mesh liner.

TABLE 8.—THE NUMBER OF TOWS AND THE CATCH PER TOW OF HADDOCK BY DAY AND NIGHT IN THE GULF OF MAINE - GEORGES BANK AREA, SEPTEMBER 1955, NOVEMBER 1956 AND OCTOBER 1958.

		Day (0730 - 1629)			Night (1930 - 0429)		
	Year	No. of tows	No. of fish	C/T	No. of tows	No. of fish	C/T
Young-of-the year haddock	1955	46	218	4.7	53	732	13.8
	1956	34	72	2.1	37	58	1.6
	1958	46	264	5.7	50	1216	24.3
	Total	126	554	4.4	140	2006	14.3
One-year-old haddock	1955	42	45	1.1	54	349	6.8
	1956	35	74	2.1	37	48	1.3
	1958	46	286	6.2	50	548	11.0
	Total	123	405	3.2	141	945	6.7
2+ year haddock	1955	42	466	11.0	54	270	5.0
	1956	35	285	8.1	37	212	5.7
	1958	46	958	20.8	50	732	14.6
	Total	123	1709	13.9	141	1214	8.6

The day and night effort did not vary markedly, although in all years more tows were made during the night than during the day. The catch per tow of young-of-the-year haddock was slightly greater during the day in 1956 and much greater during the night in 1955 and 1958. The catch per tow of 1-year-old haddock was greater during the day in 1956 and greater during the night in 1955 and 1958. The average night/day ratio of abundance was greater for young-of-the-year haddock than for 1-year-old haddock. In all years the catch per tow of 2+ year haddock was greatest during the day as is the case in the commercial catch. The day/night ratio of abundance of 2+ year haddock was of the same order of magnitude during all years, but the abundance of young-of-the-year and 1-year-old haddock was only greater at night in the years when the survey cruises indicated that these two age groups were most abundant (1955 and 1958).

Year-class strength estimates based on the abundance of young-of-the-year haddock during both day and night would indicate that the 1955 and 1958 year classes were strong. The night time data would not only indicate that the 1955 and 1958 year classes were considerably stronger than indicated by the day time data, but that the 1958 year class was approximately twice as strong as the

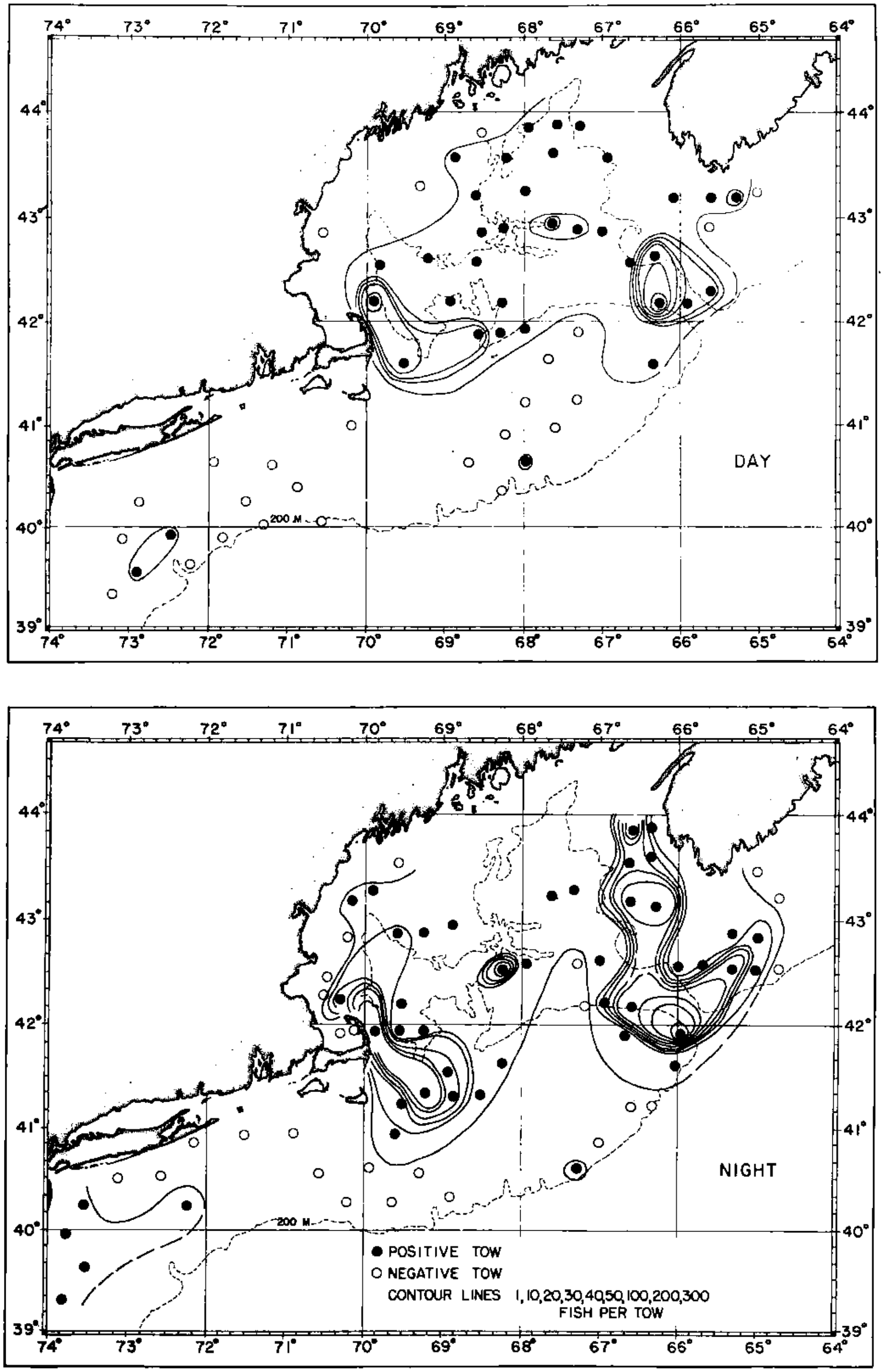


Fig. 4. Distribution of young-of-the-year haddock during the day and night, October, 1958.

1955 year class. The day time catch of 1-year-old haddock would indicate that only the 1957 year class was strong, while the night time catch would indicate that both the 1957 and 1954 year classes were strong. Although not as marked, significant yearly differences in the relative abundance of 2+ year haddock also occurred between the day and night data.

Not only do estimates of abundance of haddock based on day and night observations vary, but also the distribution pattern is different if based on night observations than if based on day observations. This is demonstrated in Fig. 4 showing the distribution of young-of-the-year haddock as determined during the day and night tows in October, 1958. Young-of-the-year haddock were found over a much wider area at night and also areas of high abundance (off southeastern Nova Scotia) were not indicated by the day time data.

When the 3-year average catch per tow of young-of-the-year, 1-year-old and 2+ year haddock was determined for hourly intervals, the plots showed marked hourly fluctuations in the abundance of all age groups. Although in general the catch per tow of young-of-the-year and one-year-old haddock tended to be higher during the night time hours and the catch per tow of 2+ year haddock tended to be higher during the daylight hours, the fluctuations in the number of fish caught, between individual tows within a given hour, were too great to attach any significance to the abundance figures. The main cause for these fluctuations appears to be the marked regional variations in the abundance of haddock. Obviously there were many tows made during the night in areas where there were few or no young-of-the-year and 1-year-old haddock, or many 2+ year haddock, and tows made during the day where the reverse situation existed. In any event, the day/night variability in the catch is real, but special sampling programs in which tows are made at set time intervals within relatively small areas for an appreciable number of days are needed before this variability can be accurately assessed.

Diurnal migration appears to be the cause of the variation in the day and night catch of 2+ year haddock. Although no sampling has been undertaken to determine if haddock move off the bottom during the night, trawling experiments and echo sounder observations have shown that haddock move off the bottom at night in other areas (Woodhead, 1961). Indications are that this is also the case in the Gulf of Maine - Georges Bank area where the commercial catch of haddock is greater during the day than at night. Diurnal migration cannot explain the variation in the day and night catch of young-of-the-year and 1-year-old haddock unless, unlike older haddock, these young fish move up in the day and down at night. It is also possible that young-of-the-year and 1-year-old haddock do not move off the bottom at night. However, observations on the diurnal migration of herring in the North Sea (Lucas, 1936) and of haddock in the Barents Sea (Woodhead, 1961) have demonstrated that smaller fish show more tendency to leave the sea bed than do larger fish. It appears that the day time decrease in the catch of young-of-the-year and 1-year-old haddock is due to a variation in the catching efficiency of the otter trawl between day and night. This variation in catching efficiency could be due either to an increase in the avoidance of the trawl during the day, as has been demonstrated in the case of larval and juvenile fish, or to an increase in escape through the unlined meshes of the trawl wings (12.7 cm stretched mesh) during the day. No doubt haddock of all ages are able to avoid the otter trawl to some extent, but it appears that the younger fish may exhibit a more rapid visual and auditory response to the trawl and that the day and night variability in the catch of young-of-the-year and 1-year-old haddock due to avoidance or escapement is greater than that due to vertical migration.

There would appear to be only two possible methods of increasing the daytime catching efficiency of the otter trawl. One would be to increase the towing speed, but this does not appear practical for it is difficult to keep the trawl on the bottom at high speed and the amount of backwash and turbulence at the mouth of the net would be increased. Another, and possibly more effective way of reducing escape, would be to decrease the mesh size of the trawl wings. It appears quite possible that all age haddock enter the net at the same rate, but the smaller fish (young-of-the-year and 1-year-olds) are able to escape through the meshes of the wings and are better able to do this during the day than during the night. In order to determine if this is in fact the case, it would be necessary to make a duplicate series of tows during the day and night with and without a fine mesh liner in the wings.

It is evident that one of the causes of the variability in fishing efficiency between years is the diurnal variation in the catch. If the various age haddock were randomly distributed and if the diurnal cycle was similar for all age haddock and for all depths, due allowance could be made for this diurnal variation. However, in addition to the variance caused by day and night differences in depth distribution there is apparently also bias caused by a variation in the fishing efficiency of the otter trawl with age of fish and time of day. Until this variance is allowed for and the bias eliminated, the relative abundance of haddock between areas and years can only be made for a specific age group and on a basis of data collected either by day or night.

SUMMARY AND CONCLUSIONS

The analysis of the data on the vertical distribution of haddock eggs collected in 1931, 1932, .940, 1941, 1953, 1955 and 1956 in the Gulf of Maine - Georges Bank area demonstrated that, although ıaddock eggs occurred throughout the water column, eggs in all stages of development were concen:rated in the surface layers and there was a decrease in abundance with an increase in depth. The :elative abundance of haddock eggs in the upper 20 m of the water column was similar to the relative ıbundance of eggs based on a sample of the whole water column.

Surveys made in 1940, 1941, 1953, 1955, 1956 and 1958, in which quantitative data on the vertical listribution of prolarval and postlarval haddock were obtained, demonstrated that haddock up to 21 mm .n length were concentrated within a limited depth stratum, the depth limits of which were defined by :he thermocline. At stations in which simultaneous samples were taken at depths down to 75 m over ·0% of the larvae were found between the 10-and 40-m levels and within the thermocline.

In studies of the vertical distribution of juvenile haddock conducted in 1957 and 1958 in which amples were taken at specific depths down to 110 m, over 75% of haddock, ranging in length from 7 mm to 124 mm, occurred between depths of 10 and 40 m and within the thermocline. No juvenile addock of this size range were found at depths greater than 80 m.

In surveys in which high-speed samplers having a high ratio of effective filtering area to samling aperture were used, there were no significant differences in the day and night catch of larval nd juvenile haddock and no variation in the depth distribution between day and night.

It appears that not only would it be possible to obtain a reliable estimate of the relative bundance of the eggs, larvae, and pelagic juveniles of haddock as well as other species on a basis f samples confined to a limited depth stratum, but also that the areal distribution and thus the time nd location of spawning and the drift and migrations of larval and juvenile fish could be obtained by ampling a restricted depth stratum.

In studies of the early life history and year-class strength fluctuations of most species of marne fish it does not seem feasible or expedient to attempt to determine the absolute abundance of eggs nd larvae. Indeed, no conclusive correlation has been demonstrated between the abundance of eggs and arvae and the brood strength of these fish as measured by their contribution to the fishery in suceeding years (Thompson, 1929*a* and 1929*b*; Poulsen, 1931 and 1941; Heegard, 1947; Carruthers *et al.*, 951; Rae, 1953; and Radovich, 1962). The time and location of spawning and the subsequent disperal of larvae and juveniles are likely to have greater influence on brood strength than the absolute umber of eggs or larvae produced. The data on the vertical distribution of haddock eggs, larvae, nd juveniles indicates that such information can be obtained from samples taken within a relatively arrow depth zone. Because sampling of a limited depth stratum would be more rapid than sampling the hole water column, a greater number of samples could be obtained in a given period. Reliable estiates of abundance over broad geographical areas would be possible and more accurate data obtained n the fluctuations in abundance in time and space.

To define the vertical distribution of the eggs or larvae of any species of fish it would be dvisable to use high-speed, simultaneous, horizontal tows. Once the vertical distribution is ascerained, it would be expedient to make high-speed oblique tows with samplers of high filtering capaity to eliminate avoidance and to insure adequate samples. The studies of Bridger (1956, 1958) and f Southward (1962) show that with modifications the Gulf III high-speed sampler (Gehringer, 1952) s ideally suited for this purpose. A simple closing mechanism for this sampler has been described y Kinzer (1962).

The analysis of data on the distribution and abundance of haddock during otter trawl surveys of roundfish populations in the Gulf of Maine - Georges Bank area in 1955, 1956 and 1958 showed that ıe catch of young-of-the-year and 1-year-old haddock fluctuated in the same way, both being high in ll areas in 1955 and 1958 and low in 1956. The variation in abundance between years appears to reılt from a decrease in fishing efficiency during daylight hours, for the average catch per tow of ung-of-the-year and 1-year-old haddock was markedly greater during the night than during the day ı years when the abundance figures were high. This day and night variation in the catch of young ıddock is opposite to that of 2+ year haddock, the catch of which was greater during the day in all ars as is the case in the commercial catch. The variation in the catch of young-of-the-year and -year-old haddock is not due to a change in availability resulting from a movement off the bottom during the night as in the case of 2+ year haddock, but appears to be due either to an increase in avoidance or escape through the trawl wings during the day. Special sampling programs are needed to determine the cause and to assess accurately the degree of this day and night variation in the catch. Regardless of the cause, the effect is real in that there are marked differences in abundance and distribution as determined from day and night observations.

This analysis of the catch of haddock eggs, larvae and juveniles shows that in studies of the early life history and brood strength fluctuations of fish we have to deal with populations of such complexity that special investigations on the nature of the distribution of the various developmental stages should be undertaken to improve sampling programs and the design of collecting gear with a view of minimizing variance and eliminating bias.

REFERENCES

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

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

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

1958. On efficiency tests made with a modified Gulf III high-speed tow-net. *J. Cons. int. Explor. Mer*, 23(3): 357-365.

CARRUTHERS, J.N. *et al.* 1951. Variations in brood-strength in the North Sea haddock, in light of relevant wind conditions. *Nature*, 168 (4269): 317-319.

CLARKE, G.L. , E.L. PIERCE, and D.F. BUMPUS. 1943. The distribution and reproduction of *Sagitta elegans* on Georges Bank in relation to hydrographical conditions. *Biol. Bull.*, 85(3): 201-226.

CLARKE, G.L. and D.F. BUMPUS. 1950. The plankton sampler -- An instrument for quantitative plankton investigations. *Am. Soc. Limnol. and Oceanog., Spec. Pub.*, 5: 1-8. Revised.

COLION, J.B., K.A. HONEY, and R.F. TEMPLE. The effectiveness of sampling methods used to study the distribution of larval herring in the Gulf of Maine. *J. Cons. int. Explor. Mer*, 26 (2): 180-190.

COLTON, J.B. and R.R. MARAK. 1962. Use of the Hardy Continuous Plankton Recorder in a fishery research programme. *Bull. Mar. Ecol.*, 5 (49): 231-246.

FARRIS, D.A. 1961. Abundance and distribution of eggs and larvae and survival of larvae of jack mackerel (*Trachurus symmetricus*). *Fish. Bull. U.S.*, 61 (187): 247-279.

GEHRINGER, J.W. 1952. 2. An all metal plankton sampler (Model Gulf III). *Spec. sci. Rep. U.S. Fish Wildl. Serv. - Fish.*, No. 88, p. 7-12.

HEEGAARD, P. 1947. Investigations of the breeding season and the quantities of eggs of the food fishes of the Kattegat and the northern Belt Sea 1929-1941. *Medd. Komm. Danm. Fisk. Havundersøg.*, 11(4): 1-20.

JOHANSEN, A.C. 1925. On the diurnal movements of young of some fishes in Danish waters. *Medd. Komm. Danm. Fisk. Havundersøg.*, 8(2): 1-27.

KELLY, G.F. and A.M. BARKER. 1961. Vertical distribution of young redfish in the Gulf of Maine. *Rapp. et Proc.-Verb.*, 150: 220-233.

KINZER, J. 1962. Ein einfacher Schiessmechanismus für die Planktonröhre "Hai" (A simple closing mechanism for a modified Gulf III plankton sampler). *Kurze Mitteilungen aus dem Institut für Fiskereibiologie der Universität Hamburg*, No. 12, Dec., 1962: 13-17.

KRAMER, D. 1960. Development of eggs and larvae of Pacific mackerel and distribution and abundance of larvae 1952-56. *Fish. Bull., U.S.*, 60 (174): 393-438.

LUCAS, C.E. 1936. On the diurnal variation of size-groups of trawl-caught herring. *J. Cons. int. Explor. Mer*, 11 (1): 53-59.

MILLER, D. 1961. A modification of the small Hardy plankton sampler for simultaneous high-speed plankton hauls. *Bull. Mar. Ecol.*, 5 (45): 165-172.

MILLER, D., J.B. COLTON, and R.R. MARAK, 1963. A study of the vertical distribution of larval haddock. *J. Cons. int. Explor. Mer*, 28 (1): 37-49.

POULSEN, E.M. 1931. Biological investigations upon the cod in Danish waters. *Medd. Komm. Danm. Fisk. Havundersøg.*, 9 (1): 1-148.

1941. On fluctuations in the size of the stock of cod in the waters within the Skaw during recent years. *Rept. Danish Biol. Sta.*, 46: 1-36.

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

RAE, B.B. 1953. The occurrence of lemon sole larvae in the Scottish plankton collections of 1929, 1930, and 1931. *Mar. Res. Scot.*, 1953, No. 1: 1-36.

RUSSELL, F.S. 1928. The vertical distribution of marine macroplankton. VIII. Further observations on the diurnal behaviour of the pelagic young of teleostean fishes in the Plymouth area. *J. Mar. Biol. Ass., U.K.*, 15 (3): 829-850.

SETTE, O.E. 1950. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America Part I: Early life history, including growth, drift, and mortality of the egg and larval populations. *Fish. Bull., U.S.*, 50 (38): 149-237.

SILLIMAN, R.P. 1943. Thermal and diurnal changes in the vertical distribution of eggs and larvae of the pilchard (*Sardinops caerulea*). *J. Mar. Res.*, 5 (2): 118-130.

SOUTHWARD, A.J. 1962. The distribution of some plankton animals in the English Channel and approaches. II. Surveys with the Gulf III high-speed sampler, 1958-60. *J. Mar. Biol. Ass., U.K.*, 42 (2): 275-375.

THOMPSON, H. 1929*a*. 2. Haddock biology (North Sea). A brief survey of recent data, methods and results. *Rapp. et Proc.-Verb.*, 54: 135-163.

1929*b*. General features in the biology of the haddock (*Gadus aeglefinus* L.) in Icelandic waters in the period 1903-1926. *Rapp. et Proc.-Verb.* 57: 1-73.

WALFORD, L.A. 1950. Effects of currents on distribution and survival of the eggs and larvae of haddock (*Melanogrammus aeglefinus*) on Georges Bank. *Fish. Bull., U.S.*, 49 (29): 1-73.

WIBORG, K.F. 1948. Investigations on cod larvae in the coastal waters of Northern Norway. Occurrence of cod larvae, and occurrence of food organisms in the stomach contents and in the sea. *Fiskeridir. Skr. Havundersøk.*, 9 (3): 1-27.

1960. Investigations on eggs and larvae of commercial fishes in Norwegian coastal and offshore waters in 1957-58. *Fiskeridir. Skr. Havundersøk.*, 12 (7): 5-27.

WOODHEAD, P.M.J. 1961. Diurnal variation in the trawl catches of haddock. *Cons. int. Explor. Mer, Comparative Fishing Committee,* No. 71: 1-5. (unpublished manuscript).

B-6

FACTORS CONTROLLING DISPERSAL OF THE PELAGIC STAGES OF FISH AND THEIR INFLUENCE ON SURVIVAL

By

Alan Saville [1]

ABSTRACT

The part which dispersal of the planktonic stages may play in generating differential recruitment to a fish stock is discussed in relation to the habitat of the stock. Wind is considered to be the dominant factor in bringing about differences in dispersal between years. Evidence for the effect of wind on the distribution of haddock eggs and larvae at Faroe and in the North Sea, and of herring larvae in the Clyde is reviewed. It is concluded that there is a relationship between wind direction and strength and the distribution of larvae for Faroe haddock and Clyde herring but not for North Sea haddock. The impact of this on subsequent year-class strengths of these stocks is discussed.

INTRODUCTION

Appreciation of the major role played by variation in the success of year-classes, in generating the fluctuations in productiveness to which most fisheries are subject, has made the investigation of the factors controlling this variation a major preoccupation of fisheries research. For the majority of fish stocks it has now been clearly established that the size of a year-class is fixed at least by the end of the planktonic phase (Parrish, 1950), although opinion is still divided as to the part of this phase in which the operative factors principally exert their effect.

The planktonic nature of the early spawning products, both the eggs in the majority of species of commercially important fish, and larvae for all but an insignificant proportion, must mean that dispersal could play a vital part in determining the fate of a year-class. The possible importance of dispersal was first propounded by Hjort (1914) who encountered great numbers of cod larvae over deep water in the Norwegian Sea and suggested that such drift into an unsuitable environment might be a major cause of differential mortality between years. Although differential survival of the initial production between years seems to be a feature of virtually all spawning stocks, the operative factors producing this differential survival must be expected to differ between stocks and indeed within the same stock in different years. This must be particularly true for the effects of variations in dispersal.

Stocks of fish spawning on isolated shallow banks surrounded by deep water, or on narrow shelves bordering oceanic depths would be expected to be much more vulnerable to this source of mortality than those whose chosen spawning areas are surrounded by large areas of suitable ground for the settlement and growth of the post-metamorphic stage. The presence of self-contained spawning stocks on such banks would seem to demand a current system over them, such as an eddy, which would tend to retain the planktonic stages of the life-cycle over the bank. The part played by eddy systems in maintaining benthic populations with planktonic larvae in such situations has been pointed out for bivalves by Orton (1937) and the role of convection currents in similar situations for lobsters at Bermuda by Boden (1952). Whether the planktonic stages carried beyond the habitat of the spawning stock survive to recruit to another area or perish is a moot point and must be dependent on the length of the planktonic phase, on any ability of the organism to postpone the change over to the adult mode of life until a favourable environment is reached (such as Wilson 1952 has demonstrated for the planktonic larvae of certain invertebrates) and on the proximity of alternative areas suitable for settlement. Unless, however, one postulates a reverse migration of the organism to the spawning site of the parents, whether the organism survives in a new habitat or not does not affect the generation of differential survival of the initial stock.

---

[1] Marine Laboratory, Aberdeen, Scotland.

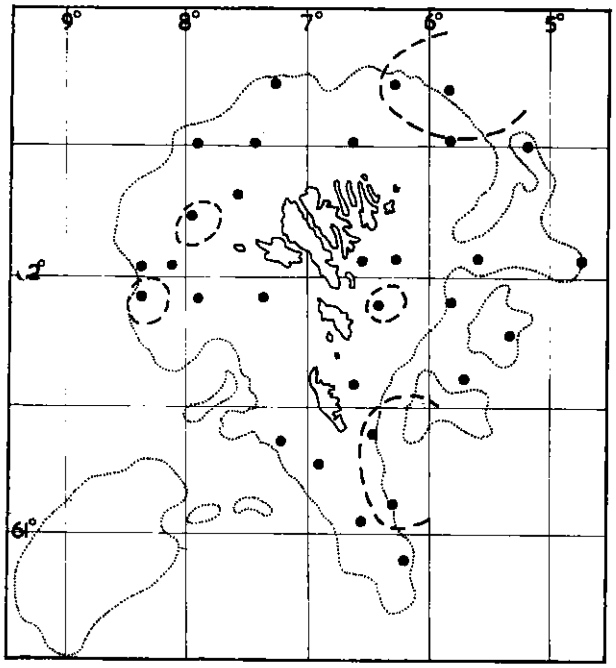


Fig.1. Distribution of haddock larvae at Faroe, June 1950. Dots show the positions of the stations; the abundance of the larvae is shown by contours at 1 to 5 per haul (broken line) and >5 (unbroken line).

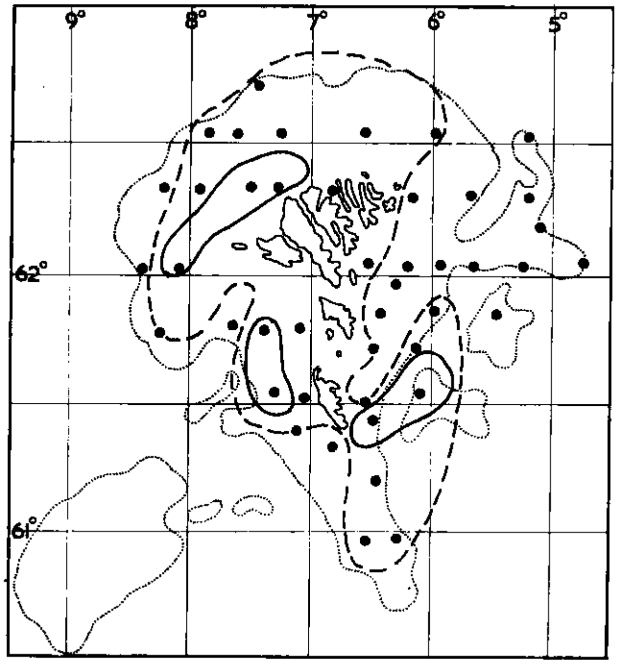


Fig. 2. Distribution of haddock larvae at Faroe, June, 1952. Contour levels as in Fig.1.

Thus the maintenance of a permanent spawning stock demands a current system over the spawning area which under normal circumstances retains the planktonic stages within that area or alternatively brings about dispersion within an environment suitable for subsequent settlement and growth, and permits of a contranatant migration back to the original spawning area. Any short-term distortion of the current system, during the spawning season, which results in a dispersion not fulfilling these conditions, could be expected to result in a poor recruitment from that year class.

Of the factors which would bring about such a distortion of the normal current pattern an abnormal persistence of wind from one direction seems the most likely. The major part of this paper deals with a consideration of wind effects on egg and larval dispersion and subsequent year-class size in different types of spawning situations.

DISTRIBUTION OF HADDOCK EGGS AND LARVAE AT FAROE

The Faroe plateau, which forms part of the submarine ridge connecting Scotland and Iceland, comprises an area of about 23,000 sq km within the 200 m contour. This area is intensively fished, largely for cod and haddock, - the haddock landing in a typical year amounting to something of the order of 400,000 cwt. Tait (1934), largely on the basis of drift-bottle returns, postulated an anti-cyclonic eddy system around the islands and this is supported by the fact that the plateau appears to maintain its own plankton population, which is quite different from the typical oceanic fauna of the surrounding waters (Fraser 1939; Hansen, 1955). The haddock stock of the area is considered to be a self-contained one (Raitt, 1936) and, considering the extensive area of deep water separating Faroe from the contiguous haddock stocks of Iceland and off the north and west Scottish coasts, it is difficult to believe that haddock larvae carried off the Faroe plateau and possibly reaching these areas to settle subsequently are able to return. On this basis the Faroe stock would appear to be an almost classic case, in which any influence which disrupts the normal eddy system operating over the Faroe shelf will have very serious repurcussions on the size of the recruitment to the year class born in that year.

In the years 1950-53 inclusive an intensive investigation of this area was carried out by Scottish research vessels to sample the planktonic stages of the haddock. This material has been reported by Saville (1956) with particular reference to the demarcation of the spawning season and locations, and the assessment of egg

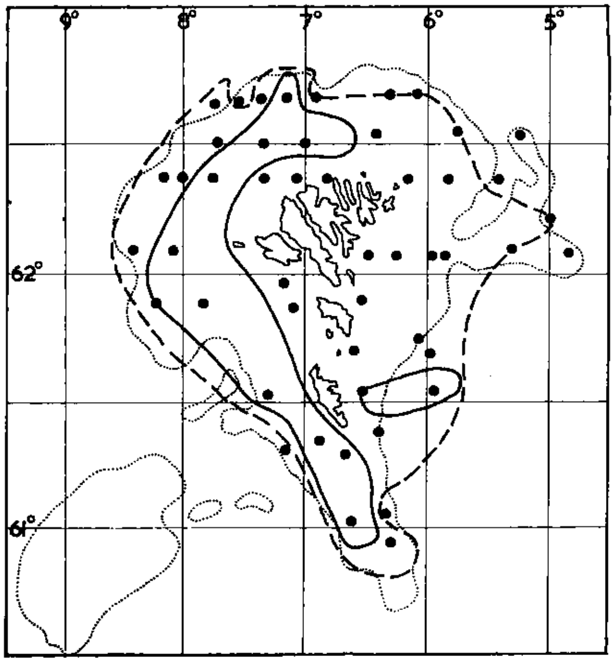


Fig. 3. Distribution of haddock larvae at Faroe, June 1953. Contour levels as in Figure 1.

production and of the subsequent larval mortalities in the different years. The favoured centres of spawning were markedly constant from year to year and it is noteworthy that they are situated near the edge of the shelf where the spawning products would seem particularly liable to displacement over the adjoining deep water. Unfortunately in all years the cruises were too widely spaced in time to allow the drift of the eggs and larvae to be traced in any great detail. Figures 1-3 however show the distribution of haddock larvae in June for the years 1950, 1952 and 1953. It is clear from these that in June, when the larvae are near the end of the planktonic phase in 1952 and 1953 a considerable body of haddock larvae was still present in the area, with a generalised distribution over the Faroe shelf such as one would expect from the operation of an eddy system around the islands. The 1950 picture is very different; larvae in that year were very scarce in the area, with the greater number on the eastern edge of the shelf in June. This situation in June was to some extent forecast by the May cruise of that year when, although a considerable body of larvae was still present within the area, they were very markedly concentrated to the east of the islands compared with the distribution in the same month in 1951. The distribution of the planktonic haddock stages over this period would seem to suggest that in the years 1951-53 the bulk of them were retained within the Faroe plateau but that in 1950 there was a major loss of these spawning products over the deep water to the east. The same may also have been true of cod larvae which were also markedly scarce in June 1950 compared with 1952 and 1953.

From these data the best index of recruitment to the adult stock was considered to be the abundance of larvae in June when they were nearing the end of the planktonic phase. As these covered a variable size range between years, from the calculated mortality and growth rates their abundance were first converted to the equivalent numbers at a standard size and then to the mean number at this size below 10 sq m of surface. The figures so derived, for the years 1950, 1952 and 1953, showed a satisfactory degree of agreement with the strength of these broods in their first year of life assessed from trawl surveys, and published by Jones (1951) and Jones and Main (1953, 1954). This suggests that in these years at least there is no appreciable differential loss of haddock larvae from the area after June and, as the assessment of juvenile haddock is a satisfactory index of their subsequent strength throughout their fishable life, that any loss from the area through larval drift is not subsequently made good by a compensatory return migration during the adolescent or adult phase.

Thus from these data it appears that the planktonic haddock spawning products at Faroe are normally retained within the eddy system overlying the Faroe plateau and that their abundance there late in the planktonic stage gives a valid index of the resultant year-class strength. In 1950 however there was a marked scarcity of haddock larvae within the area in June and the resulting year-class was a poor one. Events during the planktonic stage make it probable that this scarcity of larvae was due to many having drifted out of the area and over the deep water to the east. The most likely force to bring about such a distortion of the normal circulation pattern seemed to be persistent winds from the west. Wind directions and strengths for Faroe are available in the daily reports of the British Meteorological Service. These were plotted during the course of the planktonic phase of the haddock (March-June) and resultants calculated for each month. Normally one quarter of the annual production of haddock eggs are present in the area in March and the total has been produced by the end of April. As March winds must therefore exert a lesser effect than those of the ensuing months the strength of the March resultant was reduced to one quarter of its real value. The resultant for the season as a whole was then calculated and the water transport assessed on the assumption that it would be 45° to the right of the wind direction. The easterly component of transport was then calculated for each of the years on a comparative basis taking 1953 as a standard with an arbitrary value of 1.

These data are given in Table 1 along with the assessment of haddock larval abundance in June for those years in which the area was sampled in that month, and the abundance of haddock in their first year of life from trawl surveys given by Jones (1951) and Jones and Main (1952, 1953, 1954).

TABLE 1.—EASTERLY WIND COMPONENT AND ABUNDANCE OF FAROE HADDOCK AS LARVAE AND AS 1-GROUP.

Year	Easterly wind component	Larvae abundance in June	Abundance of haddock as 1-group
1950	14.8	1.2	228
1951	-25.0	?	538
1952	6.0	2.4	488
1953	1.0	2.7	495

The data are admittedly based on a very short series of years but they do suggest that a persistence of strong winds from the west is inimical to the retention of haddock larvae in the Faroe area and to the subsequent recruitment to the demersal stocks.

This situation at Faroe seems to parallel closely that of haddock on Georges Bank. There too there is a considerable population of spawning haddock more or less surrounded by natural hazards; by high temperatures to the southwest; by oceanic depths along the southern edge; and by deep water and muddy bottom along the northern edge. On the eastern edge is a deep channel which probably forms at least a partial trap on that side (Walford, 1938). Chase (1955), by using the winter temperatures to estimate the time of the spawning season and calculating the off-shore wind component for the period of planktonic life so assessed, got a very satisfactory correlation with the brood-strengths of haddock for the 24 years for which brood-strength data were available.

NORTH SEA HADDOCK

Considerable interest was aroused in the part played by wind induced transport of fish larvae in the North Sea following on the work of Carruthers and his collaborators. These authors presented a series of correlations between fluctuations in wind direction and strength and the strength of the corresponding year-class of various species of commercial fish (Carruthers, 1950; Carruthers *et al.*, 1951; Carruthers *et al.*, 1951; Veley, 1951). The mechanism underlying these correlations was in no case categorically stated but in general terms it was inferred that the surface currents induced by the winds controlled whether the larvae were dispersed into environments favourable or unfavourable for survival.

In particular for North Sea haddock the close correlation found between the wind function used and resulting year-class strength led to the suggestion that the poor brood survival found with south-westerly winds was due to the planktonic spawning products being carried by the surface currents induced by such winds, north-eastwards into the north-going stream along the Norwegian coasts. Winds from other quarters were in general found to be favourable and this was explained as being the result of dispersion over the main body of the North Sea, which is the customary haddock nursery area.

In the period 1952-57 research vessels of the Department of Agriculture and Fisheries for Scotland carried out a series of cruises to investigate the planktonic stages of haddock in the northern North Sea and in particular to trace their drift and its variations from year to year. The material collected on these cruises has already been reported by Saville (1959). The most striking conclusion arrived at from this investigation was that any drift of the planktonic haddock stages in the northern North Sea, at least during the years covered by the investigation, was extremely small. In Figures 4 and 5 are shown the distributions on successive cruises of eggs and the resulting larval stages in 1955 and 1956. The other years investigated gave very similar distributions. It will be seen that any transport which took place must have been exceedingly small and certainly inadequate

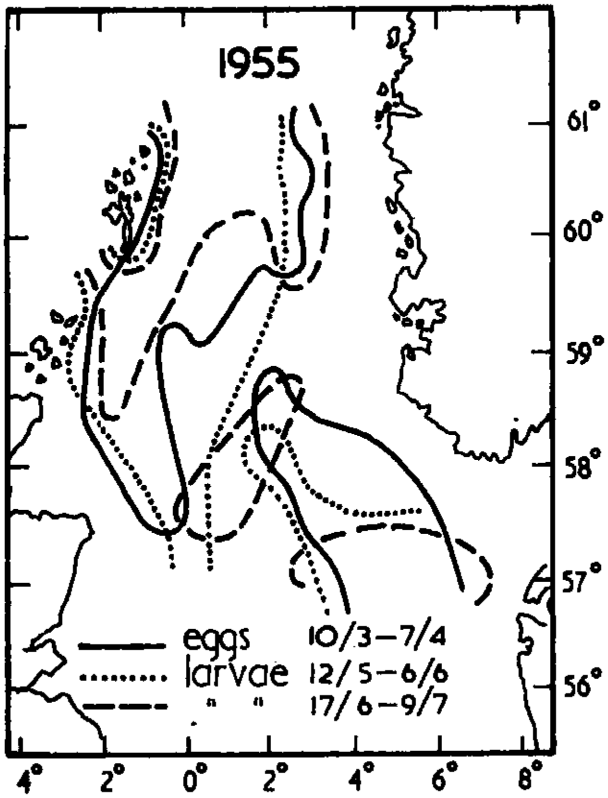


Fig. 4. Distribution of haddock eggs and larvae in the North Sea on successive cruises, in 1955.

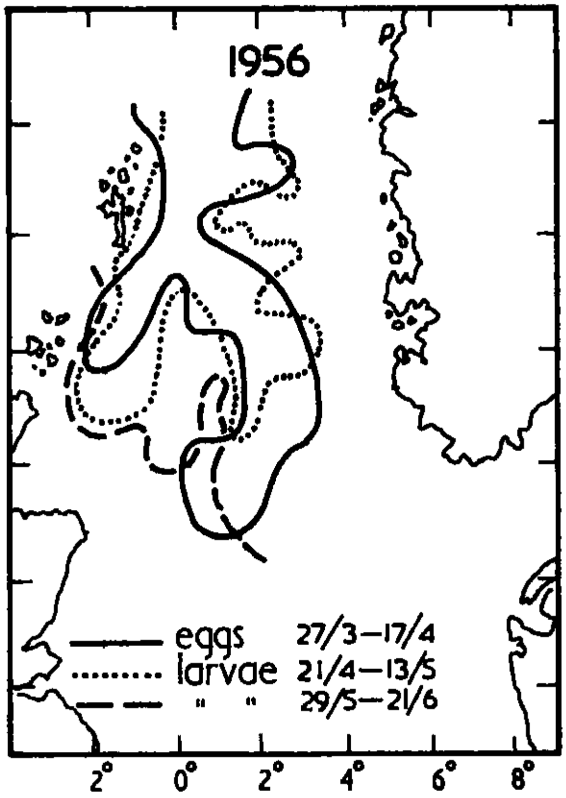


Fig. 5. Distribution of haddock eggs and larvae in the North Sea on successive cruises, in 1956.

to account for major variations in year-class strength. In Table 2 are given the average northerly and easterly components of the wind for the months April-June inclusive for each of the years investigated and the strength of the south-west component over these three months all in terms of sea miles per day.

TABLE 2.—ANNUAL VARIATIONS IN WIND IN APRIL-JUNE OVER NORTHERN NORTH SEA 1952-57.

1952			1953			1954			1955			1956			1957		
N	E	SW	N	E	SW	N	E	SW	N	E	SW	N	E	SW	N	E	SW
-73	-120	140	-23	-36	42	- 8	-75	61	+ 39	-93	40	+ 28	-95	46	+ 57	-82	18

With the exception of 1952, with a very large component of wind from the S.W., and 1957 with a rather small one, there was not much variation in this respect between the various years. The year class of 1952 was a fairly good one - up to the mean of the series of good broods produced between 1951 and 1955. On the other hand 1956 and 1957 were both particularly poor broods. On this limited evidence it would seem that winds from the south-west bear little relation to brood prospects and, in view of the rather static distributions of haddock spawning products found over these ranges of wind strength and direction, it would seem doubtful whether wind plays any major part in inducing transport in the North Sea. Steele (1957), discussing the hydrography of the northern North Sea in spring and summer, states that in this area at this time the water below the thermocline is relatively stationary. Above the thermocline the dominating influence is the westwards spread of low salinity water coming from the Baltic out-flow. The fact that this spread is in the opposite direction from that of the prevailing wind implies that the wind effect is not predominant. It is probable that the balance produced between this westwards spread and the westerly wind component accounts for the relatively static distributions of haddock eggs and larvae found in this area.

Rae (1957) was able to relate the distribution of *Metridia* in the northern North Sea in the winter months to the direction and strength of the prevailing winds and showed a relationship between the wind function at this time and the strength of the haddock brood born in the following spring. In autumn and winter the hydrographic picture in the northern North Sea is completely different from that of the spring and summer with the dominating influence being inflow of Atlantic water. The extent of the easterly spread of this water might well be affected by wind stress. Rae tentatively suggested that the principal effect of the wind function he used on haddock year-class strength was in orientating mixed oceanic-coastal water, of which *Metridia* is an indicator, over the haddock spawning grounds, and that such water provided a favourable environment for the development of the planktonic haddock stages. Saville (1959), using data on the distributions of plankton indicator species, was able to show a high degree of correlation between the proportion of the haddock spawning area occupied by such mixed water conditions and the size of the haddock broods over the period 1936-57.

CLYDE HERRING

Although not strictly applicable to a consideration of ground-fish stocks, the situation of the Clyde herring is of considerable interest in illustrating another situation where dispersion could play a major role in determining recruitment. The Clyde herring stock is a spring-spawning one with spawning taking place on Ballantrae Bank — a small bank of around 12 sq miles in extent situated near the entrance to the Clyde estuary. In addition to the fishery on the adult spawning shoals there is throughout the rest of the year a fishery within the estuary on adolescent fish and fish approaching first maturity. After spawning these fish leave the Clyde for feeding grounds off the Scottish west coast. The indications are that the Clyde adolescent fish recruit to the Clyde spawning stock and that the strength of a brood in its first and second years of life in the adolescent fishery is closely related to its subsequent strength as three year old first time spawners in the spawning fishery (Wood, 1960). This situation led to the hypothesis that the Clyde estuary formed a nursery ground for the recruits to the Clyde spawning shoals and that little if any recruitment to these shoals of first time spawners took place from any other nursery areas. In view of the situation of Ballantrae Bank — the major if not only spawning ground — it appeared highly probable that variations in direction and speed of drift could play a major role in determining year class strength. The situation of the spawning ground is such that minor variations in drift pattern could result in larvae going northwards into the Clyde estuary, southwards into the Irish Sea or westwards into the Atlantic and the Scottish west coast. If the interpretation of the stock characteristics is correct, then drift northwards into the Clyde would result in recruitment to the Clyde adolescent and subsequently to the Clyde spawning fishery whilst drift in other directions would mean poor recruitment to both branches of the Clyde fishery.

In 1957 a programme was commenced to investigate this situation and has been continued each year since. This programme took the form of a close grid of plankton stations over the spawning ground, repeated at short time intervals, to measure the production of larvae throughout the hatching season; and a grid of more widely spread stations, at less frequent intervals, to trace their subsequent dispersal. Each year, in the first fortnight of May, a survey of the upper reaches of the Clyde estuary was carried out to give a measure of the abundance of larvae, near the end of the planktonic phase in this region, as an index of recruitment to the Clyde stock.

In the 1958 season sampling over the spawning ground showed that over 90% of the season's hatching took place in the period 9th to the 15th March. Unfortunately sampling on the wider grids at this time was rather inadequate both in timing and in the extent of the area covered. The grids sampled on the 11th and 12th of March however both showed high concentrations of larvae over and to the south-west of the spawning area (Fig. 6). There was then a gap in the sampling until the 19th March. By then herring larvae were very scarce but the contoured distribution was suggestive of higher concentrations of larvae to the south and west of the area sampled (Fig. 7). In the remaining cruises of the 1958 season very few herring larvae were taken and the May cruise in the upper reaches of the estuary yielded the smallest numbers of herring larvae of any year in which the area was investigated.

The 1960 season showed a rather similar picture. The overwhelming preponderance of a fairly large hatching took place in the period 10th-18th March. A cruise covering a major part of the outer Clyde estuary on the 16th March yielded an abundance of early herring larvae with the contours open to the west and south of the area sampled (Fig. 8). On the next cruise to this area between the

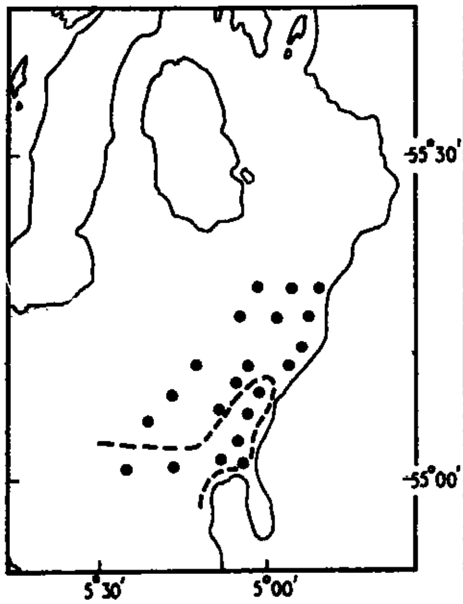


Fig. 6. Distribution of herring larvae in the Clyde on the 11th March 1958. Broken line 50 larvae per 15 min tow, 1 m net.

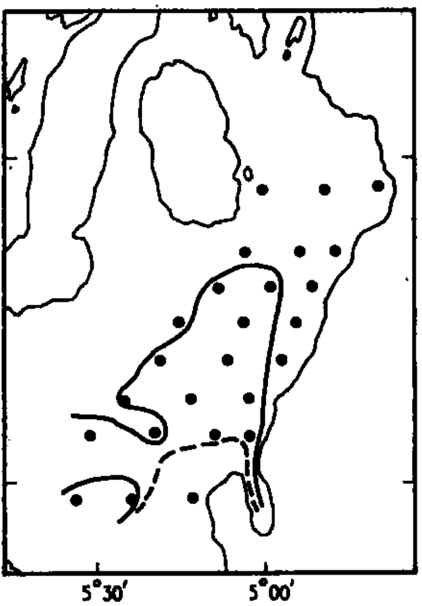


Fig. 7. Distribution of herring larvae in the Clyde on the 19th March 1958. Broken line 50 larvae, solid line 1 larva per 15 min tow, 1 m net.

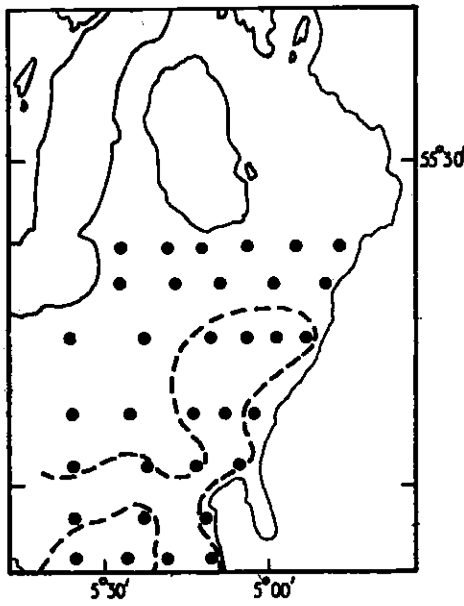


Fig. 8. Distribution of herring larvae in the Clyde on the 16th March 1960. Broken line 50 larvae per 15 min tow, 1 m net.

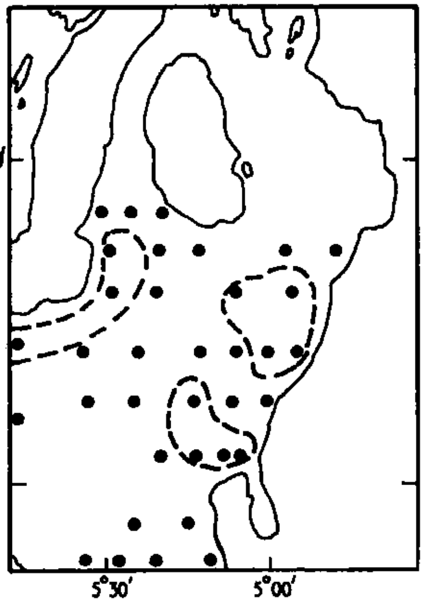


Fig. 9. Distribution of herring larvae in the Clyde on the 30th March 1960. Broken line 50 larvae per 15 min tow, 1 m net.

29th - 31st March the numbers of larvae had been very markedly reduced - giving an apparent mortality rate of almost 18% per day - and again there was evidence of a leakage of larvae westwards beyond the area sampled (Fig. 9). In 1959 and 1961 - the only other years for which the data have so far been completely analysed - the picture is rather different. In both years the centres of larval abundance on all cruises showed a marked restriction to the eastern part of the outer Clyde estuary and a steady progression northwards into the inner estuary between successive cruises (Figs. 10-12). In the years (1959, 1961) when the dispersal took place into the inner estuary the pattern is clear from the distribution on successive cruises. In the case of apparent dispersal outwith the area the evidence from this source is less conclusive - probably because of the short time it took the main body of larvae to drift from the spawning area to the limit of the surveyed area. As a result the distribution shown on succeeding cruises probably largely represents the proportion of larvae which were retained rather than the main body of larvae. This is supported by Fig. 13 which illustrates the reduction in larval numbers on succeeding cruises in each of the years considered. In 1958 and in 1960 larval abundance within the surveyed area suffered a very marked reduction within a short time of the main hatching peak with apparent mortality rates of 35% and 18% a day; in the years when dispersal was into the Firth the initial reduction in abundance was lower at under 10% per day.

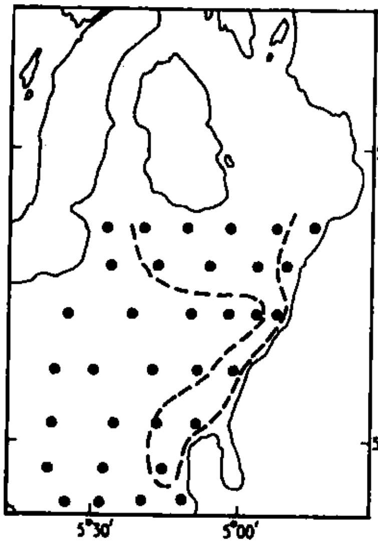


Fig. 10. Distribution of herring larvae in the Clyde on the 21st March 1961. Broken line 50 larvae per 15 min tow, 1 m net.

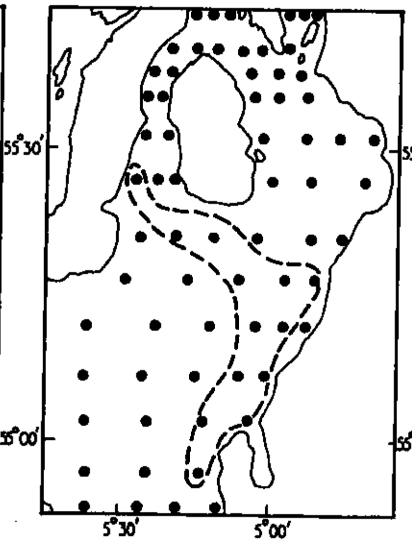


Fig. 11. Distribution of herring larvae in the Clyde on the 25th March 1961. Broken line 50 larvae per 15 min tow, 1 m net.

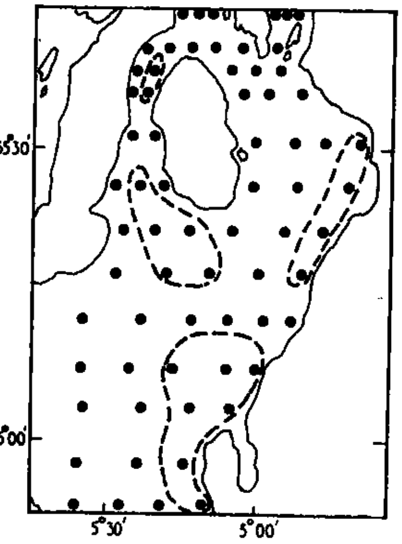


Fig. 12. Distribution of herring larvae in the Clyde on the 5th April 1961. Broken line 50 larvae per 15 min tow, 1 m net.

As previously mentioned, in the first fortnight of May in each year the upper reaches of the Clyde estuary were sampled to gauge the numbers of larvae which had reached this area. This number must be a function of three factors - initial number of herring larvae hatched in that year, larval mortality between the time of hatching and the time of the survey, and the proportion of larvae which were transported northwards into the area. In the years considered there were very marked variations in the amount of hatching which took place. In order to estimate the proportion of larvae reaching the upper Clyde these have been allowed for by dividing the abundance of larvae in the inner estuary (expressed as the mean catch per haul) by the ratios of the hatching in the year in question to that of 1959 taken as a standard. The material on the amount of hatching in 1963 has not yet been fully analysed but a preliminary value has been assigned to that year from a cursory inspection of the samples. This will be at least of the right order of size. No correction can be made for mortality because of the absence of any criterion to distinguish between transport out of the area and mortality *sensu stricto*. If however transport is a major factor in determining recruitment to the upper estuary any relationship between factors inducing transport and the proportion of larvae reaching the upper estuary should emerge in spite of the effects of other causes of loss in disturbing the relationship.

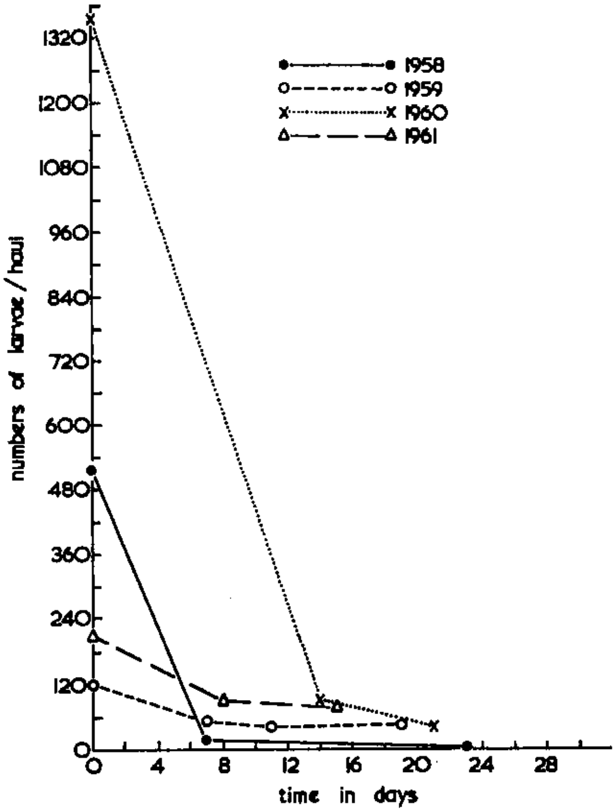


Fig. 13. Reduction in the abundance of herring larvae on succeeding cruises, 1958-1961.

These values for proportionate recruitment to the Clyde estuary are given in Table 3.

TABLE 3.—ABUNDANCE OF HERRING LARVAE IN CLYDE ESTUARY IN MAY 1957-63.

Year	Larval Abundance in May	Larval Abundance in May corrected for variations in hatching
1957	5.0	5.0
1958	0.05	0.01
1959	3.2	3.2
1960	7.1	0.8
1961	78.0	2.7
1962	1.0	0.3
1963	10.6	3.5(?)

It will be seen that in the corrected data the values for these years fall into two well-defined groups —1958, 1960 and 1962 with very low values and the remaining years with high values.

Additional information which supports the view that much of the variation in recruitment of larvae to the inner Clyde estuary is the result of water movements is supplied by drift bottle releases. In the years 1958-63 inclusive, whilst sampling of the spawning ground was in progress 10 drift bottles were released on each day the research vessel was over the spawning grounds. I am indebted to my colleague Mr R. E. Craig for information on the returns derived from these drift bottle releases. For the present purpose only returns from these releases made whilst hatching of herring larvae was in progress have been utilised. In Table 4 are given the number of drift bottles released during the period in each year, the number of returns from within the Clyde estuary and the numbers returned outwith the Clyde. These latter were principally from N. Ireland, the west coast of Scotland, and from the shores of the Irish Sea.

TABLE 4.—RETURNS OF DRIFT-BOTTLES RELEASED OVER CLYDE SPAWNING GROUNDS 1958-63.

Year	No. of D.B.'s released	No. returned from Clyde	Returns outside Clyde	% of returns from Clyde
1958	70	2	10	17
1959	80	26	0	100
1960	60	4	11	27
1961	35	15	0	100
1962	75	11	11	50
1963	90	33	0	100

These data show that the years also fall into the same two well-defined groups - 1959, 1961 and 1963 when all the returns came from the Clyde and 1958, 1960 and 1962 when half or more of the returns came from outwith the Clyde estuary. In 1957 when this work in the Clyde was begun the programme was more of an exploratory nature. In that year drift bottle releases were widely spread over the south-eastern part of the outer estuary and took place in two periods only, namely 4-5th March and the 25th-26th March. The returns from the releases of that year have already been reported by Craig (1959) who states: "The earlier releases suggested that most of these larvae would be carried into the Firth while the deduction from the second series is that most of the larvae produced near the later date would be carried out of the Firth". In view of the fact that the preponderance of hatching of herring larvae took place almost half way between these two release periods this information is not in itself of much value in deciding the role played in larval dispersion by water transport in that year (see however p.345).

In view of the major role played by wind in determining water movement wind data were extracted from the Daily Weather Reports of the British Meteorological Office. These give observations, at six hourly intervals, of wind direction and speed in knots at certain specified stations. For this purpose the observations selected were those taken at Renfrew, as being the closest to the Clyde area, and an arbitrary choice was made of the observations taken at 1200 hours on each day as being reasonably representative of the twenty-four hour period. For this purpose the daily wind values were considered over a three-week period, chosen to cover the three weeks occurring immediately after the inception of considerable hatching in that year. This period was chosen because experience of the course of hatching during the spawning seasons sampled, and the speed of drift experienced, suggested that this would be the maximum time necessary to determine whether the bulk of the season's production of larvae would reach the inner Clyde estuary or be lost to it. The winds for the days so selected were plotted in direction and strength and the northerly and easterly components for each week were calculated. These are given in Table 5.

TABLE 5.—NORTHERLY AND EASTERLY WIND COMPONENTS IN CLYDE DURING HATCHING PERIOD 1957-63.

Year	Week 1		Week 2		Week 3		Mean	
	N	E	N	E	N	E	N	E
1957	6.7	- 6.3	3.6	+ 0.8	3.8	+ 1.7	4.7	- 1.3
1958	1.8	+ 7.3	0.8	+ 6.7	- 1.0	+ 6.0	0.5	+ 6.7
1959	1.0	- 6.0	5.7	- 0.5	2.7	- 1.0	3.1	- 2.5
1960	0.5	+ 6.3	- 2.0	+ 6.7	- 1.0	+ 7.7	- 0.8	+ 6.9
1961	2.3	- 7.3	1.7	- 9.0	0.8	- 4.3	1.6	- 6.9
1962	- 0.3	+ 3.5	- 1.0	+ 0.8	0.3	- 1.1	- 0.3	+ 1.1
1963	2.7	- 0.5	- 2.0	- 4.7	0.3	+ 0.5	0.3	- 1.6

It will be noted that, as in the larval data of Table 3, and the drift bottle release data of Table 4, the years 1958, 1960 and 1962 are distinguished as being years with a prevalence of winds from the east, and with a weak northerly component, in contrast to the other years when the prevailing winds were from the west. This relationship would however seem to be of a qualitative rather than a quantitative nature; the particularly strong component of wind from the west in 1961, with a particularly low northerly value, did not result in an improved recruitment to the inner Clyde in that year when compared with the years of less strong westerly components; similarly the rather weak easterly component of 1962 appears to have been as deleterious as the much stronger one of 1960. This is only to be expected in view of the other factors which must play a part in controlling larval survival.

In view of the apparent relationship between wind and drift bottle returns shown in Tables 4 and 5 it seemed worth re-examining the wind data for 1957 in the light of Craig's (1959) drift bottle results. This showed winds consistently from the west in March up to the 22nd of that month with a reversal thereafter for the remainder of the month into winds from the east. It would appear likely therefore that the change in the current system in the Clyde, which Craig found between the 5th and the 25th March, took place probably as late as around the 22nd March. By that time the main hatching of herring larvae was over and the current system depicted by Craig for the first series of releases probably played the major role in determining larval drift. From this evidence, 1957 would fall into the same group as the years 1959, 1961 and 1963 (Table 4). Barnes and Goodley (1961), also concluded that the pattern of surface drift in the Clyde is markedly wind dependent.

There thus seems to be reasonably strong evidence that the direction of dispersal of spring-spawned larvae from Ballantrae Bank is largely determined by the east-west and north-south wind component over a short period after hatching and that this influences the abundance of later stage herring larvae in the inner reaches of the Clyde. It would seem however that the abundance of such larvae in this area is by no means a criterion of future year-class strength in the commercial fishery. In Table 6 are given the catch per unit effort of each of the year classes investigated in their planktonic phase which have so far recruited to the fishery as adolescents between 1 and 2 years old and as recruit spawners spawning as 3 year olds. These were computed from routine landing statistics and from the age composition of the landings assessed from one or two random samples taken each week.

TABLE 6.—CATCH PER UNIT EFFORT OF YEAR CLASSES OF CLYDE HERRING.

Year Class	Catch/effort as 1+ fish	Catch/effort 3 year old spawners
1957	10.28	17.22
1958	14.38	5.84
1959	2.13	0.32
1960	5.87	0.41
1961	7.80	?

The two indices of year class strength are not in as close agreement as one might wish - particularly with respect to the low index of the 1958 brood as spawners compared with their abundance in the adolescent fishery. This has also been a feature of this year class in subsequent years and deserves further investigation. Both of these indices however are in agreement in marking 1958 as a successful year class in the scale of this series of years and 1959 as a very poor one, in contrast to their rating in Table 3. The evidence from these data with regard to the 1958 year class would suggest therefore that drift out of the Clyde is not necessarily inimical to the prospects of a year class and presumably a return movement may take place during the post-planktonic stage. A comparison of the data of Tables 3 and 6 would also suggest the possibility of considerable differential mortality between year classes in a late planktonic or post planktonic stage in herring.

DISCUSSION

The early work of Carruthers (1937) and Carruthers and Hodgson (1937) suggested a relationship between both year-class strength of North Sea haddock and Southern Bight herring and the wind regime prevailing during the planktonic stages in the life-cycle. This suggestion of a relationship between brood-strength and wind was further formalised and extended to cover a wider range of species in the post-war papers of Carruthers and his collaborators. A similar relationship between wind and year-class strength was demonstrated for Georges Bank haddock by Chase (1955). In spite of these apparent associations between wind and brood strength, there appear in the literature to be few authenticated cases of a direct effect of wind on the transport of eggs and larvae. In particular successful predictions have been few, although Graham (1925) was able, in a very generalised way, to predict the distribution of cod larvae in the central North Sea in one year from a consideration of wind direction and strength.

In the present paper some evidence is produced that under an unusual wind regime the normal distribution of haddock larvae at Faroe is disrupted, and for herring larvae in the Clyde the effect of wind variations on larval transport seems well authenticated. In the North Sea haddock, on the other hand, wind variation, within the range found in the years investigated, seems to have no appreciable effect on larval transport. It would appear, on this evidence, that only in certain situations, where comparatively minor variations in wind from the normal pattern can produce wide ranging effects is wind variation likely to produce marked differences in dispersal pattern. One such situation is where isolated stocks occupy banks of small extent when short periods of persistent winds from one quarter can push the planktonic fauna overlying the bank over oceanic depths or into well-defined stream currents. This situation is well illustrated at Faroe and on Georges Bank. In the north Atlantic there are several such banks which maintain what are apparently self-contained stocks of ground fish. Fraser (1958) has discussed the problem of the retention of the planktonic stages within the habitat of the stock in such situations. It is of interest in this connection that what little is known about the population structure in such habitats suggests that year-class fluctuations are more violent than in populations with less restricted distributions. This would seem to be so for the haddock stocks on Porcupine Bank in the north-east Atlantic (Hickling, 1946) and on St. Pierre Bank in the north-west Atlantic (Beverton and Hodder 1962).

The Clyde situation is probably a peculiar case where comparatively slight northwards transport brings the larvae within the sheltering arms of the Firth while initial southerly or westerly transport of limited extent results in larvae being carried into a current system which militates against subsequent return in the planktonic phase. Even here however there seem to be no demonstrable relationship with the subsequent number of recruits to the commercial shoals.

REFERENCES

BARNES, H. and E.F.W. GOODLEY, 1961. The general hydrography of the Clyde Sea Area, Scotland. Part 1: Description of the area; drift bottle and surface salinity data. *Bull. Mar. Ecol.*, 5: 112-150.

BEVERTON, R.J.H. and V.M. HODDER, 1962. Report of working group of scientists on fishery assessment in relation to regulation problems. *I.C.N.A.F. supplement to Annual Proc.* Vol. 11.

BODEN, B.P.,1952. Natural conservation of insular plankton. *Nature, Lond.*, 169 : 697-699.

CARRUTHERS, J.N. 1937. A note on plaice fluctuations in the southern North Sea. *Rapp. Cons. Explor. Mer*, 105: 14-15.

1950. An attitude on fisheries hydrography. *J. Mar. Res.*, 10: 101-118.

CARRUTHERS, J.N. and W.C. HODGSON, 1937. Similar fluctuations in the herrings of the East Anglian fishery and certain physical conditions. *Rapp. Cons. Explor. Mer*, 105: 10-13.

CARRUTHERS, J.N., A.L. LAWFORD, and V.F.C. VELEY, 1951. Fishery hydrography: brood strength fluctuations in various North Sea fish with suggested methods of prediction. *Kieler Meeresforsch.*, 8: 5-15.

CARRUTHERS, J.N. *et al.* 1951. Variations in brood strength in the North Sea haddock, in the light of relevant wind conditions. *Nature, Lond.*, 168 : 317-319.

CHASE, J. 1955. Winds and temperatures in relation to brood strength of Georges Bank haddock. *J. Cons. int. Explor. Mer*, 21: 17-24.

CRAIG, R.E. 1959. *Ann. biol. Copenhague*, 14 (1957) : 63.

FRASER, J.H. 1939. The distribution of chaetognatha in Scottish waters in 1937. *J. Cons. int. Explcr. Mer*, 14: 25-34.

1958. The drift of the planktonic stages of fish in the northeast Atlantic and its possible significance to the stocks of commercial fish. *Spec. Publ. int. Comm. Northw. Atlant. Fish.*, No. 1, 289-310.

GRAHAM, M. and J.N. CARRUTHERS, 1925. The distribution of the pelagic stages of the cod in the North Sea in 1924 in relation to the system of currents. *Fish. Invest., Lond.*, *Ser 2*, 8 (6): 1-31.

HANSEN, V. 1955. Zooplankton and hydrography in the southern part of the Norwegian Sea. *Cons. int. Explor. Mer, C.M. 1955, Plankton Committee* No. 29.

HICKLING, C.F. 1946. Haddock on Porcupine Bank, September 1944. *J. mar. biol. Ass. U.K.*, 26: 398-407.

HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *Rapp. Cons. Explor. Mer*, 20: 1-228.

JONES, R. 1951. *Ann. biol., Copenhague*, 7:(1950): 28-31.

JONES, R. and W. MAIN. 1952. *Ann. biol., Copenhague*, 8(1951): 36-39.

1953. *Ann. biol., Copenhague*, 9(1952): 35-38.

1954. *Ann. biol., Copenhague*, 10(1953): 32-35.

ORTON, J.H. 1937. Some interrelations between bivalve spatfalls, hydrography and fisheries. *Nature, Lond.*, 140: 505.

PARRISH, B.B. 1950. Brood fluctuations in the North Sea haddock population. *Challenger Soc. Abstracts*, 3 (2): 18.

RAE, K.M. 1957. A relationship between wind, plankton distribution and haddock brood strength. *Bull. Mar. Ecol.*, 4: 247-69.

RAITT, D.S. 1936. The haddock stocks of the north-east Atlantic, 1916-35. *Sci. Invest. Fish. Scot.*, *1936*, No. 1: 1-32.

SAVILLE, A. 1956. Eggs and larvae of haddock at Faroe. *Mar. Res. Scot., 1956*, No.4: 1-27.

1959. The planktonic stages of the haddock in Scottish waters, *Mar. Res. Scot., 1959*, No. 3: 1-23.

STEELE, J.H. 1957. The role of lateral eddy diffusion in the northern North Sea. *J. Cons. int. Explor. Mer*, 22 : 152-62.

TAIT, J.B. 1934. Surface drift-bottle results in relation to temperature, salinity and density distributions in the northern North Sea. *Rapp. Cons. Explor. Mer*, 89: 68-79.

VELEY, V.F.C. 1951. Fishery hydrography; brood strength fluctuations in the hake with a suggested method of prediction. *Ann. Biol. Copenhague*, 7(1950): 44-46.

WALFORD, L.A. 1938. Effects of currents on distribution and survival of the eggs and larvae of haddock (*Melanogrammus aeglefinus*) on Georges Bank. *Fish. Bull. U.S.*, 49 (29): 1-73.

WILSON, D.P. 1948. The relation of the substratum to the metamorphosis of Ophelia larvae. *J. mar. biol. Ass. U.K.*, 27: 723-60.

WOOD, H. 1960. The herring of the Clyde estuary. *Mar. Res. Scot., 1960:* No. 1, 1-24.

B-7

COMPARATIVE CHARACTERISTIC OF SOME BIOLOGICAL INDICES OF THE BOTTOM STAGES OF 0-GROUP COD BELONGING TO THE 1956, 1958, 1959, 1960 AND 1961 YEAR-CLASSES.

By

I.Ja. Ponomarenko[1]

ABSTRACT

Annual fluctuations in the fatness and nutritional condition of cod fry in the southern part)f the Barents Sea are governed by the availability of Euphausiacea in their food, the main item of :he diet of the 0-group of cod. The more Euphausiacea there are in their food, the higher is the level of fatness and nutritional condition of the fry.

The length of cod fry at the end of the first year of life is closely related to the tempera:ure conditions in a given year. In warmer years the fry grow faster than in colder ones. Due to :he annual fluctuations in length and condition of fry, their accessibility to small predators (for instance the young cod of age groups I, II and III) changes from year to year. The smaller and less nourished are the fry, the more can predators feed on them.

Feeding conditions and the thermal regime of the sea, affecting growth indirectly (through predators), influence the mortality of the fry; that is, the formation of the year-class strength. Due :o the faster growth rate of the 0-group, the conditions for maintaining the strength of a year-class)f cod at a high level are better in warmer years than in colder ones, all other conditions being equal, particularly the feeding conditions.

To determine the factors influencing variations in the amount of fish recruited to the commercial stock of the Barents Sea cod, the Polar Institute (PINRO) annually carries out investigations on feeding, fatness, nutritional condition and sizes of the bottom stages of 0-group cod.

In this report the following indices for cod fry belonging to the five generations are compared:

1) food composition (weight in %);
2) stomach fullness index in $^{o}/ooo$ (the relation of food weight to fish weight multiplied by 10000, *i.e.*, per decimille);
3) fatness (the relation of liver weight to fish weight in %);
4) nutritional condition (the relation of the weight of a fish to the long-term mean weight of fish of the same length in %);
5) mean length (in cm);
6) the importance of the bottom stages of 0-group cod to the feeding of cod fry of the I-II-III age groups in November-December.

These indices are compared with the abundance of the bottom stages of 0-group cod belonging to :he given year-classes and with the temperature anomalies occurring along the Kola hydrological sec:ion. The materials were collected by PINRO research vessels in November-December of 1956 and 1958 :o 1961 to determine the abundance of the young of the commercial fishes. The 25-meter bottom trawl with a fine-mesh net (10 mm), inserted into the codend was used. The quantitative analysis of young :od is carried out annually in the autumn-winter period in the Barents Sea. From the catch of the bottom stages of 0-group cod per hour, one can determine the abundance of a year-class at the first year of life. The data on catches of fry per hour's trawling are taken from the work of A.S. Baranenkova.

---

[1] Polar Research Institute for Marine Fisheries and Oceanography, Murmansk, USSR.

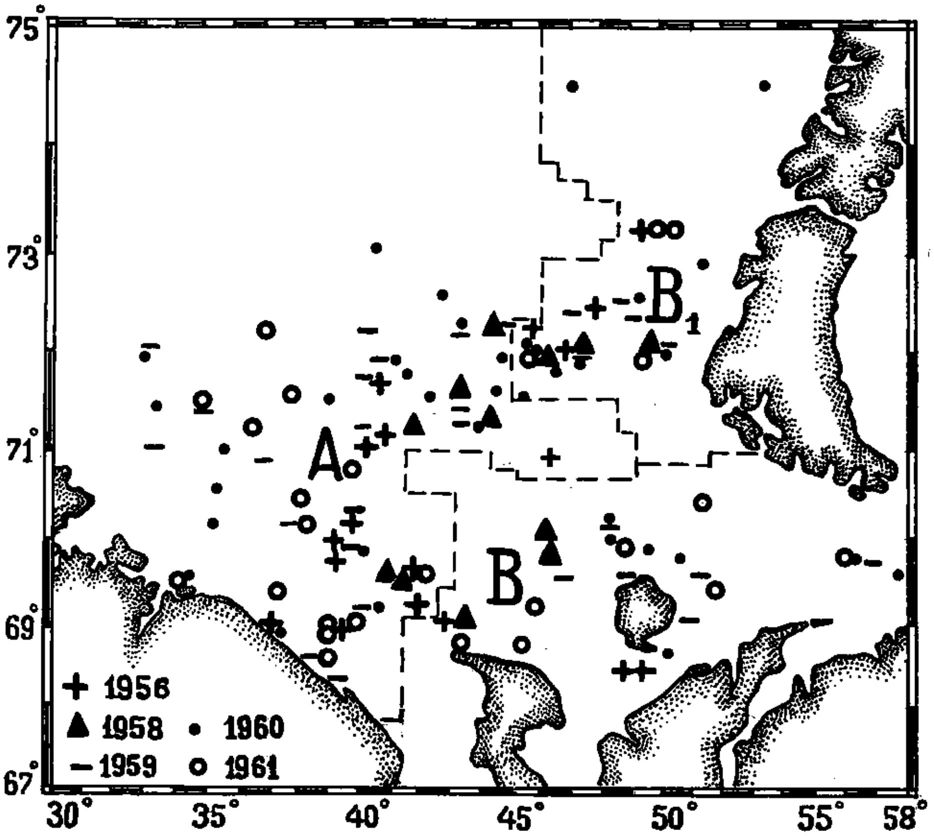


Fig. 1. Areas where samples of 0-group cod were taken for the analysis of food, fatness and nutritional condition. The dotted line separates the Central Zone (A) from the South-eastern (B) and North-eastern (B_1) zones.

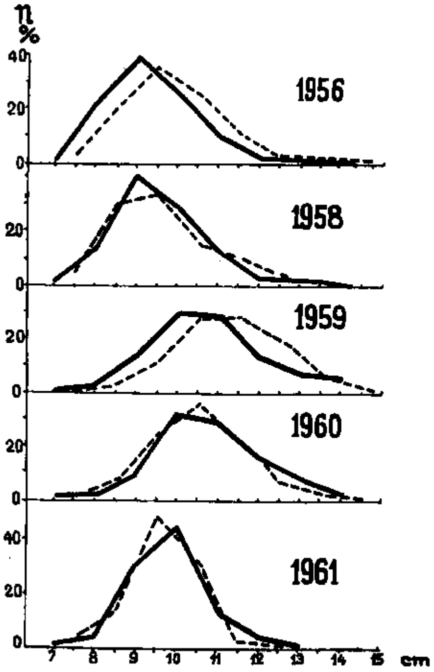
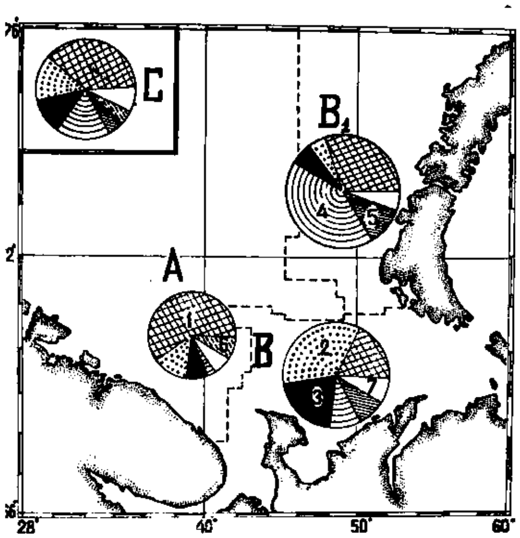


Fig.2. The size composition of the fry of 0-group cod which were examined (dotted line) and of all the 0-group fry caught by trawl during the period of the study.

Samples were collected from the Murman Coast to Novaya Zemlya Bank (Fig. 1). The length composition of the fry examined and of all fry of the 0-group taken with a trawl is given in Figure 2.

Euphausiacea (32.5% by weight), Gammaridea (15.6%), Polychaeta (10.6%) and Pisces (17.4%) were the main food items of cod fry over the average period of five years in the near-bottom layers of the Barents Sea (Figs. 3 and 4). Appendicularia (4.9%), Hyperiidea (4.5%), Decapoda (4.3%), Chaetognatha (4.1%), Mysidacea (2.0%), Cumacea (0.6%), Caprellidea (0.5%), Isopoda (0.4%), and others are of secondary importance in the food of cod fry. A total of 101 species were found in the stomachs of 0-group cod.

Local differences are traced in the feeding of the bottom stages of cod fry. On these grounds we can divide the southern part of the Barents Sea into the three conventional zones (Figs. 1, 3, 4 and 5): Central (A), where the main fry food is Euphausiacea; South-eastern (B), where Gammaridae and Polychaeta prevail; and North-eastern (B_1), where the fry of *Boreogadus saida* and the young of *Lumpenus* are the dominant food objects. All the quantitative data on feeding, represented in Figures 3, 4 and 5, were calculated separately for each of the three zones and for the whole sea.



ig. 3. Food composition (as % by weight) of the bottom stages of 0-group cod according to the five year observations:
A-in the Central zone;
B-in the South-eastern zone;
B_1-in the North-eastern zone;
C-all zones combined;
1. Euphausiacea (together with Hyperiidea and Mysidacea):
2. Gammaridea (together with Caprellidea, Cumacea and Isopoda);
3. Polychaeta;
4. Pisces;
5. Appendicularia;
6. Chaetognatha;
7. Others.

The radius of each circle is in proportion to the average index of stomach fullness.

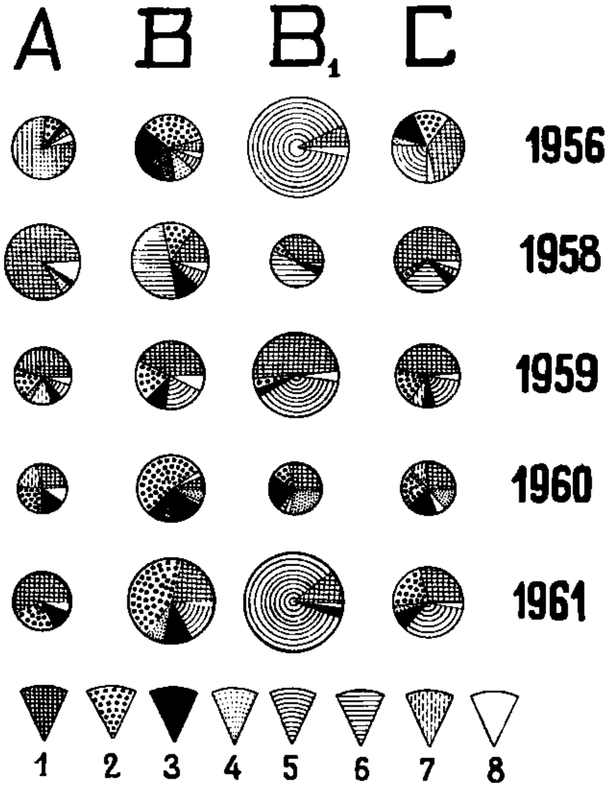


Fig. 4. Food composition (as % by weight) of the bottom stages of 0-group cod of the 1956, 1958-61 year-classes. The zones (A - C) and organisms (1-7) are the same as those shown in Figure 3.

Food composition of cod fry in 1956 and 1958 to 1961 is shown in Figure 4; fatness (I), nutrit-onal condition (II), stomach fullness index (III) and the single index of Euphausiacea (the relation f the weight of the Euphausiacea eaten to fish weight in %) are presented in Figure 5. The percen-age of feeding specimens did not differ greatly from one year to another (from 76% to 86.3%) and ver the course of five years it averaged 82.8% in the Central zone, 83.8% in the South-eastern zone nd 82% in the North-eastern zone.

Most of the material was collected in the Central zone, where the greatest abundance of the bot-om stage of 0-group cod occurred in the years investigated (Fig. 5). Annual variations in fatness, utritional condition and stomach fullness index of 0-group cod in the Central zone are closely con-ected with the annual changes in importance of Euphausiacea in the diet of fry. Thus, the highest in 1958) and the lowest (in 1960) fatness, nutritional condition and stomach fullness index cor-espond to the greatest (98°/ooo in 1958) and the least (7.8°/ooo in 1960) importance of Euphausiacea n the food of fry (Fig. 5, A.I,II,III). The importance of Euphausiacea in the diet of fry deter-ines the annual variations in fatness and nutritional condition of the bottom stages of 0-group cod n the southern part of the Barents Sea. The stomach fullness index, fatness and nutritional con-ition of cod fry belonging to the moderately abundant 1956, 1958, 1959 year-classes were similar. he relative importance of Euphausiacea in the food of fry was approximately the same during these ears (special index 39.2, 51.7 and 48.8 respectively). The fry of the 1960 and 1961 year-classes ccurred in low numbers in the southern part of the Barents Sea and were characterized by lower

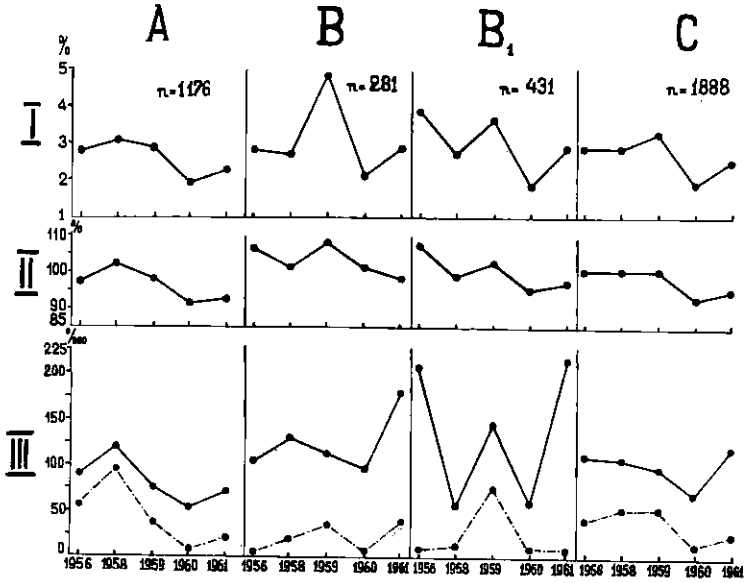


Fig. 5. Quantitative index of feeding of the bottom stages of 0-group cod in November/December. The zones (A - C) are the same as those shown in Figure 3.
I - Fatness.
II - Nutritional condition.
III - Total index of stomach fullness (solid line).
Index for Euphausiacea (broken line).

fatness, and nutritional condition, which corresponded to the lesser importance of Euphausiacea in the food of cod (Fig. 5, C, I, II, III Table 1). Probably, Euphausiacea play a great part in the diet not only of the bottom but also the pelagic stages of 0-group cod. This assumption is confirmed by the PINRO data on feeding of the pelagic fry of cod (Sysoeva and Degtereva, 1964, and Wiborg's data, 1960). The transition of cod fry to the near-bottom life is evidently closely associated with the descent of Euphausiacea to the bottom layers.

For the five years investigated, the three values change almost in parallel from one year to another: 1) importance of Euphausiacea in the diet of 0-group cod at the bottom stages; 2) nutritional condition of 0-group cod; 3) abundance of 0-group cod. Such interdependence can probably be explained by the drift of cod fry and the young of Euphausiacea from the west to the east and by the greater survival-rate of cod fry during the years when the young of Euphausiacea are abundant. However, further investigations are necessary.

No link was traced between the temperature conditions during the year and the quantitative data on the feeding of the bottom stages of 0-group cod. Thus, in the cold years (1956 and 1958), when the annual temperature anomalies in the 0-200 m layer in the Kola section were -0.65° and -0.58°, and in the relatively warm year (1959), the fry of cod had similar stomach fullness index, fatness and nutritional condition. In 1959 and 1960, when similar temperature conditions occurred (anomalies +0.18° and +0.17°C), the fatness and nutritional condition indices of fry strongly differed (Fig. 5). However, a close relationship between the sizes of cod fry in November-December, and the temperature in February-October was found (Fig. 6). The growth rate of 0-group cod was somewhat lower in the cold years than in the warm years. In November-December, the average length of fry of the 1956 and 1958 year-classes was 9.29 and 9.57 cm and of fry of the 1959 and 1960 year-classes was 10.79 and 10.81 cm. Temperature and the length of fry are average for the other years, 1957, 1961 and 1962.

One of the most numerous small predators of cod fry in the bottom layers of the Barents Sea is small cod of the I, II and III age groups (length 15-35 cm). The importance of fry in the diet of cod of these age groups depends upon the abundance of the 0-group, and also upon the length and nutritional condition of fry. Our data show that in November-December the small cod feed mainly on cod fry not over 10 cm in length (Ponomarenko, 1961). The larger fry, however, are fed on only if they have a low nutritional condition value. The fry of the 1956 and 1958 year-classes, having the lowest length, and the fry of the 1960 year-class, having the lowest nutritional condition, were eaten in the greatest quantity. The large fry of the 1959 year-class, with high value for nutritional condition, were eaten in the smallest quantity. (Table 1). If one now considers the small size and low nutritional condition of fry of the 1961 year-class, one would expect these fry to be found in numbers in the stomachs of cod of the I, II and III age groups. The fry of this generation were, in fact, fed upon in small numbers. This is another demonstration of the low abundance of the 1961 year-class in the southern part of the Barents Sea. Thus, in the years when the bottom stages of 0-group cod are small or in low nutritional condition or both, they become more available to the predators and the number of predators which are able to live on the fry in the bottom layer increases.

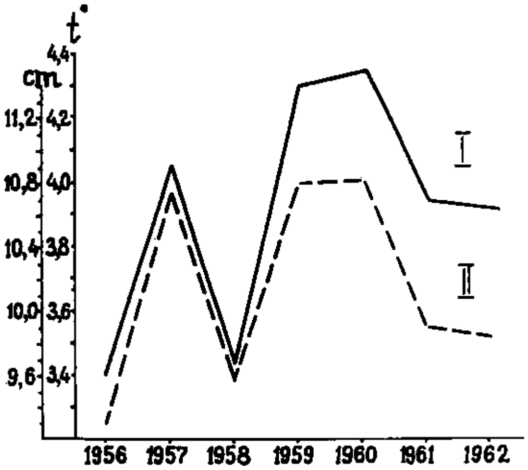


Fig. 6. Relation between the mean water temperature (I) in the 0-200 m layer in February/October (along the Kola section) and the mean length of the bottom stages of 0-group cod in the Southern part of the Barents Sea in November/December (II).

TABLE 1.—THE IMPORTANCE OF THE BOTTOM STAGES OF 0-GROUP COD IN THE DIET OF COD FRY OF AGE GROUPS I, II AND III* IN COMPARISON WITH THE ABUNDANCE OF 0-GROUP FRY, THEIR SIZES AND NUTRITIONAL CONDITION.

Year-classes:	1956	1958	1959	1960	1961
Importance in the diet					
% by weight	42.8	55.0	4.4	20.7	5.2
occurrence	31.7	25.5	2.9	13.2	5.4
Average catch per hour of 0-group cod in the southern part of the Barents Sea	12	11	11	7	3
Average length of 0-group cod	9.29	9.57	10.79	10.81	9.9
Nutritional condition of 0-group in % of the long-term mean	100	100	100	93.1	94.0

The thermal regime of the sea and the feeding conditions of 0-group cod influence the sizes and nutritional condition of fry. The latter two indices determine the degree of fry mortality caused by the small predators. Owing to the more intensive growth of 0-group cod, their survival-rate in the warm years will be better than in the cold years.

---

* Samples for study of the feeding of cod fry of the I, II and III age groups, 15-35 cm in length, were taken in the same areas and in the same way as the samples for study of the 0-group feeding. Age-composition was approximately the same during all the years. A total of 2289 stomachs were examined. The analysis of stomachs was made by the quantitative-weight method.

REFERENCES

PONOMARENKO, I.Ja. 1961. On Possible Influence of Feeding of Cod Fry upon their Abundance. *Trud. Soveshch. ikhtiol. Kom.*, XIII.

SYSOEVA, T.K. and A.A. DEGTEREVA. 1964. The Relation Between the Feeding of Cod Larvae and Pelagic Fry and the Distribution and Abundance of their Principal Food Organisms. *This symposium, Contribution No. B-16.*

WIBORG, K.F. 1960. Investigations on Pelagic Fry of Cod and Haddock in Coastal and Offshore Areas of Northern Norway in July-August 1957. *Fiskeridir. Skr. Havundersøk.* (Report on Norwegian Fishery and Marine Investigations), XII (8).

B-8

DRIFT MIGRATIONS AND THEIR SIGNIFICANCE TO THE BIOLOGY OF FOOD FISHES OF THE NORTH ATLANTIC

By

Ju.Ju. Marty[1]

ABSTRACT

The passive transport of fish by water currents is discussed in relation to the evolution, feeding and development of the fish stocks. It is shown that knowledge of such drift migrations is needed for assessing the productivity of a sea area and for predictions of recruitment to the commercial stocks. In calculating growth rates it is necessary to remember that different contingents of a species may have differing histories of drift migration and hence of feeding and development. Detailed investigations of the dynamics of fish stocks are needed and international collaboration will be necessary.

Drift migrations, *i.e.*, the passive transport of living organisms by water masses, are common amongst representatives of the animal world living in the hydrosphere. These migrations occur not only among planktonic organisms, whose possibilities for horizontal movement are very limited, but among nekton as well and particularly among various species of fish. Drift migrations are especially characteristic of fishes inhabiting the boreal waters of the North Atlantic (Meek, 1916; Schering, 1929; Schmidt, 1947; Zenkevitch, 1963). The drift of eggs, larvae and fry has been well studied for cod, haddock, herring and redfish of the Norwegian, Greenland and Barents Seas (Hjort, 1914; Lea, 1929; Baranenkova, 1957, 1960; Baranenkova and Khokhlina, 1959, 1961; Maslov, 1944, 1957 and 1960; Marty, 1941, 1956 and 1961). Eel larvae brought by the Gulf Stream to the European shores serve as a classic example of a prolonged drift migration (Schmidt, 1929). Passive dispersal starts either at the stage of developing egg (gadoids; flatfishes), or at that of hatching for demersal eggs (herring) (Marty, 1961).

Drift migrations result in the extension of the species habitat and wider utilization, as feeding areas, of enormous sea spaces which for various reasons cannot be used by a given species for reproduction. Through the resulting extension of the habitat, drift migrations reduce the possibility both for interspecific and intraspecific competition.

Drift of eggs, larvae and fry represents the first stage in the migration cycle of immature fish. The second stage of this cycle is a return migration of fish to the spawning grounds. For the majority of species the drift migration lasts for about 6-8 months. During this period the young are carried from the spawning grounds to the feeding areas over a distance of 500 to 800 or more miles. The return migration is accomplished within 3 to 8 years depending on the rate of growth and maturation of particular species.

Passive dispersal of living organisms takes place not only in the hydrosphere but also in the atmosphere where the air currents carry, first of all, plant seeds. However, there are some radical differences in the passive dispersal of living organisms in the atmosphere and in the hydrosphere (Marty, 1961). Plant seeds can be carried and deposited by air currents into various, even lethal conditions. Eggs and larvae of fish and of other marine animals are transported with water masses within which their development began and which are characterized by a very slow and gradual change of their physical and chemical qualities. Yet, even in the hydrosphere, it is possible that the young may find themselves in unusual environmental conditions. For example, the young of the coastal fish can be carried out to the open sea; pelagic eggs and larvae can drift into areas occupied by floating ice etc. Such conditions are known to exist in a number of areas of the Pacific Ocean.

---

[1] All-Union Research Institute of Marine Fisheries and Oceanography, Moscow, USSR.

The main condition for drift migration of the young is the proximity of the spawning grounds to the permanent currents. The next condition for favourable drift of the young of the bottom and demersal fishes is the direction of the currents along the shelf or towards the shallow waters. Pelagic fishes and herring, in particular, can be carried even to the remote areas of the open sea. There are a variety of ways in which the young may "withdraw" from the drift. The young may cease to drift when the movement of the water masses stops, or if they get into the eddy zones, sink to the bottom, or swim out of the areas of the permanent currents.

Habitats of the main commercial species in the Barents Sea (Figs. 1,2,3,4,5) are quite different. These differences are based, first, on the different starting points of the drift, *i.e.*, on the location of the spawning grounds and, second, on the biological peculiarities of the young.

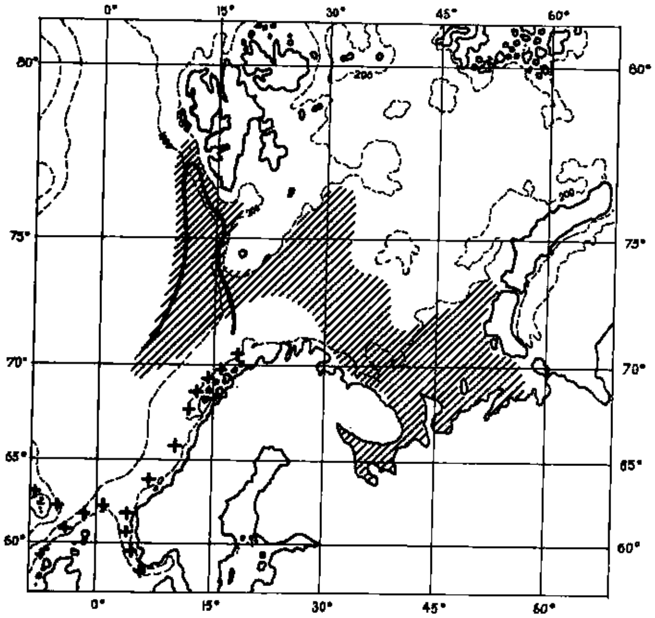


Fig. 1. Atlanto-Scandian Herring. Showing distribution of fingerlings (shading), spawning areas (crosses), limits of distribution of adults (heavy line). (from Marty and Shutova-Korzh).

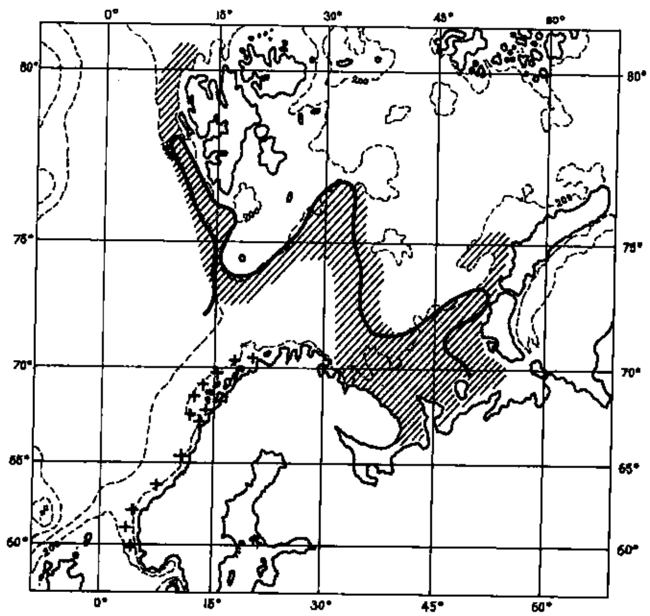


Fig. 2. Cod. Showing distribution of fingerlings (shading), spawning areas (crosses), limits of distribution of adults (heavy line). (from Maslov and Baranenkova).

It is not yet clear to what extent the habitat of the young of certain commercial species reflect the natural mortality of the young in different areas as being influenced by the abiotic factors or predation.

The greatest habitats of the young herring as a pelagic fish are mostly found in the Norwegian, Greenland and Barents Seas. They are encountered in the eastern part of the Norwegian Sea and in the Spitsbergen Current up to 76 - 77°N and further north. The young herring inhabit both the southern part of the Barents Sea and the White Sea.

The distribution of young cod in the Barents Sea is similar to that of herring. In the Norwegian Sea young cod are observed in the eastern branch of the Norwegian Current and in the Spitsbergen Current — along the whole western coast of Spitsbergen. Some of the young cod, according to observations made by the Polar Institute, are carried into the Arctic Ocean. The young cod are undoubtedly carried to the White Sea as well, though to a much less extent than herring. Haddock are characterized by a more westerly distribution. The young of the "golden redfish" are found predominantly in the northwest areas of the Sea, as well as along the main branch of the Norwegian Current. The young of *Sebastes mentella* inhabit the northwest areas of the Barents Sea and do not occur in its central part.

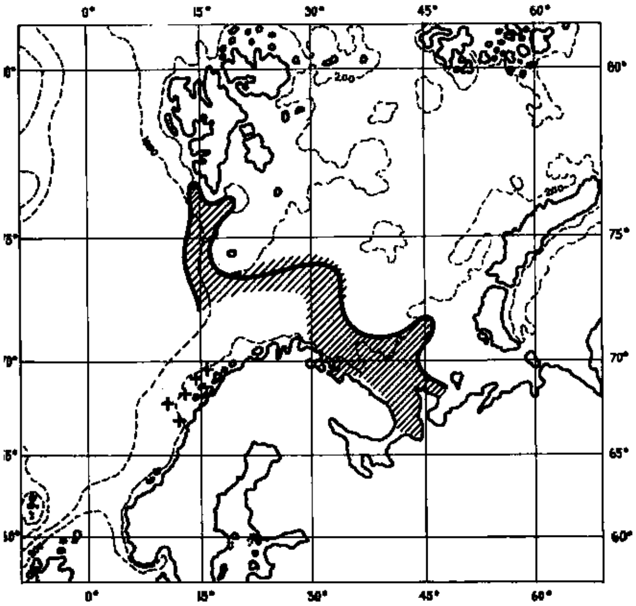


Fig. 3. Haddock. Showing distribution of fingerlings (shading), spawning areas (crosses), limits of distribution of adults (heavy line). (from Baranenkova and Sanina).

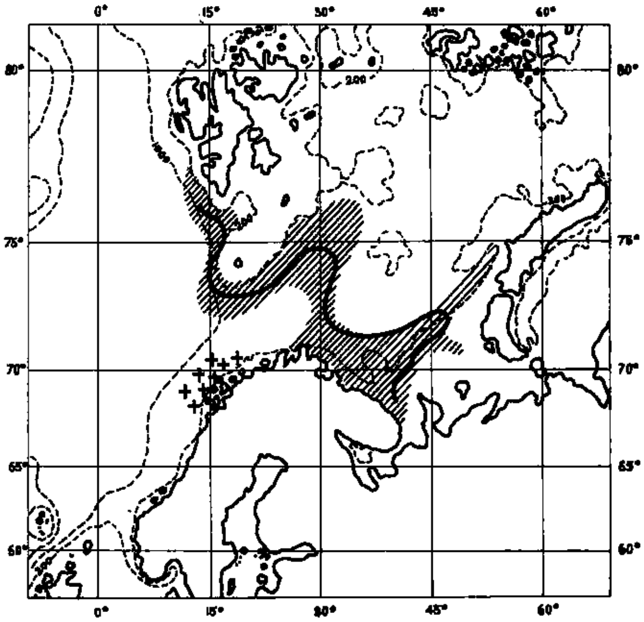


Fig.4. *Sebastes marinus*. Showing distribution of fingerlings (shading), spawning areas (crosses), limits of distribution of adults (heavy line). (from Baranenkova and Khokhlina).

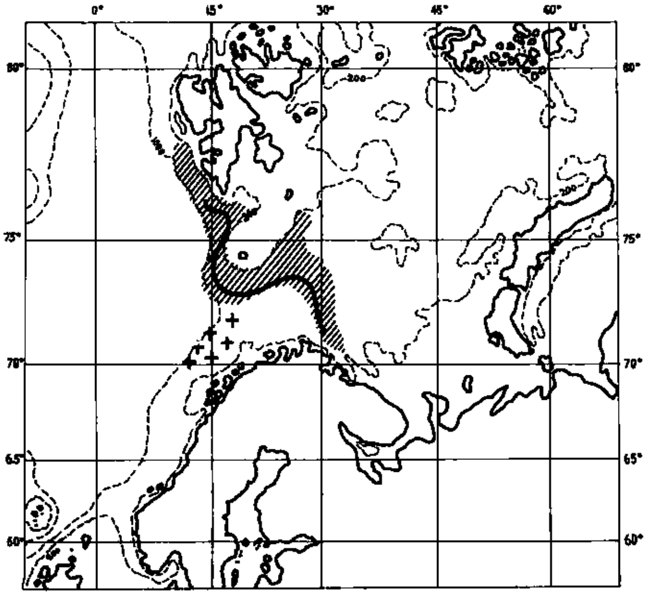


Fig. 5. *Sebastes mentella*. Showing distribution of fingerlings (shading), spawning areas (crosses), limits of distribution of adults (heavy line). (from Baranenkova and Khokhlina).

Observations on the distribution of the individual year-classes of herring in the Barents Sea were begun as far back as in the thirties and have been continued to the present day by Dr Shutova-Korzh (Marty, 1941, 1956; Shutova-Korzh, 1960). The widest distribution was observed for the 1937 and 1950 year-classes. Inshore distribution characterised the abundant 1930 year-class, the bulk of which penetrated into the White Sea, returned along the Murman coasts and entered the inlets of the Motovsky Gulf. The abundant 1934 year-class had an open sea distribution. A similar pattern of distribution was registered for the 1943 and 1944 year-classes. The rich 1959 year-class was distributed widely. However, it did not penetrate into the east and northeast areas.

The drift migrations of the ichthyofauna of the boreal area probably originated during the glacial epoch; first, the reproduction of all relatively warm-water species could then occur only in the areas affected by the warm currents; secondly, the drift of the young perhaps had already been taking place in the more northward latitudes (Marty and Wilson, 1960). Alternate cold and warm periods have made the migrations a habit (Marty and Wilson, 1960). It seemed to be equally advantageous for the boreal species in the period of stabilization of the temperature regime of the sea as in the periods of temperature ups and downs.

Experience gained in the cod and herring fisheries in the North Atlantic shows convincingly that, during the periods of temperature rise of the Subarctic areas and the extension of the boreal area, the abundance of boreal species tends to go up, resulting in extended feeding areas and longer feeding migrations. In hydrologically warmer years drift migration of the young of boreal species is also extended. Research conducted by Wiborg (1957) showed that the abundant year-classes of cod relating to warm years are carried from the northwest coast of Norway much faster than poor ones. This is undoubtedly due to acceleration of the current in warmer years. The young of cod, haddock and herring are brought to the Barents Sea earlier and distributed wider and more to the east during warm years than in colder years.

Thus, there seems to be a definite relation between the spawning conditions, the abundance of the young and the factors favouring the dispersal of the latter. The great speed with which the young adapt to favourable life conditions resulting from the drift migration, is specially interesting. The extension of the boreal area due to an increased intensity of the warm currents causes a rapid "stocking" of the areas affected by the warm water masses by the young of commercial fish (Kisljakov, 1960).

Drift migrations of the young represent a most interesting example of the unity of the organism and the environment; besides, what we observe in this case is not a simple adaptation of the organism to the life conditions, but a deep assimilation of these conditions by the species. A true understanding of various aspects of the biology of commercial fish is impossible without thorough knowledge of drift migrations. Their study allows us to understand the scheme of the migration cycles of the species and to determine the conditions necessary to retain the intraspecific integrity or to form races and local stocks.

Wherever there are long drift migrations of the young and return migrations of the maturing fish, the possibility of race formation is out of the question (Marty, 1958). At the same time, a stable extension of the habitat by the species at the expense of any branch of the warm current may lead to the formation of a local tribe. An obvious case is provided by the conditions which exist in the Barents Sea. As long as the northwest Norwegian coast remains the area of reproduction owing to its favourable temperature conditions, it has one tribe of the Arctic cod, although some contingents of the maturing fish in the Southern Barents Sea and in the Bear Island-Spitsbergen area live separately.

Drift migrations result in the fact that for many species the area of distribution of the young can be just as wide as that of the adult fish performing spawning migrations. In a number of cases the habitat of the young is much wider than that of the adult fish and the limits of the habitat are determined by the pattern of distribution of the young at the age of one or two years.

Passive distribution of the young is possible only because of their exclusive eurybiotic and, particularly, eurythermal qualities which are formed in the process of phylogenesis. During the first years of life, young cod, herring and haddock are limited in their movement and the above mentioned eurythermality allows them to survive rather severe winter conditions, with temperatures of about -1°C and even lower (Marty, 1941).

Study of the age distribution of herring in the Barents Sea showed that the younger year-classes always keep more to the east and north than the older ones. Migration contours of the maturing year-classes are being constantly shifted against the current. Because maturation of fish depends not only on the age but also on the size of fish in the areas of distribution of young individuals, one can observe a stable withdrawal of specimens having the higher growth rate which move to the west with older year-classes (Marty, 1941). Our observations on the individual year-classes of herring have shown that their reaction to the temperature conditions remains unchanged for a number of years. Thus, those populations of the young that had grown up under the severe conditions of the White Sea prefer cooler waters in the subsequent years as well, and the young that had grown up in the Finmarken waters remain in the areas of higher temperature range.

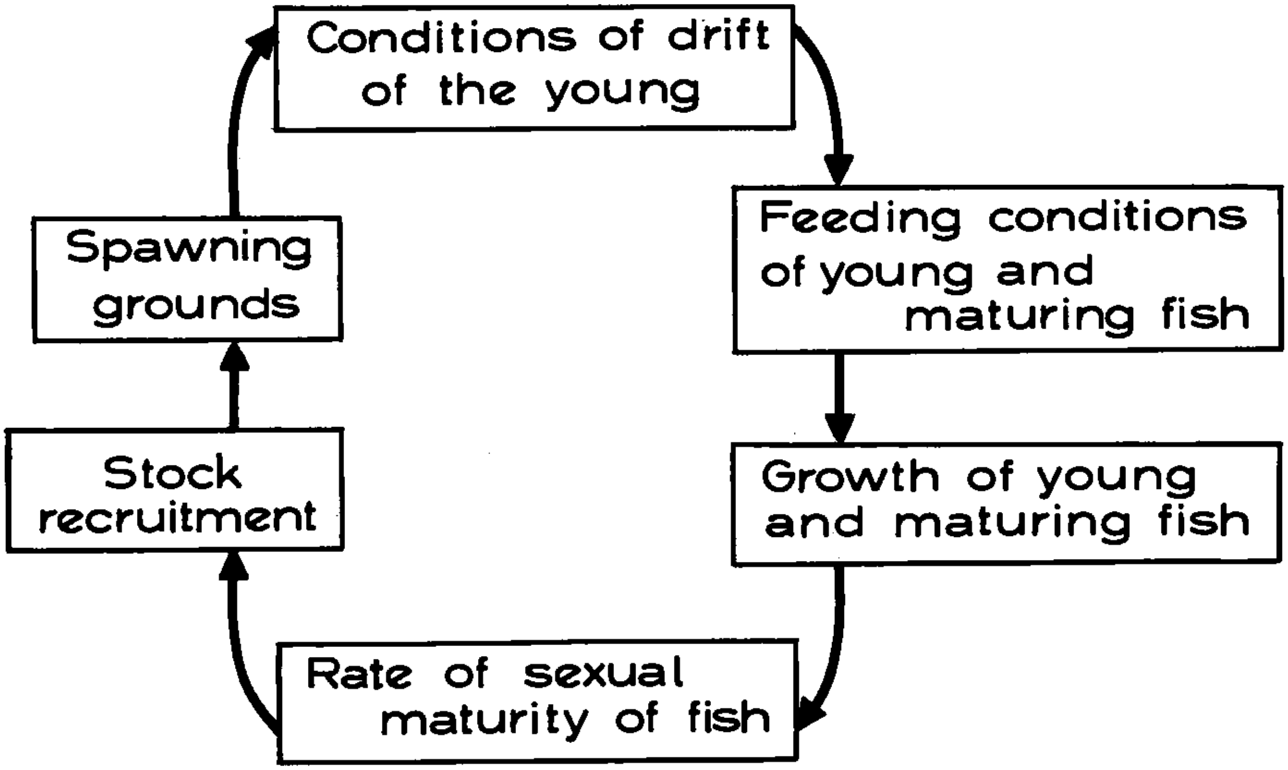
The study of the distribution of the maturing year-classes of commercial fish is of great importance for forecasting the strength of the year-classes; also for planning selective fisheries by excluding from the fishing operations the areas known to be occupied by non-commercial size fish.

Studies of the distribution of the young of commercial fish are important in assessing the productivity of the basins. Wherever drift migrations exist, the fishing productivity of the basin can be differentiated into the productivity of young fish resulting from their passive distribution, and the productivity of the adult fish performing feeding migrations. The relationship between the first and the second types of productivity depends first of all on the age composition of the populations characteristic of a given species. Changes in the age composition of the population, as shown by Maslov (1961) may reduce the feeding migrations and utilization of the feeding resources of the basin.

Knowledge of the drift migrations of the young is most important in forecasting the rate of recruitment to the commercial stocks. The extent of the drift of the young determines the extent of its feeding grounds and the growth and maturity rates of year-classes: the farther the young are carried by the drift, the slower they grow and mature. Without knowledge of the feeding grounds, it is impossible to estimate the growth of separate contingents of the young that had grown up in separate areas, and to predict the rate of recruitment to the stock. Therefore, the attempts of many investigators to describe an average growth rate of individual year-classes cannot be successful. Our experience shows that in a number of cases we have quite definite contingents of maturing fishes with noticeably different growth rates and attempts to calculate growth rate averages only complicate the problem instead of aiding its solution.

In our opinion, in order to get a true idea of the growth rate, it is necessary to study the growth of individual contingents of fish with due regard to their distribution and significance in the composition of the year-class. Such well-organized investigations can greatly help us to understand the dynamics of the formation of the commercial stock and its exploitation.

To summarize, the growth and maturity rates of the recruits are closely related to the feeding grounds and, consequently, to the conditions of the drift migrations of the young. Schematically, this interdependence seems to assume the following shape:



Drift migrations are particularly important in the northeast part of the Atlantic. In the northwest areas they should be less important, first of all because of the more limited boreal area (Marty, 1962). However, the drift migrations do exist in the northwest Atlantic and it is important that they shall be studied. International investigations into the distribution of eggs, larvae and young of fish in Davis Strait, commenced in 1963 and the recent studies of the distribution of young of food fishes by the Soviet investigators will undoubtedly help to get more accurate information on many problems pertinent to the biology of the food fishes in the ICNAF area.

REFERENCES

BARANENKOVA, A.S. 1957. Assessment of the numerical strength of cod and haddock year-classes in the Barents Sea based on the estimation of the young and on the commercial fisheries data. *Trudy PINRO*, X: 54-77.

1960. The results of estimation of young cod and haddock in the Barents Sea in 1946-1959, p. 267-275. *In* Soviet Fisheries Investigations in North European Seas. Moscow.

BARANENKOVA, A.S. and N.S. KHOKHLINA. 1959. Drift of larvae and fry of the Barents Sea cod from the spawning to the feeding grounds. *Nauch.-tekh. Biull. PINRO*, No.1 (9).

1961. The distribution and size composition of larvae and young redfish in the Norwegian and Barents Seas. *Spec. Publ. int. Comm. Northw. Atlant. Fish.*, No.3, p.177-187.

1961. The distribution of larvae of commercial fishes of the Barents Sea in 1959 and 1960. *Nauch.-tekh. Biull. PINRO*, No.2-3 (16-17).

HJORT, J. 1914. Fluctuations in the great fisheries of Northern Europe. *Rapp. Cons. Explor. Mer*, XX: 228 p.

KISLYAKOV, A.G. 1960. Fluctuations in the regime of the Spitsbergen Current, p.39-49. *In* Soviet Fisheries Investigations in North European Seas. Moscow.

LEE, E. 1929. The oceanic stage in the life history of the Norwegian herring. *J. Cons.* IV (1): 1-42.

MARTY, Ju. Ju. 1941. Investigations of life cycle of the Murmansk herring. *Trudy PINRO*, VII: 38-124.

1956. Main stages of the life cycle of Atlanto-Scandian herring. *Pishchepromizdat*, Moscow: 69 p.

1958. Race formation and Marine Herring Races. *Rapp. Cons. Explor. Mer.* 143, 11, 1958.

1961. Migrations and the problem of provision of sea fish with food. Transactions of the meeting on fish population dynamics, 1960. *Akad. Nauk. SSR.* vol. 19: 78-81.

1962. Some similarities and differences in conditions of existence of boreal fish species in the Northeast and Northwest Atlantic, p.57-68. *In* Soviet Fisheries Investigations in North-Western Atlantic. Moscow.

MARTY, Ju.Ju. and A.P.WILSON. 1960. Migrations of the Atlanto-Scandian herring, p.329-339. *In* Soviet Fisheries Investigations in North European Seas. Moscow.

MARTY, Ju.Ju. and I.G.JUDANOV. 1962. Population dynamics, stock condition and perspectives of fisheries of Atlanto-Scandian herring. *Trudy PINRO*, XIV: 151-181.

MASLOV, N.A. 1944. Bottom fish and bottom fish fisheries of the Barents Sea. *Trudy PINRO*, VIII: 3-186.

1957. On the improvement of methods of long-term forecasting the stock conditions of cod and haddock. *Trudy PINRO*, X.

1960. Soviet investigations on the biology of cod and other demersal fishes of the Barents Sea, p.185-231. *In* Soviet Fisheries Investigations in North European Seas. Moscow.

1961. A change of geographical distribution of fishery and an expected effect of the regulation. *Nauch.-tekh. Biull, PINRO*, No.1 (15).

MEEK, A. 1916. The migrations of fish. London.

SCHEURING, Z. 1929. Die Wanderungen der Fische Ergebnisse der Biologie Bd.

SCHMIDT, J. 1923. Die Laichplatze des Flussales. *Inter. Rev. ges. Hydrobiol. and Hydrogr.* Bd. XI.

SCHMIDT, P.Ju. 1947. Fish migrations.

SHUTOVA-KORZH, I.V. 1960. Peculiarities in the distribution, growth and maturation of some herring year-classes in the Barents Sea. p.361-370. *In* Soviet Fisheries Investigations in North European Seas. Moscow.

WIBORG, K.F. 1957. Factors influencing the size of the year-classes in the Arcto-Norwegian tribe of cod. *Fiskeridir. Skr. Havundersøk,* XI (8).

ZENKEVITCH, L.A. 1963. Biology of the USSR seas.

B-9

SURVIVAL OF THE YOUNGEST STAGES OF FISH, AND ITS RELATION TO YEAR-CLASS STRENGTH

By

J. A. Gulland[1]

ABSTRACT

Most fish have enormous fecundities, and there must be a correspondingly enormous mortality etween the egg and adult stages. Most of this mortality is believed to occur in the first few onths of life, and this stage is believed to be important for two other reasons; because the diffrences between good and bad year-classes are determined at this stage, and because the regulatory density-dependent) effects which prevent the population expanding without limit in favourable conitions, or dwindling to extinction under poor conditions (*e.g.* with heavy fishing), may occur in his stage.

Year-class fluctuations are presumably due to some environmental factor. Attempts to show the nvironmental effect by correlation techniques have generally not been successful; the wide range f possible environmental factors makes the usual statistical tests of significance invalid if the actor studied has been chosen on the basis of goodness of fit. Also the correlation coefficient or even an environmental factor directly responsible for year-class changes is not likely to be igh because of difficulties of estimating both the year-class strength and the environmental actor.

The relation between year-class strength in the Arcto-Norwegian stock was studied. Relations reviously suggested between year-class and wind, or plankton were shown not to be firmly supported, ut there seemed to be a relation, though not a close one, between year-class and temperature in the arents Sea.

In this, and other stocks, the mortality between eggs and recruitment (for the cod, recruitment ccurs at 4 years old) was shown to decline with increasing adult stock, and a pattern of the deline in numbers during the first years of life is proposed. It is suggested that further undertanding of the happenings in these early stages will be reached by using the techniques of populaion dynamics, *i.e.* direct measurement of growth, mortality etc. Low mortality, as deduced from the elative abundance of larger (and presumably older) larvae is shown to be related to good year-class trength in several stocks.

Most marine teleosts have enormous fecundities. A female cod in her lifetime may produce milions of eggs, but in a stable population an average of only two will survive to maturity. While he fish are of commercial size the mortality is (by these standards) low, of the order of 30-75% er year. Mortality between the end of the first few months of life and the time of reaching comercial size is not known so precisely, but is probably also fairly moderate, and the bulk of the 9.9999% mortality occurs in the first few months of life.

The mortality in these early stages is believed to be important to the study of fish populations n two ways. First, it is at this time that the difference between good and bad year-classes is esablished - certainly this difference is usually established and observable by the time the fish are ig enough to be sampled with normal fishing gear (cf. Baranenkova, 1960, for Barents Sea cod). econd, any population must have some basic density-dependent factors controlling it, preventing it rom expanding without limit when conditions improve, and from declining when conditions worsen *e.g.* when adult mortality increases due to fishing). This effect, for at least some fish stocks, robably occurs in the early larval stages (Beverton, 1962).

Variations in year-class strength are presumably due to variations in the environment at some ime in the early life. Failing the information needed to make a direct study of the effect of arious environmental factors on the survival of young fish, correlations between year-class strength nd various environmental data have been made for several fisheries. Thus Carruthers and his olleagues (Carruthers *et al.* 1951) used wind data, mainly because these were regularly and easily

---

Fisheries Laboratory, Lowestoft.

available without the need of any special investigation, and wind could reasonably be expected to influence other more direct factors such as the distribution of larvae in unfavourable areas, rather than because of its direct effect on young fish.

The use of correlations to establish a connection between environment and year-class strength is made more difficult by the small number of pairs of observations available (one per year). On one hand there is the statistical danger, pointed out by Gulland (1953), that with the wide range of possible environmental factors available, including the choice of precise season, a high degree of correlation between some factor and year-class strength is likely to arise merely by chance. On the other hand the estimates of year-class strength, and probably also of the environmental factors, are likely to contain considerable observational variance. Thus Beverton and Holt (1957, p. 270), comparing for the North Sea haddock the variances of year-class strength and of the total annual catch, concluded that, for the period 1922-37, the variance of the estimated year-class strength was considerably greater than the variance of the real year-class strength. Also, as shown below, there appear to be discrepancies in later data between changes in year-class indices and in catch per unit effort of the fishery. Thus, however close the real relation may be, the correlation between the estimates of year-class and environmental factor cannot be very large, perhaps not large enough to be significant except when determined over a considerable number of years. For example, estimates of year-class strength have been made for the Bear Island cod - a stock for which the data are probably rather better than average - based on the abundance of 7- and 8-year old fish. The correlation between these two estimates is 0.896, and this is about the best degree of correlation that could be expected between either of these (fairly good) estimates and an environmental factor which could be measured precisely, and which determined the true year-class strength absolutely precisely. Even this fairly high correlation needs seven pairs of observations (*i.e.* seven years) to be significant at 1%. Thus tests of statistical significance give only a poor guide to the reality of a derived correlation and, as Saville (1959) points out in his survey of such correlations for the North Sea haddock, the best test is given by the passage of time, and by the relation between variables in the years after the correlation was first suggested.

Despite these difficulties, it is worth examining the relation between the estimated year-class strength of the Arcto-Norwegian cod and some environmental factors, particularly where such a relation has already been suggested (*e.g.* Hill and Lee, 1958; Corlett, 1958*a*). Hill and Lee, working with very limited data, both in number of years and precision of year-class strength in the Bear Island-Spitsbergen area, suggested that there was a correlation between good year-classes and strong southerly wind during the period when the larvae were drifting from the Lofoten spawning grounds to the Bear Island area, the latter causing increased northerly water transport. Mr Lee has kindly put the complete series of wind data at my disposal. A series of pairs of observations of wind (mean southerly component at Bear Island during April and May) and year-classes (using the data of Gulland, 1964) can be obtained for twenty-eight years between 1921-56. These data have been plotted in Fig. 1; distinct symbols have been used for the periods 1921-32, 1937-41 and 1946-55. No clear relation emerges, nor, examining the early and late years separately, does there appear to be any relation in these shorter periods. The correlation between the two variables is 0.1, which is not significant.

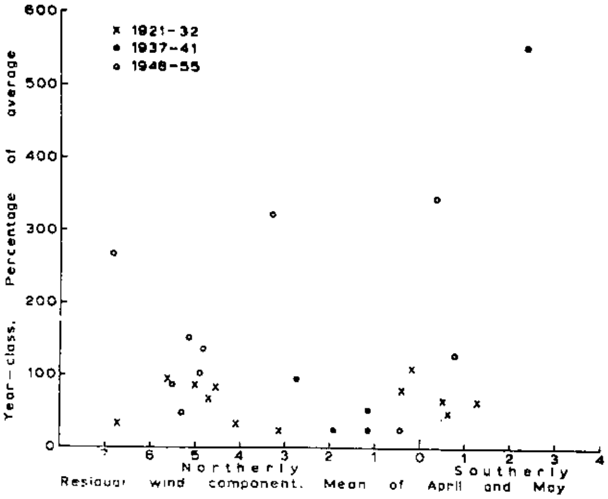


Fig. 1. The relation between year-class strength (expressed as the percentage of average) in the Bear Island region, and the mean wind component at Bear Island.

Another correlation has been suggested by Corlett (1958*a*) between dry weight of summer plankton and year-class strength. Only one year (1956) can be added to his series, but with the year-class strengths expressed in quantitative terms it is possible to calculate a correlation coefficient. For the eight years 1949-56, this is 0.56 ($P>0.1$, not significant). Corlett (this symposium) also correlates year-class strength with plankton and wind. Using different periods of years, and another estimate of year-class strength (one based on only one year's data, and likely to be affected by the amount of fishing in the previous year or two), he obtains correlation coefficients of 0.758 between plankton and year-class, and 0.594 between wind and year-class. This again illustrates the degree to which the value of the correlation coefficient obtained depends on precisely which sets of data, of both year-class strength and environmental factors, are used, often from a considerable choice. Under these conditions the levels of significance as given in statistical tables can be very poor measures of the probability of the observed relation between the selected pairs of year-class indices and environmental factors occurring by chance, and the level of significance may be grossly overestimated.

This of course in no way disproves the hypothesis that plankton or wind in fact affects year-class strength, but merely that the correlation approach is unlikely to provide useful evidence one way or another. In fact other evidence on growth, as discussed later in this paper, suggests that plankton - or rather the indices of plankton used by Corlett - is not related to year-class survival. Also, even ignoring the fact that the depth from which samples were taken was different in 1949-53 and in 1953-59, it is extremely doubtful if the single figure used by Corlett, based on a few irregularly timed samples, can adequately represent the changing plankton standing crop throughout the period of nearly six months from mid-April to the end of September. Even with perfect sampling the mean standing crop of total plankton over this period is likely to be a poor measure of the food available to the cod at the critical period, when in any case it is possibly only certain preferred species that are of vital importance. This critical period, as defined later in this paper, is likely to occur fairly early in the year, but the correlation coefficient between year-class strength (using Corlett's indices) and dry weight of plankton in April and May for the seven years available - 1950 to 55 and 1957 (Corlett, 1953, 1958*c*) is +0.01. This last calculation probably attempts to make more use of the data than is profitable. Further research into the factors determining year-class strength in the Arcto-Norwegian cod stock, or any other stock, requires detailed quantitative study of the dynamics of the eggs and larvae, such as the surveys of eggs, larvae and 0-group cod made by Russian scientists, and reported to this Symposium by Baranenkova.

For the other main feeding/nursery area of the stock in the Barents Sea, data collected by PINRO are available for the mean temperature in the 0-200 m zone along the Kola meridian (33 1/2°E), together with corresponding brood indices for twenty-five years between 1924-56. These are plotted in Fig. 2. Again separate symbols are used for the periods 1924-32, 1937-40 and 1945-55. There is some slight relation, as indicated by the fitted regression, though the correlation coefficient is only 0.23, which is not significant. The lack of statistical significance, of course, does not prove that there is no relation, but only that the data are not inconsistent with the hypothesis that the year-class strengths are independent of the environmental factor considered. Probably, in fact, at least in the Barents Sea, the temperature may have an influence, but if the true correlation is only 0.23, then, purely by the statistical method of correlation, it would take seventy years of observation to establish it, even at the 5% level of significance. Another relation with temperature has been derived by Kislyakov (1961). He related the temperature off the west Norwegian coast (*i.e.* close to the spawning grounds) to year-class strength, as measured by the total yield, in arbitrary units, and obtained a correlation coefficient of 0.91. When comparing his results and the present ones in detail, the most striking discrepancy is not so much in the greater value of the correlation coefficient observed by Kislyakov (if the critical phase is very early in life it is presumably more closely related to temperature nearer the spawning ground) as in the apparent differences in year-class strength. It is not precisely clear how his estimates were obtained, nor to what group of fish they refer - to the whole stock spawning at Lofoten, or to some part of it - but taking the same data of year-class strength for regions I and IIb as used earlier in this paper, and also a single weighted mean (factors of 2:1) to give a best estimate for the whole Arcto-Norwegian stock, and relating this to the temperature data in his Table 1, the following correlation coefficients were obtained.

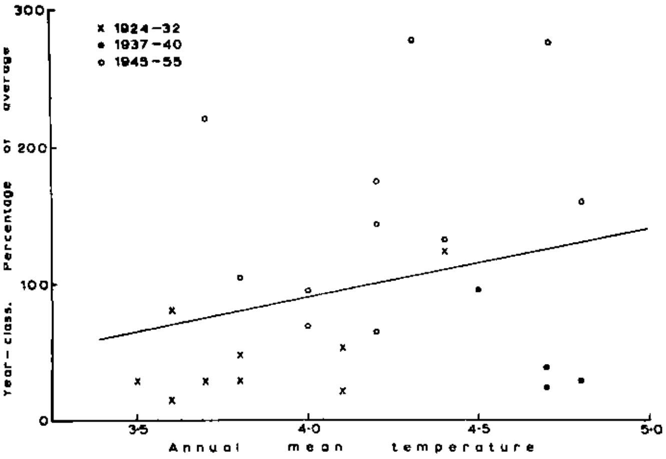


Fig. 2. The relation between year-class strength in the eastern Barents Sea, and the spring temperature on the Kola meridian.

Region I : 0.48
Region IIb : 0.55
Weighted mean of both areas : 0.66.

These are considerably smaller than the correlation coefficient of 0.91 mentioned above, which is in fact larger than the correlation between the two most reliable single estimates of year-class strength based on English data. This suggests that the closeness of Kislyakov's observed relation between temperature and year-class strength, based on a rather short series of data, is fortuitous. The basic weakness of the correlation approach is illustrated by the different conclusions reached by Kislyakov and in the present paper, and particularly by the fact that, without using different techniques, the discrepancy will only be settled by the passage of time, possibly of quite a large number of years.

In fact, though many such correlations between year-class strength and environmental factors have been suggested, few if any have stood the test of time. Thus one of the most promising, relating wind force and direction to year-classes of North Sea haddock (Carruthers, 1938), which at the time when it was proposed fitted data for some fifteen years extremely closely, has given an extremely bad fit for the post-1945 data (Saville, 1959). Attempts could be made to improve matters by considering additional environmental factors either in the initial analyses, so as to produce a very high correlation coefficient, or later, when the simple relation fails to hold. Such attempts have to be made with caution because the danger of introducing spurious correlations is very great.

Density-dependent mortality

It is easy to show that if a population of animals is to remain reasonably stable under different conditions, for example if a fish population is to be able to stand the large additonal mortality caused by fishing without declining to extinction, then one or more of the vital parameters (mortality, growth, reproduction) must change with the abundance of fish. While growth can decrease with increased stock abundance, the more important factor seems to be the recruitment. This has often been assumed to be independent of the abundance of the parent stock, and this is equivalent to assuming that the average survival from eggs to recruits decreases with increasing adult stock. This decreased survival has been clearly shown for such different stocks as the Karluk River sockeye salmon (Rounsefell, 1958), the North Sea plaice (Beverton, 1962) - a marine stock where the recruitment does not vary much, - and the Californian sardine (Radovich, 1962), where there is much greater variation independent of stock abundance. It is probable that this relation would be found for most fish stocks but at present sufficient data on adult stock and subsequent recruitment are available for only a few stocks.

The following data have been obtained for the Arcto-Norwegian cod. Recruitment has been taken as the sum of the numbers of fish at four years old in regions I and IIb. Stock estimates are based on the catch (in weight) per man at Lofoten (which gives the longest series of data) converted to actual numbers of eggs. From the Arctic Working Group (ICES, 1959), it is known that the effort in region IIa from 1951-58 was equivalent to 40,000 men at Lofoten. During this period the total mortality coefficient was 0.99, so that allowing for natural mortality (*ca.* 0.2), and for fishing mortality due to fishing in other regions, we may take 40,000 men as causing a fishing mortality coefficient of 0.4, so that the estimate of stock is obtained by multiplying the catch per man by $\frac{40,000}{0.4} = 10^5$.

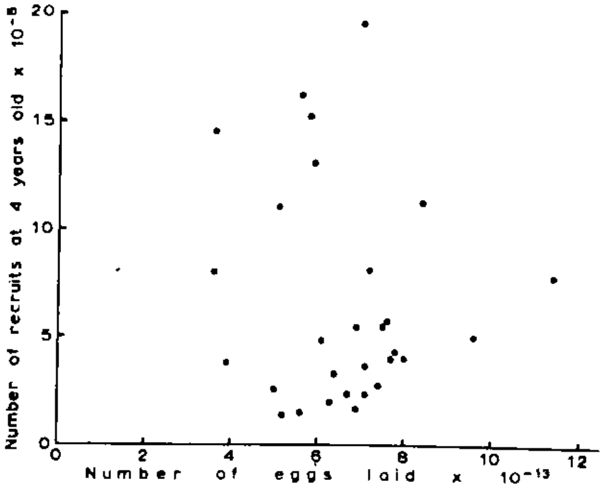


Fig. 3. The relation between the number of eggs laid at Lofoten and the resulting number of recruits.

The fecundity has been estimated by Mrs Woodhead (personal communication) to be closely, though not exactly, proportional to weight, and as equal to about 1.5 x 10^6 eggs per female of 85 cm, *i.e.*, *ca.* 8 kg, so that a catch per man of 1 kg is equal to an egg production of, say, $1/2 \times 10^5 \times \frac{1.5 \times 10^6}{8} = 10^{10}$ (taking a sex ratio of unity). In Fig. 3 the estimated number of recruits has been plotted against estimated egg production. There is clearly no significant relation ($r = 0.13$). In Fig. 4 the survival from eggs to recruits, *i.e.* the number of fish surviving to four years old per million eggs laid, has been plotted against the number of eggs laid. There does seem to be a relation, as indicated by the curve drawn by eye. The correlation coefficient is significant (≃ = 0.434, P 0.02). This test is not the most sensitive, because of the probable true curvilinear relation, but a relation of

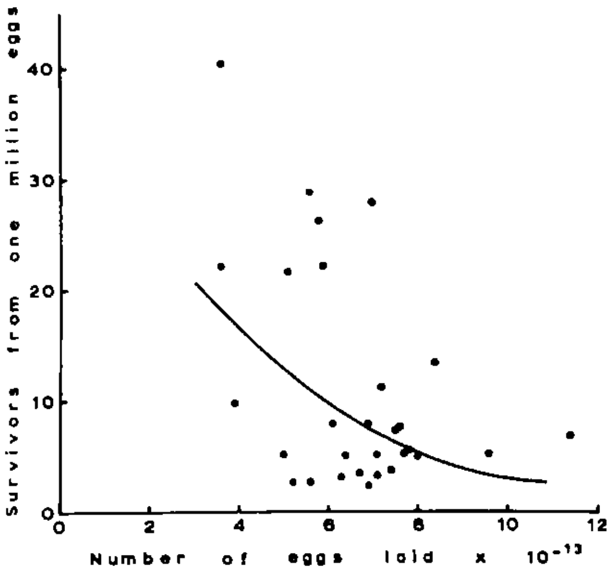


Fig. 4. The relation between the number of eggs laid and their survival.

this type could be developed by chance due to errors in estimating the egg-production. These are probably not very large, and we may conclude that there is a real difference of about two-fold in average survival over the observed range of stock density.

While the survivals above were calculated from egg to four years old, the surveys by Baranenkova (1960) show that year-class strength is already determined by two-three years old. In the table below, the data from her Tables 1 and 3 are grouped to give a single average value of catch per hour for each age-group.

Area	Catch per hour's fishing of each age			
	0+	1+	2+	3+
Southern Barents Sea	13.1	19.7	20.1	16.6
Near Bear Island	5.3	40.9	32.8	10.6

The results suggest that mortality among these ages is not very high (even allowing for probable lower vulnerability of the younger ages); probably it is of the same order as the natural mortality in the older fish, 20-30% per year. Thus, of the total mortality between eggs and four-year-olds, which reduces the numbers by a factor of 2 x 10^5, *i.e.*, *ca.* 5.3 logarithmic units, the last three years account for 3 x 0.1-0.15 log units. Taking an upper limit of this mortality leaves nearly 5 log units for the mortality in the first year, *i.e.* half a unit (nearly 70%) per month, or *ca.* 3% per day. This decline in numbers is shown diagrammatically in Fig. 5, for average conditions of stock and year-class. Even if an extreme upper limit of mortality after the first year (0.2 log units or 35% per year) is taken, the survival curve in the first year must be very much steeper than in the next three years.

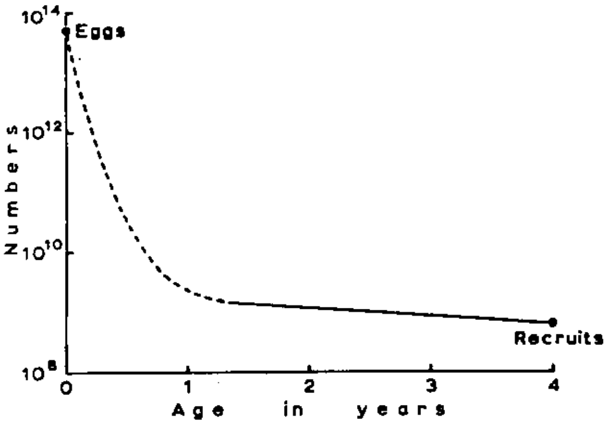


Fig.5. The mortality of Arctic cod during its first years of life.

A curve, or set of curves may now be drawn to represent the presumed decline in numbers of a given year-class from eggs through the first few months of life. This curve must firstly show a very high mortality of around five orders of magnitude, common to all year-classes. At some point during these months there is what may be defined as the density-dependent phase, in which mortality is higher for year-classes with an initially high number of eggs than for one with an initially low number of eggs. There is also the critical phase, which in the sense used here is the phase during which the strength of a year-class is determined, *i.e.* the phase during which the mortality of an ultimately poor year-class is higher than that of an ultimately rich year-class. These definitions do not imply anything about the duration or timing of, or total mortality during, either phase. If, however, the density-dependent mortality is caused by competition between larvae of the same age (*e.g.* for some scarce food at a critical stage of development) rather than say competition with, or predation by, the adults, then the density-dependent phase must at least in part precede the critical phase. Otherwise the differences caused by the latter would be removed by the density-dependent effect.

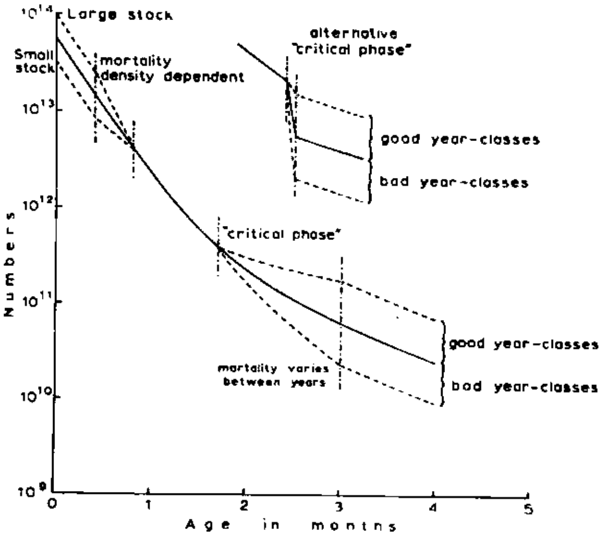


Fig. 6. Hypothetical mortality curves of eggs and young fish.

Hypothetical examples of the decline in numbers in the early stages and the differential mortality in the density-dependent and critical phases are shown in Fig. 6. Two possible critical phases are shown, one of short duration in which mortality for a good year-class is small, and much less than that for a poor year-class, and one of longer duration, in which the differences in mortality rate for good and poor year-classes is only slight. For simplicity the general mortality rate has been shown as fairly steady, but it is not denied that there may be certain stages (*e.g.* when larvae first start to feed) at which mortality may be very much higher than for older or younger stages. However, such a stage is not a critical stage, in the sense defined here, unless the mortality during this stage is different in good and bad year-classes.

Population dynamics of young stages

From the discussion in the preceding section it is clear that further advance in these studies requires the use of the same type of population techniques as have been used for commercial-sized fish; that is, the study of mortality rates (if possible split up between different causes), growth rates, etc. For young fish, mortality and growth are closely linked, poor growth not only being a sign of adverse conditions likely to increase mortality, but also directly affecting mortality by increasing the time during which the young fish are vulnerable to the smaller invertebrate predators.

Few surveys of eggs and young fish have been published in a form suitable for detailed population studies. Some of the best of these, *e.g.* that of the Atlantic mackerel (Sette, 1943), cover only one year or, though covering more than one year, include years in which conditions and also subsequent year-classes were nearly identical, *e.g.* the Pacific sardine (Ahlstrom, 1954). In neither case is it possible to observe differences in mortality which may be related to ultimate year-class strength, or to differences in the parent stocks.

Some other studies of young stages have been made, which though not so detailed and hence less suitable for direct estimation of mortality rates, etc., do enable comparisons to be made between years. Wiborg (1957) made studies of the Lofoten cod. He examined some hypotheses about year-class strength and found that there was no relation between numbers of eggs and early larvae and subsequent strength of year-class; in fact the outstanding year-class of 1950 corresponded to the lowest number of eggs and larvae observed in the period 1948-56. Data were also presented on the size of larvae caught each year, and the striking feature is that the years when large larvae (over 12 mm) were caught coincided with good year-classes (1948, 1949, 1950, 1954, 1956). The data cannot be used directly to give quantitative estimates of the mortalities of larvae, because of lack of information on growth and possible changes in growth from year to year, and because the drift of eggs and larvae through the area makes repeated samplings of the same group of eggs and larvae very difficult. They do suggest however that in the early months of life there is an observable difference in the size composition of the larval catches between years, corresponding to the differences in mortality and hence in ultimate year-class strength.

Saville has given such data for haddock in the North Sea (Saville, 1959), and at Faroes (Saville, 1956). For the North Sea, data on size of larvae are given for 1953, 1956 and 1957. The year 1956 had an outstandingly poor year-class, and in this year very few larvae of over 15 mm were caught, even though small larvae were abundant. However, there was no difference in abundance of larger larvae between 1953 and 1957, though the 1957 year-class was appreciably poorer than that of 1953. For the Faroes, length data for larvae caught in June are given for 1950, 1952 and 1953. The numbers of larvae of over 15 mm beneath 100 m^2 surface were 14, 21 and 27 respectively, which agree well with the indices of year-class strength obtained by research vessel surveys of I-group fish of 228, 488 and 490 per 10 hours fishing.

Simpson's (1959) surveys of the North Sea plaice were concentrated principally on the eggs, ut some data on larvae were also given. Sizes of larvae were not given, but taking his post-larvae *i.e.* those with the yolk-sac completely absorbed), it is possible to calculate the mean number aken per haul for each cruise. Taking the mean of the catch per haul for each cruise (omitting ecember cruises), one obtains indices of the abundance of later larvae of 0.95, 0.56 and 0.36 for he years 1947, 1948 and 1950 respectively. The corresponding year-class strengths, in terms of umbers of fish caught per hour's fishing as four-year-old fish by Lowestoft trawlers, are 46, 22 nd 23. These data do suggest that, in each of the stocks examined, the critical stage (in the ense defined above) occurs very early, and its effect can, at least to some extent, be measured. f this is so the study of the effect of environment on year-class strength will be greatly helped, ot only by defining more precisely the timing of the important critical step, and hence narrowing he range of possible factors, *i.e.* only those directly or indirectly operative at that time, but lso by increasing the number of possible comparisons above the one pair of year-class strength and nvironmental factor per year. That is, mortality rates may be calculated for different groups of arvae of the same year-class, *i.e.* those spawned at various times or in slightly different areas, nd these mortalities may be compared with the conditions affecting each group. Shelbourne (1957) ound two patches of plaice larvae in the Southern Bight of the North Sea; in one *Oikopleura* (the avourite food of larval plaice) was abundant, the larvae were in good condition, and late stage arvae were not uncommon; in the other food was scarce, the larvae were in poor condition, and late tage larvae were rare. This example does not give complete proof of poor feeding causing high ortality, because Shelbourne was not able to maintain continuous sampling on the same patch, so hat it is not certain whether the scarcity of larger larvae was due to high mortality, or to an riginally smaller number of newly hatched larvae. Even when there are no data on the relative bundance of different sizes, and hence probably of ages of larvae, many other less detailed pieces f information may be used to narrow down the possible factors or the timing of the critical phases ffecting larval survival or year-class strength. Fraser (1961) has suggested some differences beween types of water in the North Sea. This difference is reflected as relatively fewer larvae in he type of water, even though the numbers of eggs are much the same in the two water-masses. This ould be due to differential mortality at any time between the youngest eggs and quite late stage arvae. For cod and haddock, however, three stages or "age-groups" can be determined from the data - arly eggs (which for cod and haddock are indistinguishable), late eggs, and larvae. These data, aking the two species together, are summarized below, together with the survival from one stage o the next.

Cod + haddock	Type of water *S. elegans* present	 *S. elegans* present
Average No. per haul		
Early eggs	24.45	33.63
Late eggs	4.24	1.66
Larvae	1.24	0.38
Survival: %		
Early to late eggs	17	5
Late eggs to larvae	29	23

he big difference between the types of water is that the survival from early to late eggs is much ess when *Sagitta elegans* is absent; there is very little difference in the survival from late eggs o larvae. The difference therefore lies somewhere in the egg stage, due to predation, or possibly isease, rather than to feeding.

Observations other than those on the relative numbers of different stages of eggs or larvae an often be of help. Thus food shortage affecting year-class strength, or indeed competition for food causing density-dependent mortality, is likely to affect growth first. Differential mortality, therefore, is unlikely to take place without some change in growth. Thus seaward migrating sockeye salmon smolts from Karluk River are longer in the more abundant broods (Rounsefell, 1958). Growth changes are rather easier to detect, either simply from size at a given time (when spawning is restricted to a short known season), or from the progression of modes in length composition, or as done by Shelbourne (1957) by the appearance of the larvae - robust when food is abundant, but thin when food is scarce. For the cod round Bear Island, Corlett (1958*a*) has suggested that the abundance of planktonic food in the summer influences the year-class strength. Corlett (1958*b*) gives some data on size of 0-group cod in October, *i.e.* at the end of the period to which the plankton data refer. These data are summarized below.

Year	1950	1951	1953	1954
Dry weight of plankton	54	15	26	46
Size of 0-group cod (cm)	11.25	11.5*	10.0	10.5

*Cod were caught in two areas; west of Bear Island and west of Spitsbergen; mean lengths 10.6 and 12.4 cm respectively.

There does not seem to be any relation between size of cod and abundance of plankton, nor are the years of good year-classes (1950, 1954) years of particularly good growth. While such analyses do help to get some insight into the causes of variations in larval survival and in year-class strength, and are far more satisfactory than mere correlations between annual pairs of values of year-class strength and some feature of the environment, they are a poor alternative to a thorough egg and larval survey designed to measure mortality directly.

Such surveys are however very time-consuming. If the form of the decrease in numbers is to be defined with any precision the individual surveys have to be quite frequent, *e.g.* at intervals of a week to ten days. This work is likely to need several research vessels if it is to be done satisfactorily, and it therefore appears to be a field where international cooperation, with several research vessels, is likely to be very productive. The stock to be investigated should be chosen with some care. It should be one in a small and fairly well defined area, so that the actual survey work taken as little time as possible. More important, the strength of year-classes should be very variable, so that say three years of surveys should give a good chance of including one year-class of unusual strength, from the data on which the critical phase might be determined fairly precisely. If possible, the abundance of the parent stock should also be variable, thus giving a better chance of observing any density-dependent effect. One stock that satisfies these conditions is the North Sea haddock, which has the advantage of being located not far from several laboratories, but there are several other suitable stocks.

REFERENCES

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

BARANENKOVA, A.S. 1960. The results of surveys on young cod and haddock in the Barents Sea during the period 1946-1959. *Soviet Fish. Invest. North European Seas.* Moscow, VNIRO and PINRO, p. 267-278. (MAFF Translation, 1961).

BEVERTON, R.J.H. 1962. Long-term dynamics of certain North Sea fish populations. In: *The Exploitation of Natural Animal Populations*, Eds. Le Cren and Holgate, Oxford. Blackwell Sci. Publs., 242-264.

BEVERTON, R.J.H. and S.J. HOLT. 1957. On the dynamics of exploited fish populations. *Fish. Invest., Lond.*, (2), 19, 533 p.

CARRUTHERS, J.N. 1938. Fluctuations in the herrings of the East Anglian autumn fishery, the yield of the Ostend spent herring fishery, and the haddock of the North Sea - in the light of relevant wind conditions. *Rapp. Cons. Explor. Mer*, 107(3): 10-15.

CARRUTHERS, J.N., A.L. LAWFORD, and V.F.C. VELEY. 1951. Fishery hydrography: brood-strength fluctuations in various North Sea fish, with suggested methods of prediction. *Kieler Meeresforsch.*, 8: 5-15.

CORLETT, J. 1953. Dry weight and fat content of plankton near Bear Island, 1949-1952. *Ann. biol., Copenhague*, 9: 8-9.

1958*a*. Plankton in the western Barents Sea and the year-class strength of the Arcto-Norwegian cod. *J. Cons.*, 23: 354-356.

1958*b*. Distribution of larval cod in the western Barents Sea. *Spec. Publ. int. Comm. Northw. Atlant. Fish.*, No. 1, p. 281-288.

1958*c*. Dry weight of plankton in the western Barents Sea, 1953-1956. *Ann. biol., Copenhague*, 13: 39-40.

1964. Winds, currents, plankton and the year-class strength of cod in the western Barents Sea. *This symposium, Contribution No. B-10.*

FRASER, J.H. 1961. The survival of larval fish in the northern North Sea according to the quality of the sea water. *J. mar. biol. Ass. U.K.*, 41: 305-312.

GULLAND, J.A. 1953. Correlations on fisheries hydrography. *J. Cons.*, 18: 351-353.

1964. The abundance of fish stocks in the Barents Sea. *Rapp. Cons. Explor. Mer*, 156.

HILL, H.W. and A.J. LEE. 1958. The effect of wind on water transport in the region of the Bear Island fishery. *Proc. Roy. Soc.*, Ser. B, 148: 104-116.

I.C.E.S. 1959. Second Progress Report of the Working Group on Arctic Fisheries. Copenhagen, 1959, Mimeo.

KISLYAKOV, A.G. 1961. The relation between hydrological conditions and the fluctuations in the abundance of cod year-classes. *Trudy Soveshch. ikhtiol. Kom.*, 13: 260-264. (MAFF Translation, 1963).

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

ROUNSEFELL, G.A. 1958. Factors causing decline in sockeye salmon of Karluk River, Alaska. *Fish. Bull., U.S.*, 58: 83-169.

SAVILLE, A. 1956. Eggs and larvae of haddock (*Gadus aeglefinus* L.) at Faroe. *Mar. Res. Scot.*, No. 4.

1959. The planktonic stages of haddock in Scottish waters. *Mar. Res. Scot.*, No. 3.

SETTE, O.E. 1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part 1: early life history, including the growth, drift, and mortality of the egg and larval populations. *Fish. Bull., U.S.*, 50: 149-237.

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

SIMPSON, A.C. 1959. The spawning of the plaice (*Pleuronectes platessa*) in the North Sea. *Fish. Invest., Lond.* (2), 22, (7).

WIBORG, K.F. 1957. Factors influencing the size of the year-classes in Arcto-Norwegian tribe of cod. *Fiskeridir. Skr. Havundersøk.*, 11 (8).

B-10

WINDS, CURRENTS, PLANKTON AND THE YEAR-CLASS STRENGTH OF COD IN THE WESTERN BARENTS SEA

By

John Corlett[1]

ABSTRACT

The early life history of the Arcto-Norwegian cod is described. The first few months of life are discussed in relation to winds, water transport and plankton abundance in the Bear Island area. The first reliable estimate of the year-class strength is from the commercial fishery when the fish are fully recruited at 5 years old. Correlations between year-class strength and wind and plankton indices are presented. It is suggested that wind and plankton data can be used as a basis for prediction of cod year-class strength 5 years in advance. Predictions for the year-classes of 1958 to 1963 in 1963 to 1968 are given.

INTRODUCTION

One of the aims of fishery research is to predict the size of a stock of fish as far ahead as possible. The ideal is to be able to estimate the size of a year-class soon after its birth and, from this estimate, to predict its strength when recruited to the fishable stock. In looking at the early life history of a fish stock and its environment in this context, we hope to find some factors which will help in making the predictions. This paper is a short account of the early life history of cod of the Arcto-Norwegian stock in the western Barents Sea, with a discussion of the possible influence of some environmental factors; from this a basis for early predictions of the size of a year-class is suggested. The discussion is confined to the western Barents Sea because most of the English work has been done there and because similar studies in the south-eastern Barents Sea are described by Russian scientists in Contributions B-7, B-15 and B-16 from this symposium.

LIFE HISTORY OF ARCTO-NORWEGIAN COD

The mature cod of the Arcto-Norwegian stock are found over most of the Barents Sea during summer and autumn and come together to spawn each spring off the Lofoten Islands. The main spawning is in the Westfjord, but spawning also takes place along the Norwegian coast to the north and south (Fig. 1). The spawning season is from late February to late April, with the peak usually in the second half of March. The distribution of eggs and larvae around the Lofoten Islands in spring has been described in several papers by Wiborg (*e.g.* 1950, 1952 and 1960*a*). From the spawning grounds many of the eggs and larvae are carried by the surface currents north-eastwards along the coast in the Atlantic Current, and when this divides to form the West Spitsbergen Current and the North Cape Current the larvae are separated; some are carried northwards towards the Bear Island, Hope Island and Spitsbergen Banks, and others are carried into the south-eastern Barents Sea (Corlett, 1958*a*; Wiborg, 1960*b*). Some of the eggs and larvae also find their way among the fjords and islands of the Norwegian coast. By late summer the young cod are beginning to descend towards the sea bed, and from late September onwards are found as 0-group cod on the nursery grounds all over the Barents Sea (Baranenkova, 1960; Corlett, 1958*a*). The codling grow up on these banks and eventually form the basis of extensive trawl fisheries. Many are caught when 4 years old, but they are not fully recruited into the fishery until they are 5 years old. Trout's (1957) work on otolith types has shown that yound cod tend to remain until they are mature in the area in which they begin their demersal life.

The numbers of eggs and young larvae near the spawning grounds have been estimated for many seasons by Norwegian scientists and the work has been summarized by Wiborg (1957). In spite of the difficulty of estimating the total production of eggs over a large area and throughout an extended spawning season, using only one ship, Wiborg could give estimates of egg numbers for several seasons.

---

[1] Fisheries Laboratory, Lowestoft, Suffolk, England.

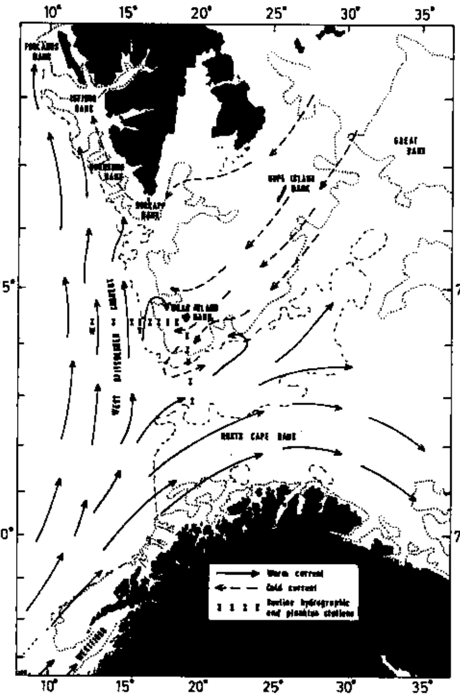


Fig. 1. Surface currents in the western Barents Sea.

But he could show no correlation between the abundance of eggs and young larvae and the subsequent strength of the corresponding year-classes.

During the early summer, when the larvae are larger and more widely dispersed, their numbers are very difficult to estimate, because of the inadequacy of the nets used and the large area that has to be covered. No full scale survey has yet been attempted.

When they are demersal from October onwards, 0-group cod can be caught in ordinary otter trawls using covered cod-ends. Some attempts to estimate numbers at that stage have been made by the *Ernest Holt* in the north-western Barents Sea in October in several years. But in the time available one ship was not able to cover adequately the large area involved. Russian workers using several ships during the autumn and winter in the southern Barents Sea have been much more successful in estimating the abundance of young cod (*e.g.* Baranenkova, 1960 and 1963).

Our first reliable estimate of the size of the year-class is obtained from market measurements of commercial catches. Four-year-old fish are not fully recruited and when caught are not always kept by the trawlers because they are too small for the market; so our earliest good estimate of abundance is at 5 years old. After this the abundance of the year-class is affected by fishing. What we would hope to predict as many years beforehand as possible, is the size of the year-class at 5 years old.

EARLY LIFE HISTORY AND ENVIRONMENT

The size of the year-class is generally considered to be decided in the first few weeks or months of pelagic life of the brood. After discussing the factors affecting the numbers and distribution of cod eggs and larvae on the north Norwegian coast, Wiborg (1957) concludes:- "the transport of eggs and larvae from the spawning areas to the nursery grounds in the Barents Sea and adjacent areas is probably of greatest importance for the abundance of a rich year-class. But in addition, other conditions, such as the number and kind of predators, the food organisms available, and the physical and chemical properties of the surrounding medium, are undoubtedly of great importance for the survival of the cod larvae". Of these other conditions the availability of food is probably most important; transport and food will now be considered further.

Cod larvae are carried to the banks of the western Barents Sea in the West Spitsbergen Currents and its various offshoots (Fig. 1). If the current is strong in spring and early summer the larvae should have a good chance of being widely distributed over the nursery grounds, and of not being carried westwards into the Norwegian Sea. During the period between 1949 - 59 the *Ernest Holt* regularly worked a line of hydrographic stations across the current west of Bear Island. Values of the volume transport above 400 m depth have been calculated for each crossing between stations "S" and "W" (Fig. 1). The values of this transport have been published by Hill and Lee (1958) and Lee (1961). In the spring and early summer the largest number of crossings was made in the month from mid-April to mid-May, and the values for these six years are given in Table 1. By this time the eggs have hatched and the young larvae are being carried between the Norwegian coast and Bear Island. Hill and Lee (1958) and Lee (1961) have discussed the relation between the wind and water transport in the eastern Norwegian Sea, and have shown that in the "non-summer" months of September to June, that is before thermal stratification occurs in the surface layers, there is a significant positive correlation between the southerly wind component and the volume transport between 2 and 20 days later. The correlation coefficient has its greatest significance around 10 days later, with $P<0.01$. The wind data are obtained from the records of the Bear Island Meteorological Station, and in Table 1 the mean southerly wind for April for each year from 1947 to 1959 is listed. Since we have the early summer transport values for so few years we have had to use the wind data instead to relate to the year-class strength.

TABLE 1.—ENVIRONMENTAL FACTORS AND YEAR-CLASS STRENGTH OF ARCTO-NORWEGIAN COD IN THE WESTERN BARENTS SEA.

Year	Southerly wind. April mph W	Water transport mid-April to mid-May km^3/hr	Summer plankton mg/m^3 P	0-group cod. October no. per hr	5-yr-old cod no. per hr Y
1947	-5.96				135.0
1948	-1.33				232.5
1949	-0.92		47		157.6
1950	-0.81		54		371.1
1951	-10.89	-0.2	15		139.7
1952	-5.94		22		30.0
1953	-7.11		26		93.4
1954	+0.66	8.4	46		237.3
1955	-4.63	0.3	24		119.2
1956	-2.30		29		210.8
1957	+3.28	3.6	34	3.8	203.5
1958	+3.75	4.1	45	9.9	
1959	+2.49	5.2	35	11.3	

Wiborg (1948 and 1960*b*) examined the food of cod larvae off the Norwegian coast and in the south-western Barents Sea between April and August and found that the main food organisms were copepods, with *Calanus finmarchicus* the most important. Other common foods are euphausiids, appendicularians and, locally, *Spiratella* and the larvae of bottom invertebrates. All these foods are planktonic and their frequency in cod stomachs is about the same as their frequency in plankton samples in the area. During the 11 years that the *Ernest Holt* was working in the western Barents Sea, plankton samples were taken on most cruises at fixed stations west and south of Bear Island (Fig. 1). Details of these stations and others in the Barents Sea and the quantity of zooplankton caught in each cruise, expressed as dry weight, have already been published (Corlett, 1953, 1958*b* and 1961). For each year a mean value has been calculated to represent the standing stock of zooplankton in the Bear Island area between mid-April and the end of September - that is, in the months when the cod larvae are pelagic. These indices of summer plankton are set out in Table 1.

The first regular index of year-class strength of cod in the western Barents Sea is obtained from the English commercial fishery when the fish are 5 years old. These indices are the numbers caught per hour's fishing and are published by the Ministry of Agriculture, Fisheries and Food (Great Britain, 1962). They are listed here in Table 1, with the addition of the previously unpublished value for the 1957 year-class in 1962. Also in Table 1 are the mean catches per hour of 0-group cod obtained during three October cruises of the *Ernest Holt*, using covered codends. Each estimate comes from between 30 and 40 stations on the West Spitsbergen Banks, Hope Island Bank and the south Bear Island Bank.

CORRELATIONS AND PREDICTIONS

The relation between the strength of the year-class when five years old and the wind and plankton indices, representing transport and food, have been examined to see whether year-class strengths can be predicted from either wind or plankton. All the indices are given in Table 1. The regressions of year-class strength on plankton and wind are shown in Fig. 2 (c and b). The formula for the regression of year-class on plankton for the 9 years 1949-57 is $Y = 5.63 P - 12$: the correlation coefficient, r , is 0.758, which is between the 1% and 2% levels of significance. The possible use of plankton data for predicting year-class strength was discussed in Corlett (1958*c*), but at that time no reliable indices of year-class strength were available.

For year-class on wind for the 11 years 1947 - 57 the regression line is Y = 13.27W + 219. *r* is 0.594, which is at the 5% level of significance.

The plankton abundance for any year is not independent of the wind and water transport. In years of strong southerly wind and increased transport in the West Spitsbergen Current, plankton is richer than average in the western Barents Sea. This is shown in the regression of plankton on wind for the 11 years 1949-59 in Fig. 2*a*. The regression line is P = 1.93W + 38.24, and the correlation coefficient is 0.730, which is at the 1% level of significance.

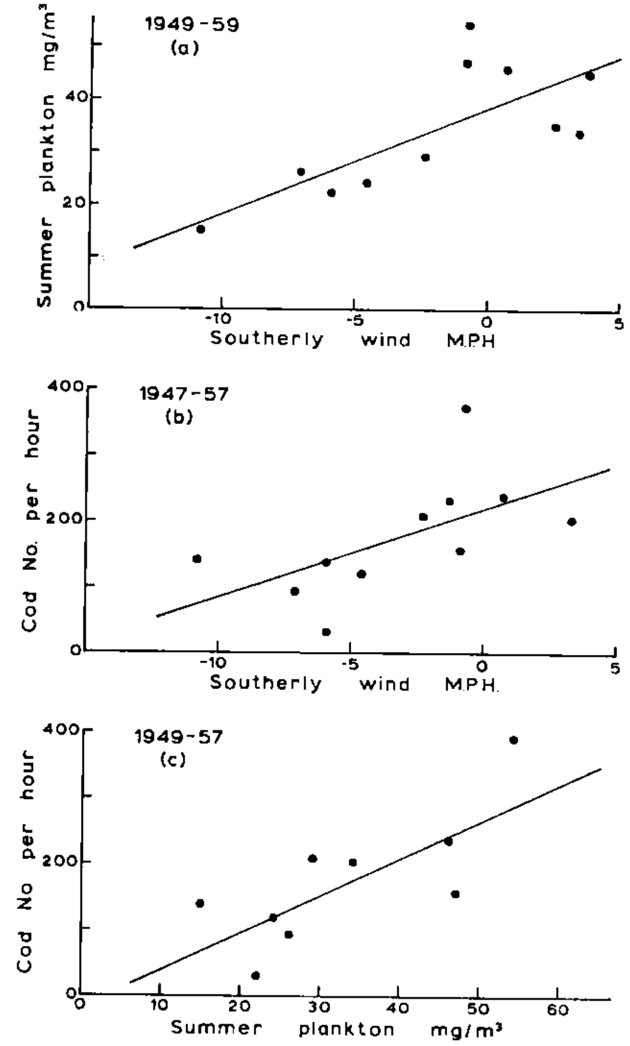


Fig. 2. Bear Island area:-

(a) Regression of summer plankton on mean southerly wind in April.

(b) Regression of cod year-class strength when 5 years old on wind in April.

(c) Regression of cod year-class strength when 5 years old on summer plankton.

Using the regression formulae the strength of the 1958 and 1959 year-classes of cod as five-year-olds in 1963 and 1964 can be predicted from both plankton and wind. These predictions are set out in Table 2, together with predictions for the 1960 - 1963 year-classes based on wind only.

TABLE 2.—PREDICTIONS OF COD YEAR-CLASS STRENGTH AT 5 YEARS OLD FROM WIND AND PLANKTON.

Year	Southerly wind mph W	Predicted year-class strength Y	Summer plankton mg/m^3 P	Predicted year-class strength Y
1958	+3.75	269	45	241
1959	+2.49	252	35	185
1960	+5.23	288		
1961	-2.69	183		
1962	-0.47	213		
1963	-0.76	209		

The estimate from plankton should be better than that from wind, because of the greater significance of the correlation. The estimates suggest that the 1958 and 1959 year-classes will be above the 1947-57 average of 175 fish per hour, and that the 1958 year-class will be stronger than that of 1959. The strong southerly wind in April 1960 should produce a particularly strong year-class. Baranenkova (1963) confirms this when she says that in October-November, 1960 "the 0-group was especially rich in the waters of West and North Spitsbergen and on the western slope of the Bear Island Bank. The occurrence of such high numbers of 0-group cod in these areas testifies to a significant drift in 1960 of fry from the spawning grounds....". She also suggests that "the 1960, 1959, 1958 and 1957 year-classes in the north-western part of the sea will not be below average".

Although the mean north-south wind component in April in each of the years 1961, 1962 and 1963 was northerly, all were less northerly than the average for the years

1947-57: so the 1961, 1962 and 1963 year-classes of cod may be expected also to be above average.

Attempts to relate year-class strengths to wind data have been made in several fisheries (Hela and Laevastu, 1961) and will no doubt continue to be made, because wind data can be obtained regularly and without any use of valuable research ship time.

POSTSCRIPT

In another paper in this section of the Symposium (p. 363-371), Gulland discusses the difficulties in the use of correlations to establish a connection between the environment and year-class strength. He quotes this paper and then, using different estimates of year-class strength and the same plankton values, obtains a correlation coefficient for the years 1949-56 of only 0.56. Gulland's estimates of year-class strength are based on the percentage age composition of the catches between 1929 and 1960 and estimates of fishing mortality during those years on fish between 4 and 9 years old. His estimates for the year-classes for 1949-51 are thus based on 6 years (4-9 years old) and for subsequent year-classes on successively fewer ages, until that of 1956 is based only on four-year-old fish. Thus his estimates are less direct than the catch of fish at 5 years old used in this paper, and, for the years in question, cannot be considered any better.

It has also been suggested that cod are not always fully recruited to the fishery at five years old. Using the catch per hour of six-year-old fish for the year-classes 1949-56 a correlation with summer plankton gives $r = 0.805$ (which is between the 1% and 2% levels of significance), compared with 0.758 for the 1945-57 year-classes as five-year-olds. In view of the controversy over estimation of year-class strengths perhaps it is best to say only that these correlations are between summer plankton and the subsequent catch per effort of five- and six-year-old fish in the Bear Island - Spitsbergen area.

REFERENCES

BARANENKOVA, A.S. 1960. The results of surveys on young cod and haddock in the Barents Sea during the period 1946-1959. *Soviet Fish. Invest. North European Seas.* Moscow. VNIRO and PINRO. p. 267-275. In Russian, with English summary.

1963. Soviet investigations on young cod in the Barents Sea. *Ann. biol., Copenhague*, 18: 105-107.

CORLETT, J. 1953. Dry weight and fat content of plankton near Bear Island 1949-1952. *Ann. biol., Copenhague*, 9: 8-9.

1958*a*. Distribution of larval cod in the western Barents Sea. *Spec. Publ. int. Comm. Northw. Atlant. Fish*, No. 1, p. 281-288.

1958*b*. Dry weight of plankton in the western Barents Sea 1953-1956. *Ann. biol., Copenhague*, 13: 39-40.

1958*c*. Plankton in the western Barents Sea and the year-class strength of the Arcto-Norwegian cod. *J. Cons. int. Explor. Mer*, 23: 354-356.

1961. Dry weight of plankton in the western Barents Sea 1957-1959. *Ann. biol., Copenhague*, 16: 68-69.

GREAT BRITAIN. 1962. Ministry of Agriculture, Fisheries and Food and Department of Agriculture and Fisheries for Scotland. *Fish Stock Record 1961.*

HELA, I. and T. LAEVASTU. 1961. *Fisheries Hydrography.* London. Fishing News (Books) Ltd. 137 p.

HILL, H.W. and A.J. LEE, 1957. The effect of wind on water transport in the region of the Bear Island fishery. *Proc. roy. Soc. (B)*, 148: 104-116.

LEE, A.J. 1961. The effect of wind on water movements in the Norwegian and Greenland Seas. *Proc. Symp. Mathematical-Hydrodynamical Methods of Physical Oceanography*, p. 353-383. Institut für Meereskunde der Universität Hamburg.

TROUT, G.C. 1957. The Bear Island cod migrations and movements. *Fish. Invest., Lond., Ser. 2*, 21 (6): 1-51.

WIBORG, K.F. 1948. Investigations on cod larvae in the coastal waters of northern Norway. *Fiskeridir. Skr. Havundersøk.*, 9(3): 1-27.

1950. The occurrence of fish eggs and larvae along the coast of northern Norway during April-June 1948 and 1949. *Ann. biol., Copenhague*, 6: 12-16.

1952. Fish eggs and larvae along the coast of northern Norway during April-June 1950 and 1951. *Ann. biol., Copenhague*, 8: 11-16.

1957. Factors influencing the size of the year-classes in the Arcto-Norwegian tribe of cod. *Fiskeridir. Skr. Havundersøk.*, 11 (8): 1-24.

1960*a*. Investigations on eggs and larvae of commercial fishes in Norwegian coastal and offshore waters in 1957-58. *Fiskeridir. Skr. Havundersøk.*, 12 (7): 1-27.

1960*b*. Investigations on pelagic fry of cod and haddock in coastal and offshore areas of northern Norway in July-August 1957. *Fiskeridir. Skr. Havundersøk.*, 12 (8): 1-18.

B-11

ON THE LIFE CYCLE OF LABRADOR COD

By

A. I. Postolaky[1]

EDITORIAL NOTE:

This paper reports on data collected on cod in the Labrador area (ICNAF Subarea 2) during the ICNAF NORWESTLANT Surveys, April-June 1963. It will be published *in extenso*, in ICNAF Special Publication Number 7 (Report of the NORWESTLANT Surveys).

---

[1] Polar Research Institute of Marine Fisheries and Oceanography, Murmansk, USSR.

B-12

CHANGES IN RECRUITMENT TO THE STOCK IN RELATION TO THE ENVIRONMENT, WITH REFERENCE TO MATHEMATICAL MODELLING

By

T.F. Dementjeva[1]

ABSTRACT

The factors governing the size of a fish stock are considered briefly. It is argued that the causes of annual fluctuations of a stock must be clearly understood before planning the regulation of a fishery. For the most part, such fluctuations are related to changes in survival rates during the early stages of the life history of the fish.

By means of illustrations taken from Russian work, it is shown that the abundance of planktonic food organisms influences the survival of young fish.

It is emphasized that the effects of the biotic and abiotic environment on brood strength should be included in mathematical models of the dynamics of fished stocks.

The efficiency of regulation of a fishery and accuracy of prediction depend in some cases on the extent of our knowledge of the causes of fluctuations in the stock. The task facing ichthyologists is to assess the quantitative effect of each factor on the dynamics of the population, and particularly the role of governing factors. Among other causes affecting the stock, the governing factor may be one which, under certain conditions, has a direct effect on the abundance of the population at one or another stage of development.

A fish population becomes specific while dwelling in a water body. This is the result of a relative consistency of the governing factors affecting the survival of the population. The governing factors may be replaced by some others only if fairly sharp changes take place in the hydrologic regime or food resources, or new fishing methods are introduced, aimed at the intensification of the fishery.

Among the main factors, it is necessary to distinguish those which bring about long-range fluctuations in the abundance of the stock, and those affecting annual fluctuations in the sizes of the year-classes. No clear distinction can be established between them due to their close relation. Nevertheless, an approach should be differently chosen to gain some knowledge of their role as a factor governing either long-term or short-term fluctuations in the stock in each case.

The annual recruitment size varies greatly, and thus the relation between recruitment and the remainder of the fishing stock also varies, particularly in fishes with a short or medium span of life, bringing about changes in the relation between catches and abundance of fish.

Consequently, it is quite obvious that the causes of annual fluctuations in recruitment should be clearly elucidated. In most species the annual fluctuations are closely related to the survival of embryos and the food supply for early larvae. It is at this time that the heaviest mortality in fish is known to occur. Great fecundity of fish is an adaptive ability to compensate for the early mortality, so that the abundance of the species can be maintained. If the early mortality was reduced even by a very small amount, it would lead to a considerable increase in the abundance of the species, assuming favourable conditions. This conclusion can serve as a basis for fishing management in the sea by increasing the food supply for larvae, and in this way increasing the

---

[1] All-Union Research Institute of Marine Fisheries and Oceanography, Moscow, USSR.

survival rate and fishery yield (Shelbourne *et al.*, 1963).

Let us consider some results obtained in the USSR during the recent decade, supporting the existence of a direct relation between the abiotic and biotic factors and the survival of young fish at the early stages.

There are many data on the relation between the availability of food plankton and survival of larvae when they begin active feeding, which undoubtedly indicate that this factor should be considered as a governing factor for the abundance of a year-class.

Lisivnenko (1961), studying material collected in the period 1955-59 on the abundance of zooplankton in the Gulf of Riga and that of larvae of the Baltic spring spawning herring, found a quite clear, quantitative, relation shown in Fig. 1 as an S-shaped curve. In some years, when the larvae of the Baltic herring began active feeding, the small plankton was poor (1 organism in more than 100 cc of water), so a shift in the normal feeding conditions could be observed and the year-classes were usually poor. On the other hand, in years when the small plankton was relatively rich, the frequency of occurrence of larvae and plankton organisms increased. If one organism occurs in less than 100. cc of water, the feeding conditions for larvae become normal and survival is high.

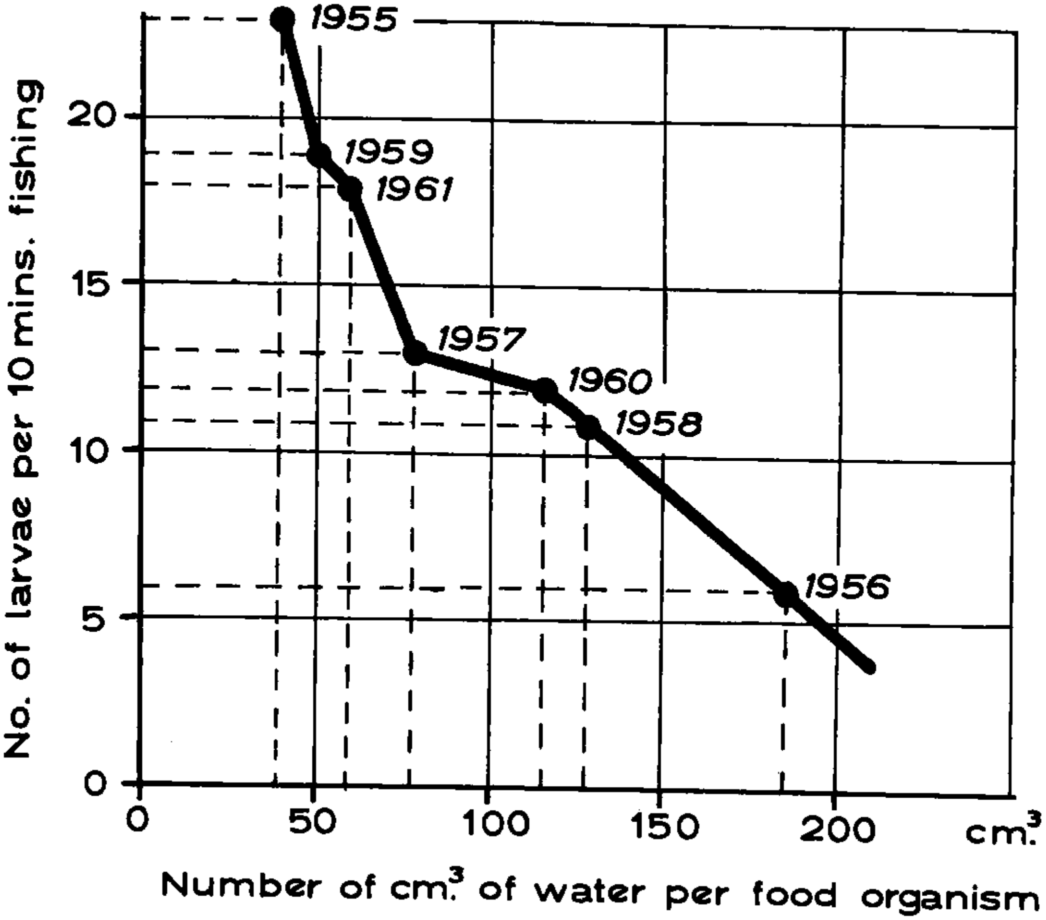


Fig. 1. The relation between the abundance of herring larvae and their food organisms (Lisivnenko, 1961). Herring larvae are shown as numbers per 10 minute haul; food as cm^3 of water per organism.

The same relation is found for the Black Sea anchovy (Pavlovskaya, 1961). As shown in Fig. 2., there is almost a direct relation between the survival of the young fish and biomass of food zooplankton in the period 1949-58. The largest generations are observed with a concentration of more than 10,000 organisms or 500 mg per m^3 of water for 4-10 mm fish larvae. Of great importance is the development of food plankton at the time when the anchovy larvae appear in large numbers.

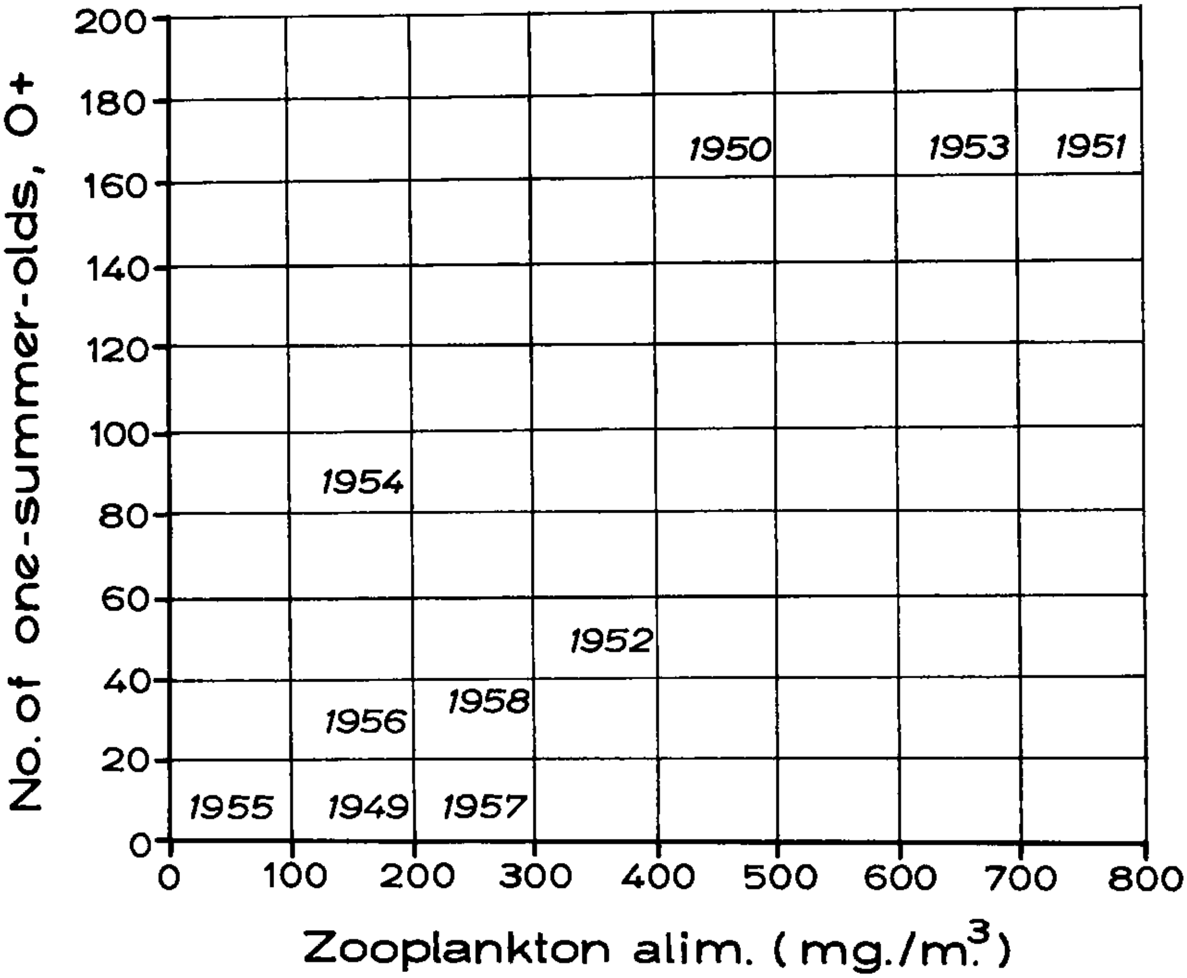


Fig. 2. The relation between the abundance of young stages of anchovy and the biomass of their planktonic food in the north-western Black Sea, during the years 1949-1958 (Pavlovskaya, 1961).

For the Baltic cod a direct relation was found between the salinity and oxygen content of off-bottom waters in the deeps (spawning places for cod) and the survival of eggs. The fluctuations in the abundance of embryos are in compliance with the fluctuations in the mean catches of one-summer-olds and catches of adult fish at corresponding ages. For the Barents Sea cod the relation between the abundance of year-classes and temperature, which seems to affect the food supply for the cod larvae, was established (Kislyakov, 1959).

In all the inland seas there is a direct relation between the abundance of the migratory and semi-migratory fishes and the volumes of the river discharges which provide suitable spawning areas and food supply for the fish at early stages. Specific research in this field was carried out by

L.A. Rannak on the Baltic herring, S.G. Kryzhanovsky on Sakhalin herring, V.I. Vladimirov on Danube herring, E.G. Boiko on bream and perch pike of the Azov Sea, T.F. Dementyeva, V.S. Tanasiychuk, A.G. Kuzmin on sea bream, perch pike and *Rutilus rutilus* of the Caspian Sea, A.A. Ostroumov on bream of the artificial Rybinsk water body and other workers, the results being similar.

The interrelation between the spawning of fish and the abiotic and biotic environment is so distinctly expressed that it enables us to work out methods of calculating the stock population by using characteristics of environmental factors (Izhevsky, 1961) in view, of course, of the fishing mortality.

Because of the above-mentioned effects, the wide range of the annual fluctuations in recruitment to the fishery stock should be included in models of the dynamics of fished populations. Calculations of the recruitment size and possible changes can be obtained from the quantitative counts of the young fish at various stages of development. For this purpose annual observations on spawning should be carried out, the result of which can be assessed in various ways, as follows:

1. By mean catches of spawned eggs at various stages of development in view of the percentage of living embryos and environmental conditions;

2. by mean catches of larvae at the stage of development after turning to the active feeding;

3. by mean catches of one-summer-olds to assess the density of their distribution per unit of area;

4. by mean catches of young age-groups (prior to maturation) per commercial or research fishing gear.

The method of counting one-summer-olds is probably most important because it enables us to assess the young fish at the stage when the heaviest mortality of eggs and larvae has already occurred. The evidence can be supported by a correlation between the fishery returns and mean catches of one-summer-olds of a certain year-class. Using this relation this index can be applied to calculations of the recruitment size to the fishing stock.

The counts of eggs and larvae may also be promising in assessing differences in the strengths of year-classes; however, the data obtained are, to a lesser extent, useful for mathematical calculations. In most cases they only indicate trends of fluctuations in the strength of the year-classes and may be suggestive in the studies of the causes conditioning the survival of embryos and larvae at early stages of development.

SUMMARY

The efficiency of measures for the regulation of fisheries and the precision of fishery forecasts depends in a number of cases on adequate knowledge of the factors affecting fish stock fluctuations.

For the majority of fish species, annual fluctuations of stock depending on the value of recruitment are noted. These fluctuations depend upon the conditions for survival of eggs and on the provision of food for larvae at the stage of their transition to external feeding. When the conditions for species are optimal, the decrease in larval mortality, even by a very small fraction, results in a considerable increase in a fish population.

During the recent decade a great number of papers were published showing a direct relationship between abiotic and biotic factors and the survival of young fish at early stages. In particular, some data on the relationship between the abundance of food plankton and the survival of larvae, allow us to consider this factor (which is not dependent on the population density) to be of extreme importance when determining recruitment abundance. The data also show that, in the case of species for which a critical period is that of transition to active feeding, there is a certain level of plankton density at which an abundant year-class survives.

Thus, to estimate an abundant year-class of the Baltic herring, it is necessary to have less

than 100 cc of water per one food organism (Lisivnenko, 1961); the density of plankton which is necessary to estimate an abundant year-class of the Black Sea anchovy is expressed in another form; such year-classes were observed when the density of food plankton for the larvae 4-10 mm long was above 10,000 organisms or 500 mg per m^3 (Pavlovskaya, 1961). These data allow us to look for ways to assess the strength of a stock of consumers on the basis of the value of plankton biomass.

Taking into consideration the wide range of fluctuations of annual recruitment to commercial fish stocks, as a result of the factors mentioned above, it is considered extremely necessary to show these fluctuations when making models expressing the dynamics of a fished population.

REFERENCES

IZHEVSKY, G.K. 1961. Oceanologic bases for fishing productivity of the seas. *Pishchepromizdat*, Moscow, p. 1-215.

KISLYAKOV, A.G. 1959. Temperature regime and yield of the year-classes of cod spawning off the north-western Norway. *Nauchno-Tech.Bull., PINRO*, No. 1 (9), p. 22-26.

LISIVNENKO, L.N. 1961. Plankton and feeding of larvae of the Baltic herring in the Riga Gulf. *Trud. nauch.-issled. Inst. ryb. Khoz., Latvian SSR*, 3: p. 105-138.

PAVLOVSKAYA, R.M. 1961. La survie des larves de l'anchois de la Mer Noire en fonction de leur alimentation. *Rapp. Comm. int. Mer. Médit.* XVI (2), p. 345-350.

SHELBOURNE, J.E., J.D. RILEY, and C.T. THACKER, 1963. Marine Fish Culture in Britain. *J. Cons.*, Vol. XXVIII, No. 1, p. 50-90; No. 2, p. 246-261.

B-13

ON PRIMARY FOOD SUPPLY - THE BASE OF PRODUCTIVITY IN THE NORTHWEST ATLANTIC

By

M. V. Fedosov[1] and I. A. Ermachenko[1]

EDITORIAL NOTE:

This paper reports on data collected during the ICNAF NORWESTLANT Surveys, April-June 1963. It will be published *in extenso*, in ICNAF Special Publication Number 7 (Report of the NORWESTLANT Surveys).

---

[1] All-Union Research Institute of Marine Fisheries and Oceanography (VNIRO), Moscow, USSR.

B-14

THE EFFECT OF TEMPERATURE AND CURRENTS ON THE DISTRIBUTION AND SURVIVAL OF COD LARVAE AT WEST GREENLAND

By

Frede Hermann[1], Paul M. Hansen[2] and Sv. Aa. Horsted[2]

ABSTRACT

The distribution of cod larvae off West Greenland is compared with the surface currents. It is shown how the westerly branch of the West Greenland Current carries great numbers of larvae away from the Greenland banks.

A comparative measure of the strength of cod year-classes between 1924 and 1951 is calculated. The year-class strengths are correlated with the water temperature during the larval stage. Significant correlation was found between year-class strength and mean temperature, surface to 45 m over Fylla Bank in June.

The number of cod larvae caught off West Greenland in different years is compared with water temperature in June and July.

The onshore wind component during the larval stage is correlated with year-class strengths. No significant correlation is found.

COD SPAWNING GROUNDS OFF WEST GREENLAND

At West Greenland the most important cod spawning grounds seem to be along the western slopes of the banks, mainly at depths between 200 and 600 m in the relatively warm water of the Irminger Current. The map (Fig. 1) which shows the distribution of these spawning grounds, is based on information from Faroese fishermen and from German, Norwegian and Russian research vessels. In addition, some spawning takes place in coastal waters and in the inner parts of some fjords, but these spawning grounds are supposed to be of lesser importance for the recruitment of the West Greenland cod stock.

DISTRIBUTION OF COD LARVAE

The distribution of cod larvae off West Greenland has been investigated for many years by R/V *Dana* taking hauls with stramin nets at a number of stations on standard sections. Figure 2 shows, as an example, the number of cod larvae caught in July 1957 (Hansen, 1958). It is seen that most of the larvae are found north of the spawning grounds, mainly in the area between Fylla Bank in the south and the southern part of Store Hellefiske Bank in the north. Furthermore it is remarkable that a great concentration of larvae is found more than 100 nautical miles west of Fylla Bank. These larvae have drifted so far westward that they are probably lost for the Greenlandic cod stock. They can possibly contribute to the recruitment of the Labrador cod stock.

In the year 1957, which was used as an example here, the number of cod larvae caught was greater than the average, but the distribution seems to be typical for the month of July, with very few larvae south of 64°N.lat, one concentration being over the West Greenland banks between 64°N. and 67°N. and another concentration far west of Fylla Bank.

CURRENTS OFF WEST GREENLAND

The surface currents off West Greenland are illustrated in Figure 3. It is well known that the main direction of the West Greenland Current is northwestward along the coast, but a branch of the current turns westward between 64°N. and 65°N. These features explain the distribution of the cod fry. From the spawning grounds the eggs and larvae are carried northward by the current. Some of the larvae are carried westward by the westerly branch of the current and, as mentioned, are probably lost for the Greenland cod stock. The fraction of the eggs and larvae which is carried away from Greenland waters is expected to have some influence on the size of the year-class of the year in question.

---

[1] Danish Institute for Fisheries and Marine Research, Charlottenlund, Denmark

[2] Greenland Fisheries Investigations, Charlottenlund, Denmark

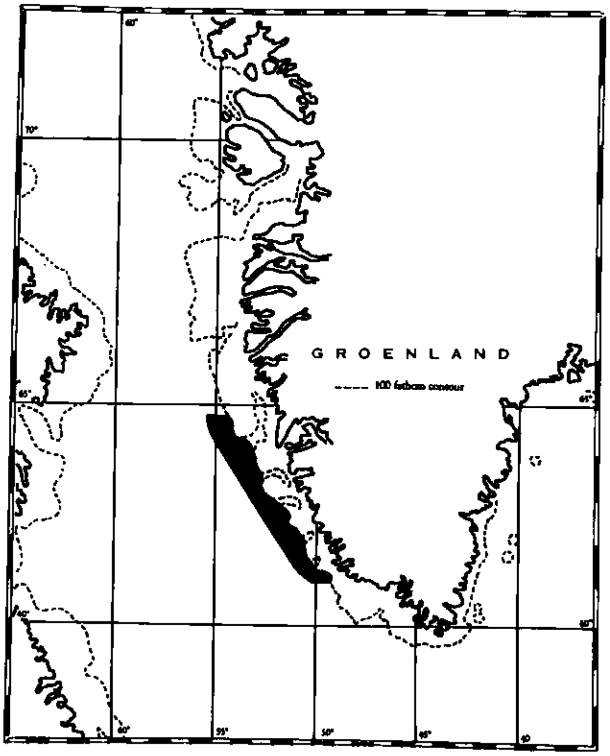


Fig.1. Offshore spawning grounds of West Greenland cod stock.

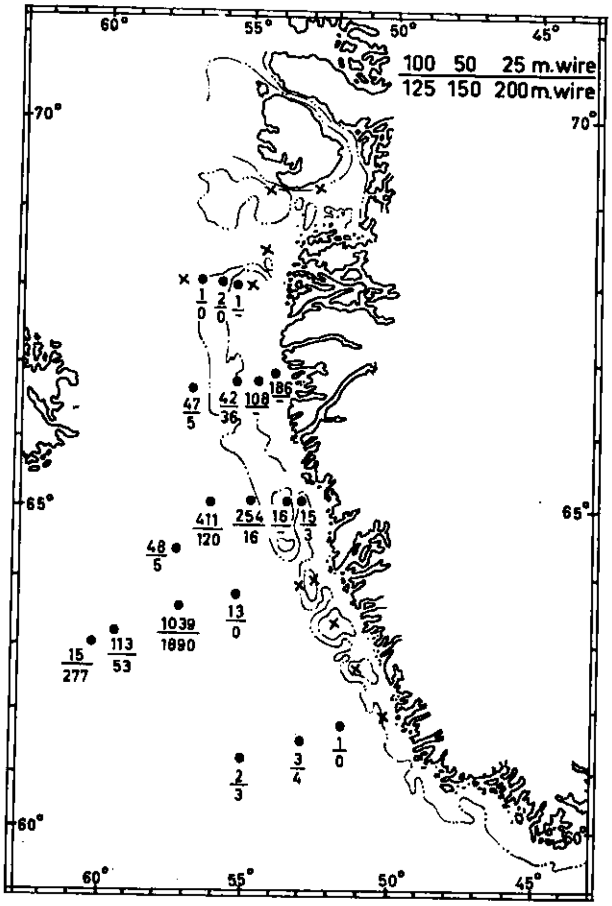


Fig.2. Number of cod larvae caught in stramin net hauls, July 1957.

The West Greenland Current is a mixture of two currents: the Polar component, which is a continuation of the East Greenland Polar Current and an Atlantic component which is a continuation of the warm Irminger Current. Off the middle part of West Greenland a considerable mixing has taken place so that the temperature differences between the two components are smaller than in the Cape Farewell region.

The water temperature over the banks and their western slopes, where the cod eggs and larvae are found, depends very much on the relative strength of the two current components.

The cod in West Greenland waters lives near its northern limit and it is therefore reasonable to assume that even small temperature variations will have great effect on the survival of the eggs and larvae. The correlation between the strength of the cod year-classes and the water temperature during the larval stage will be investigated in the following sections.

STRENGTH OF COD YEAR-CLASSES AT WEST GREENLAND

The basic material for calculating a comparative measure of the stremgth of the cod year-classes is the record of *the total catch of the Greenlanders* in the different years and *the age distribution in the single years* calculated from age determinations on samples. From this material the total catch of each year-class between age-group V and XI is calculated for all the year-classes from 1924 to 1951. In the present contribution only the catch from Godthåb district and more northern districts is considered since the cod off the southernmost part of West Greenland is

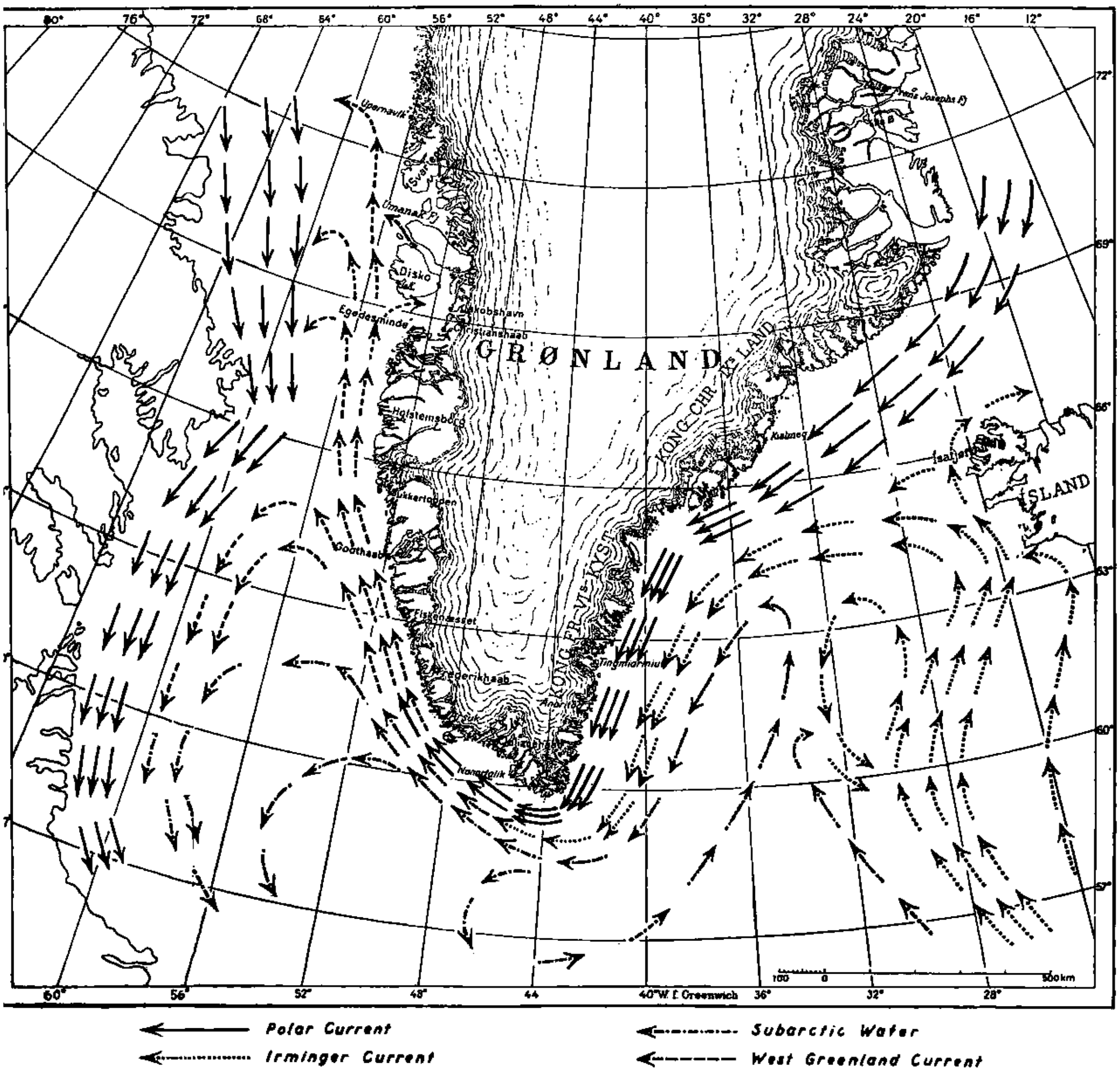


Fig.3. Surface currents in Greenland waters. (From Hansen and Hermann: Fisken og Havet ved Gronland)

supposed to be a mixture of stocks of different origin.

Had the Greenlanders' fishing effort been constant during the years, their total catch could have been used as comparative measure of the year-class strength; but, in view of the great development of the Greenlanders' fishery, especially in the years after the war, it is necessary to correct for the variation of their fishing effort. A rough measure of the relative fishing effort is obtained from the percentage of recaptures of tagged cod in different periods and from the number of boats in the Greenlanders' fishery. Table 1 gives the number of cod tagged in the Godthåb and Sukkertoppen districts (between 63°N. and 66°N. approximately) and the number and percentage of recaptures taken by Greenlanders in all districts in the year of tagging and the following three years. The mean year has been calculated with the number of cod tagged as a weighting factor for the two periods 1924-39 and 1948-58. Cod tagged in the Godthåb Fjord are not included in Table 1 as this fjord is inhabited by a local stock.

TABLE 1.

Period	Mean yr.	Cod tagged	Recaptures	Recaptures	Fishing effort relative to 1932
		No.	No.	%	
1924-39	1932	2374	66	2.78	1.0
1948-58	1954	2738	251	9.17	3.3

It appears that the percentage recaptured for the period 1948-58 was a factor 3.3 greater than the percentage recaptured for the period 1924-39.

Table 2 gives the number of rowing boats and motor boats in the Greenlanders' fishery for different years. Each motor boat has been calculated as equivalent to five rowing boats. The factor five has partly been estimated from information from fishermen, but it has also been taken into account, that with this factor the fishing effort calculated from number of boats will fit with the fishing effort calculated from tagging experiments.

TABLE 2.

Year	Rowing boats	Motor boats	Motor boats x 5	Equivalent total no. of rowing boats	Fishing effort relative to 1932
1932	1210	30	150	1360	100
1939	1410	70	350	1760	129
1945	1650	75	375	2025	149
1950	1950	360	1800	3750	276
1952	1620	450	2250	3870	285

Assuming that the fishing effort of the Greenlanders is proportional to the total number of boats as given in Column 5 of Table 2 and to the percentage recapture of tagged cod, the fishing effort of each year relative to the effort in 1932 can now be calculated. This is done in the last column in Tables 1 and 2 and plotted in Fig. 4.

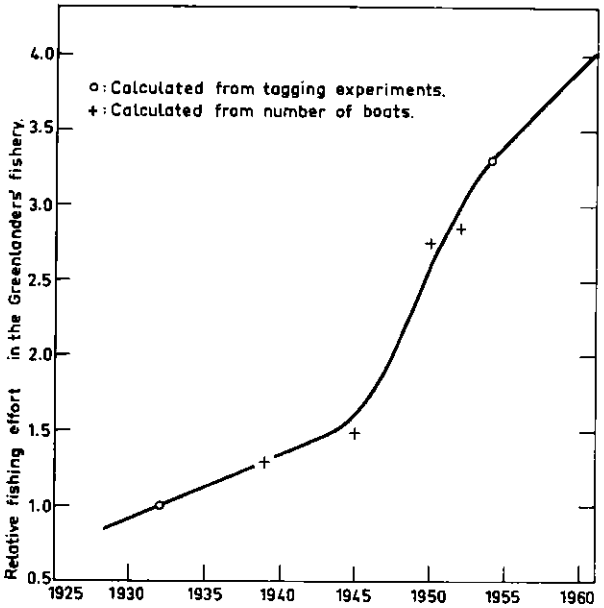


Fig. 4. Variation in relative fishing effort in the Greenlanders' Cod fishery.

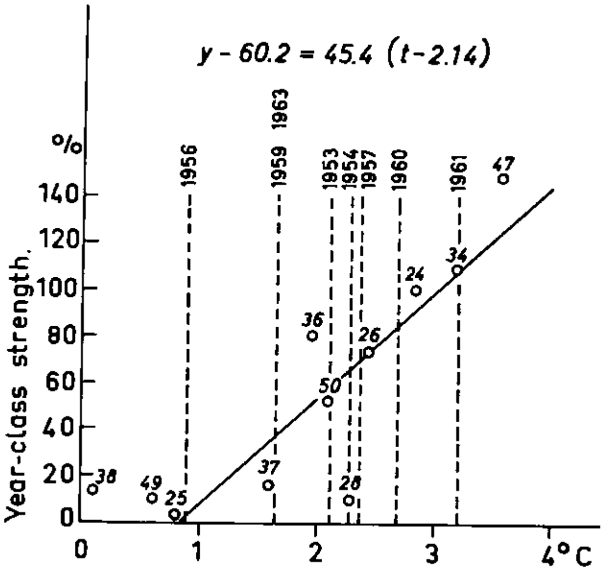


Fig. 5. Year-class strength plotted against mean temperature, surface to 45 metres over Fylla Bank in June.

The relative strength of the year-classes is now calculated in the following way: the number of cod of a certain year-class caught by the Greenlanders is divided by the relative fishing effort for the mean year of the period in which the year-class in question has been fished, *i.e.* when the year-class was 8 years old. The year-class strength is then calculated as the percentage of the strength of the 1924 year-class. The results are given in Table 3.

TABLE 3. RELATIVE STRENGTH OF THE YEAR-CLASSES 1924 - 1951

Year-class	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936	1937
Number caught in age groups V to XI in thousands	1787	57	1425	248	190	516	401	999	866	454	2741	872	2355	487
Relative fishing effort	1.00	1.03	1.08	1.12	1.17	1.22	1.25	1.29	1.33	1.37	1.41	1.47	1.56	1.66
Relative strength	100	3	74	12	9	24	18	43	36	18	109	33	81	16

Year-class	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951
Number caught in age groups V to XI in thousands	433	977	1008	1349	3950	1411	1236	3337	748	9044	1297	733	3433	1163
Relative fishing effort	1.81	1.98	2.15	2.34	2.58	2.81	2.98	3.17	3.30	3.40	3.50	3.60	3.70	3.80
Relative strength	13	28	28	32	86	28	23	59	13	148	21	11	52	17

CORRELATION BEWEEN YEAR-CLASS STRENGTH AND SEA TEMPERATURE

Table 3 shows that there is wide variation in the year-class strengths. In this section we will try to see whether this variation can be explained as an effect of the temperature conditions during the egg and early larval stage. The temperature data from West Greenland waters consist partly of surface observations from commercial vessels (collected by the Danish Meteorological Institute and published by Jens Smed, 1958, 1959 as monthly temperature anomalies for large areas) and partly of subsurface observations from research vessels.

The year-class strengths are correlated with Smed's surface temperature anomalies for Area A_1 (West Greenland waters) for the years 1924 - 39 and 1946 - 51, for the months April to July. The correlation coefficients, r, are given in Table 4.

TABLE 4.

Month	April	May	June	July	Mean temperature anomaly, April-July
r	0.14	0.53	0.15	0.42	0.38

Only the correlation coefficient for May is significant within the 0.02 probability limit. One reason for these low correlation coefficients could be that the surface temperature is not sufficiently representative of the temperature in the water layers where the cod eggs and larvae are found.

In June the cod larvae are mainly found over Fylla Bank and Lille Hellefiske Bank in the upper 50 m. The hydrographic station in this area which has been worked most frequently in June is the international station r-2 over the shallow part of Fylla Bank (63°58'N.52°44'W.). Observations have been made in June at this station in the following years: 1924,25,26,28,34,36,37,38,47,49,50,53,54, 56,57,60,61 and 1963. Thus for 11 years between 1924 and 1950 we have observations of temperature as well as strength of year-classes. In Fig. 5, year-class strength is plotted against mean temperature in June in the upper 45 m on Fylla Bank. The index numbers at the points indicate the year-classes. At the lowest temperatures it looks as though the year-class strength lies at a constant low value, but from a certain temperature the year-class strength seems to increase linearly with the temperature.

The correlation coefficient between year-class strength and the mean temperature over Fylla Bank in June is found to be $r = 0.85$. As the relationship cannot be linear over the total temperature range the correlation coefficient was also calculated omitting the observations from the "coldest" year 1938 and was found to be $r = 0.87$. Both correlation coefficients are significant ($P<0.01$). Still omitting the 1938 observations the regression line for year-class strength on temperature was found to be: $y - 60.2 = 45.4\ (t - 2.14)$. The standard deviation of the points around this regression line is equal to 25 year-class units, (25% of the 1924 year-class). This gives a measure of the accuracy with which year-class strength can be predicted from temperature observations over Fylla Bank in June.

The year-class strengths have earlier been compared with the temperatures off Fylla Bank (Hermann, 1953 and 1961). In these papers the Greenlanders' total catch of the different year-classes up to the year 1946 was used as a measure of the year-class strength and only the year-classes up to 1938 were studied. In the present paper some of the more recent year-classes have been included and, after correction for variationa in the fishing effort, they show a close relationship between year-class strength and temperature.

The mean temperatures for the water column 0 - 45 m in June for the years between 1953 and 1963 in which observations are available are indicated on Fig. 5 by hatched lines. Judging from the temperatures we would expect to get good year-classes from the years 1957, 1960 and 1961, the year-classes 1953 and 1954 should be fairly good and only small year-classes would be expected from the years 1956, 1959 and 1963.

CORRELATIONS BETWEEN NUMBER OF COD LARVAE AND SEA TEMPERATURES IN JUNE AND JULY

In 1950 and in the years 1952 - 1959 four standard sections have been worked out by the *Dana* in July in the area from Fylla Bank to Egedesminde with stramin net hauls and hydrography. From the four easternmost stramin net stations in each section and from two stations between Lille and Store Hellefiske Banks the total number of cod larvae caught has been calculated. The values for the few missing stations have been interpolated using the average percentage of the number of larvae found at stations mentioned. The catches at the westernmost stations were not included because the larvae found here will probably not benefit the West Greenland cod stock. Table 5 shows the calculated number of cod larvae.

TABLE 5.

Year	1950	1952	1953	1954	1955	1956	1957	1958	1959
Number of cod larvae	554	90	474	78	64	37	1629	187	77

It is doubtful whether these numbers are a good representation of the total mass of cod larvae off West Greenland. The larvae are not evenly distributed over the area. Thus in 1950, 554 larvae were caught on the 18 stations. Of these 319 (58%) were caught on one single station.

These numbers of larvae have been correlated with July temperatures from surface, 20 m and 40 m over both Fylla Bank, Lille Hellefiske Bank and Store Hellefiske Bank, but no significant correlations have been found. Unfortunately temperatures in June over Fylla Bank are only observed in five of these years but in these five years the number of cod larvae generally increases with increasing mean temperature (surface to bottom) over Fylla Bank in June. This confirms the hypothesis that it is during the early larval stage that the temperature conditions influence the survival of larvae.

CORRELATION BETWEEN YEAR-CLASS STRENGTH AND BAROMETRIC PRESSURE DIFFERENCES

As already mentioned a great part of the cod larvae are carried westward towards Labrador with he westgoing branch of the West Greenland Current and thus are probably lost from the West Green-and cod stock.

It is reasonable to assume that the relative strength of the two branches of the West Greenland urrent will depend to some degree on the wind conditions and specially on the onshore wind compon-nt. As a measure of this wind component, the difference in barometric pressure between Ivigtut t 61°N. lat and Jakobshavn at 69° N. lat is used. The barometric pressure differences were com-uted from the monthly means published in the Danish "Meteorologisk Årbog" for the months March to uly and correlated with the strength of cod year-classes for the years 1924 - 1951. The corre-ation coefficients found were, however, very small and very far from being significant.

Thus it looks as though the onshore wind component has no influence on the survival of the od larvae.

REFERENCES

HANSEN, P.M. 1958. Danish Research Report, 1957. *Annu. Proc. int. Comm. Northw. Atlant. Fish.*, 8: p. 27.

HERMANN, F. 1953. Influence of Temperature on Strength of Cod Year-Classes. *Ann. biol., Copenhague*, Vol. IX, p. 31.

1961. Some Considerations about Correlations between the West Greenland Stock of Cod and Environmental Factors. *Annu. Meet. int. Comm. Northw. Atlant. Fish.*, 1961. Doc. No. 34, Serial No. 844 (mimeographed).

SMED, J. 1948 to 1963. Monthly Anomalies of the Surface Temperature in Areas of the Northern North Atlantic. *Ann. biol., Copenhague*, Vol. II to XVIII.

B-15

NOTES ON THE CONDITION OF FORMATION OF THE ARCTO-NORWEGIAN TRIBE OF COD OF THE 1959-1961 YEAR-CLASSES DURING THE FIRST YEAR OF LIFE

By

A.S. Baranenkova[1]

ABSTRACT

The paper deals with the peculiarities found in the conditions of formation of the Arcto-Norwegian tribe of cod of the 1959, 1960 and 1961 year-classes during the first year of their life.

INTRODUCTION

Every year-class of cod is formed under specific conditions because of great yearly changes in the abiotic and biotic environment. It is known that the natural conditions most strongly affect the strength of year-classes during the early period of their life. A characteristic feature of cod biology is that the pelagic eggs and later, the extruding larvae are immediately exposed to the effect of local conditions on the spawning grounds. The nature of water masses (temperature and salinity, water movement and biological characteristics) determines the area of distribution of the larvae, the density of their concentrations, the feeding conditions and the predators. The direction and speed of currents result in transport of eggs, larvae and pelagic fry into various parts of the sea, thus determining the conditions of their subsequent life. The attention of investigators has long been drawn to studies of the causes of fluctuations in the strength of cod year-classes. Hjort (1914) and later, Wiborg (1957) failed to find any correlation between the numbers of liberated eggs, hatched larvae and abundance of the year-class of cod in commercial catches. From the data collected for a number of years, Wiborg (1957) concluded that the formation of rich year-classes in the Arcto-Norwegian tribe of cod was favoured by prolonged spawning, large area of spawning grounds, extension of the central spawning area to the north, prolonged period of hatching and by more rapid transport of eggs and larvae by currents to the areas of fattening of fry. The author also does not exclude such additional factors as the number of predators, availability of food and the physical and chemical characters of the environment. Wiborg assumes that the abundance of a year-class is determined during the drift of pelagic larvae or just after the fry descend to the bottom. Studying the plankton in the area of Bear Island and the western part of the Barents Sea in 1949-56, Corlett (1958) showed a relationship between the stock of plankton from mid-April to late September (*i.e.* during the pelagic larval phase) and the strength of the corresponding year-classes of cod. He also pointed out that survival of larvae and the size of the plankton stock were affected by water temperature and transport. Hill and Lee (1958) demonstrated a correlation between the volume of water transported by the West Spitsbergen Current, the strength of the south wind in April-May and the strength of corresponding year-classes of cod in the area of Bear Island. Examining the abundance of 1946-58 year-classes in the Arcto-Norwegian tribe of cod in relation to hydrological conditions, Kislyakov (1959, 1961) came to the conclusion that there is a close relationship between the yields of the year-classes and the average temperature of water masses on the spawning grounds during the spawning period. He is of the opinion that rich year-classes are associated with high intensity of atmospheric circulation, higher intensities and velocities of currents, high heat supply in water masses, dilution by coastal water, early timing of biological spring and greater depth of the 27.5-27.6 isopicnal. In warm years, due to the greater depth of the 27.5-27.6 isopicnal, eggs are found in deeper waters and are less subject to the mechanical effect of waves as compared with cold years. According to Rollefsen (1930), a number of the cod eggs are killed by mechanical damage caused by stormy weather.

In 1959-61, the Polar Institute of Marine Fisheries and Oceanography carried out special investigations on the drift of eggs and larvae of various species of fish from the spawning grounds of the north-west Norwegian coast into the Barents Sea and the area of the Bear and Spitsbergen

---

[1] Polar Institute of Marine Fisheries and Oceanography, Murmansk, USSR.

Islands. The investigations were conducted in the area limited by the latitude of Bear Island in the north, and the Lofoten region in the south, by the meridian of the Kola Gulf in the east and 5° to 10°E in the west (Fig. 1). The main routes of the drift of eggs and larvae of the Arcto-Norwegian tribe of cod pass this area. Two cruises were performed every year: one in the last ten-day period of April and in May and the other in June and early July. Standard hydrological sections were worked. The time of working the sections varied in different years, but the difference, as a rule, did not exceed two days or, occasionally, several days. Sampling of eggs and larvae of fish was accompanied by measurements of water temperature, sampling of water for hydrochemical analysis and collections of plankton. In the winters of these years the amount of "demersal" cod fry in the 0-group was estimated in the southern and north-western parts of the Barents Sea, including the areas of the Bear and West Spitsbergen Islands. The gear used for sampling plankton and ichthyoplankton during spring-summer surveys were plankton nets (gauze No. 38), egg nets (gauze No. 140) and ring trawls of perlon (3 mm mesh).

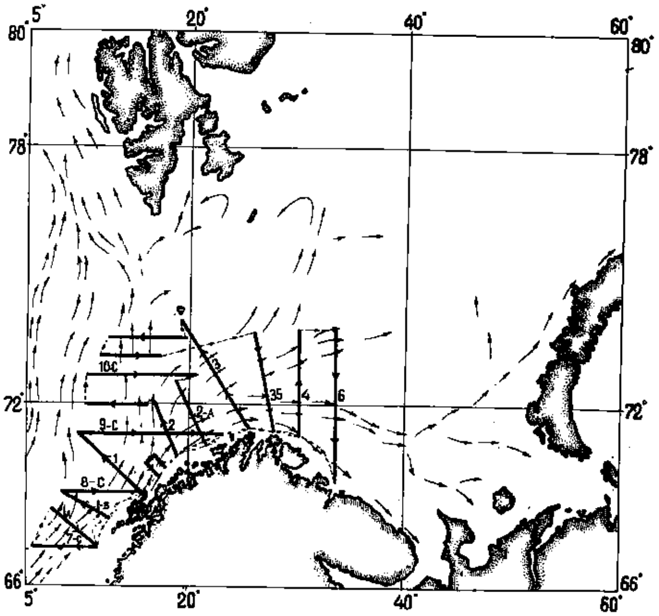


Fig. 1. Sketch map of currents and location of sections, worked during April-May and June-July 1959 and 1961. (The data on currents are taken from the works of A.I. Tantsura (1959), and A.P. Alekseev and B.V. Istoshin (1956).

For estimating the abundance of the 0-group cod, a commercial bottom trawl with a fine-mesh (10 mm) cotton net inserted into the trawl cod-end was used. Feeding of larvae (Sysoeva and Degtereva, this symposium) and "demersal" fry (Ponomarenko, this symposium) of cod of the year-classes in question was thoroughly studied.

SPAWNING OF COD

Observations on sexual maturity, stages of development of the eggs and sizes of the larvae showed a slight variation in the timing of the mass spawning of cod during these years. In 1959 and 1961, individual specimens in the area of the Rost Bank spawned in the third ten-day period of January. In January of 1960 no observations were made but in February 1960, the percentage of fish nearing the ripe and post-spawning stages was higher than in 1959 and particularly than in 1961. During these three years mass spawning started in the period from late March and April. The latest spawning period was observed in 1959. In 1960 spawning of the bulk of cod in the area of the north-west coast of Norway started and ended earlier than in 1959 and 1961. According to observations made by Wiborg (1961), mass spawning of cod in Westfjord in 1960 took place three weeks earlier than in 1959. Our analysis of material showed that mass spawning of cod in 1960 had two peak periods. This was indicated by the sizes of larvae (Table 1) and the greater percentage of eggs in early stages of development in April-May as against the same periods of 1959 and 1961. In June 1960, a group of 6-11 mm larvae was notable along with large larvae (16-26 mm). It is assumed that the second peak period of mass spawning in 1960 was caused by the approach of younger fish to the spawning grounds. In 1961 spawning was the most prolonged and ended later than in the two previous years.

DISTRIBUTION OF EGGS, LARVAE AND "DEMERSAL" FRY OF COD

The greatest numbers of eggs in April-May were found on the banks (Malang, Vesterolen and Rost banks). The distribution of eggs and larvae in the area investigated varied somewhat from year to year (Figs. 2, 3, 4). In 1961 eggs and larvae occupied a much more extensive area than in the two previous years. In 1959 the greatest drift of eggs and larvae was to the southern part of the Barents Sea. In 1960 they were carried away in great quantities to the north-west areas of the Sea. In 1961 drift was observed to the north-west areas of the Sea as well as to the southern part of the Barents Sea in the coastal branch of the current. Annual changes in the direction of

TABLE 1.

SIZES OF COD LARVAE IN mm (PERCENTAGE FREQUENCY)

Year and Month	Fishing gear	3-5	6-8	9-11	12-14	15-17	18-20	21-23	24-26	27-29	30-32	33-35	Total number	Mean size
1959 April-May	egg net	92.5	6.2	1.5									536	4.43
1960 " "	egg net	40.0	50.0	10.0									10	6.65
1961 " "	egg net	92.4	6.2	1.5									117	4.87
1959 June-July	egg net	2.2	17.8	24.5	26.6	17.8	6.7	2.2	2.2				45	12.45
1959 " "	ring trawl			2.1	22.9	31.3	28.1	5.2	4.2	1.0	4.2	1.0	96	17.70
	Combined:	0.7	5.8	9.3	23.5	27.0	21.4	4.4	3.6	0.7	2.9	0.7	141	16.02
1960 June	egg net		25.8	27.0	6.8	6.7	11.2	7.9	6.7	3.4	3.4	1.1	89	14.52
1960 "	ring trawl		3.2	3.3	-	6.4	25.8	6.5	22.5	9.7	19.4	3.2	31	23.37
	Combined:		20.0	20.9	5.0	6.6	15.0	7.5	10.8	5.0	7.5	1.7	120	16.74
1961 June-July	egg net	7.8	23.6	22.2	23.0	14.0	5.7	2.3	0.6	0.8			487	11.48
1961 " "	ring trawl			2.5	24.1	34.2	21.6	11.2	4.7	1.4	0.3		663	17.11
	Combined:	3.3	10.0	10.8	23.7	25.7	14.7	7.6	2.9	1.1	0.2		1150	14.70

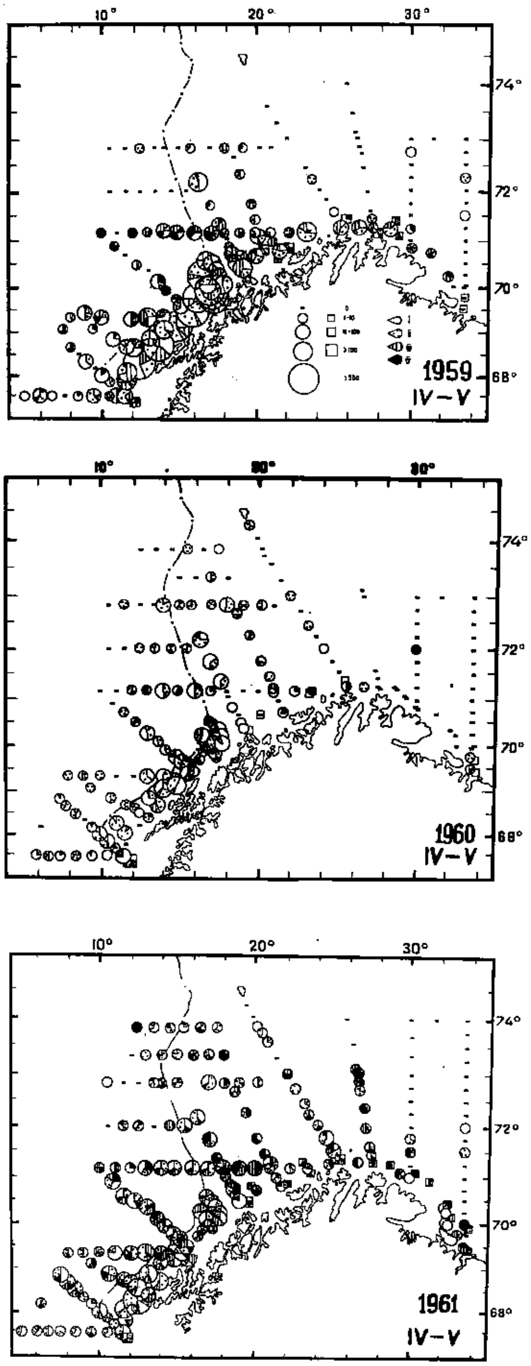


Fig. 2. Distribution of cod eggs of different stages of development in April-May 1959-1961 based on catches taken with egg net. Sizes of circles and squares indicate average amount of eggs per haul. Squares represent catches taken during second visit to the station along the paths of the route. The I-IV sectors represent the stages of development of eggs.

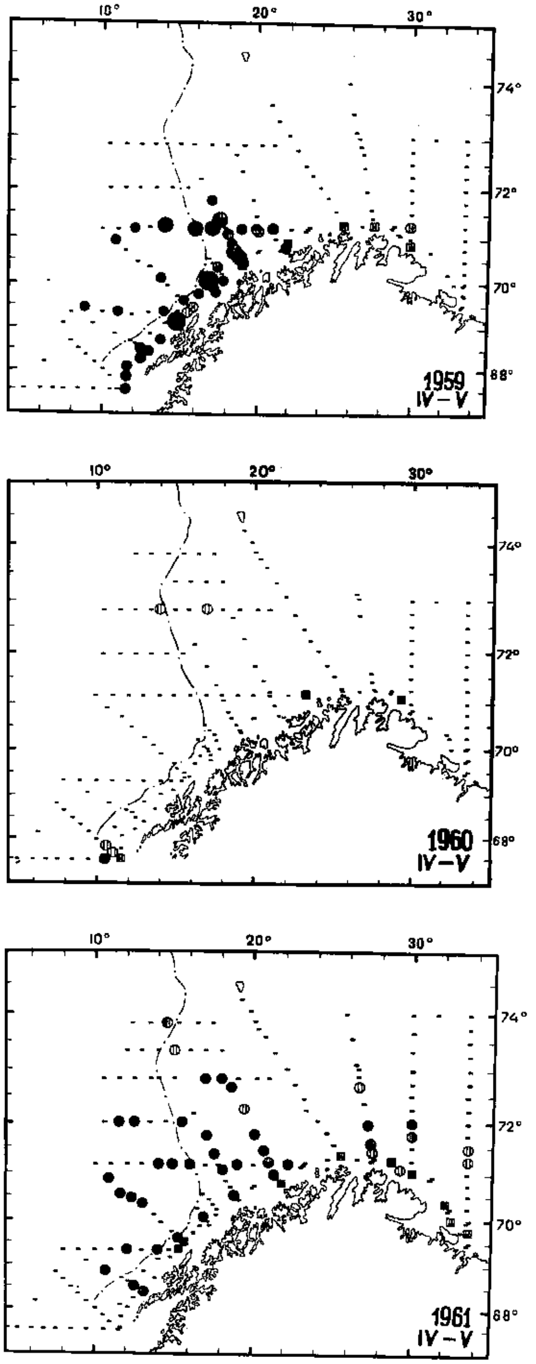


Fig. 3. Distribution of cod larvae of different sizes in April-May 1959-1961, based on catches taken with egg net.
Circles and squares indicate average amount of larvae per haul. Squares represent catches taken during second visit to the stations along the paths of the route. The key to the map is shown in Fig. 4.

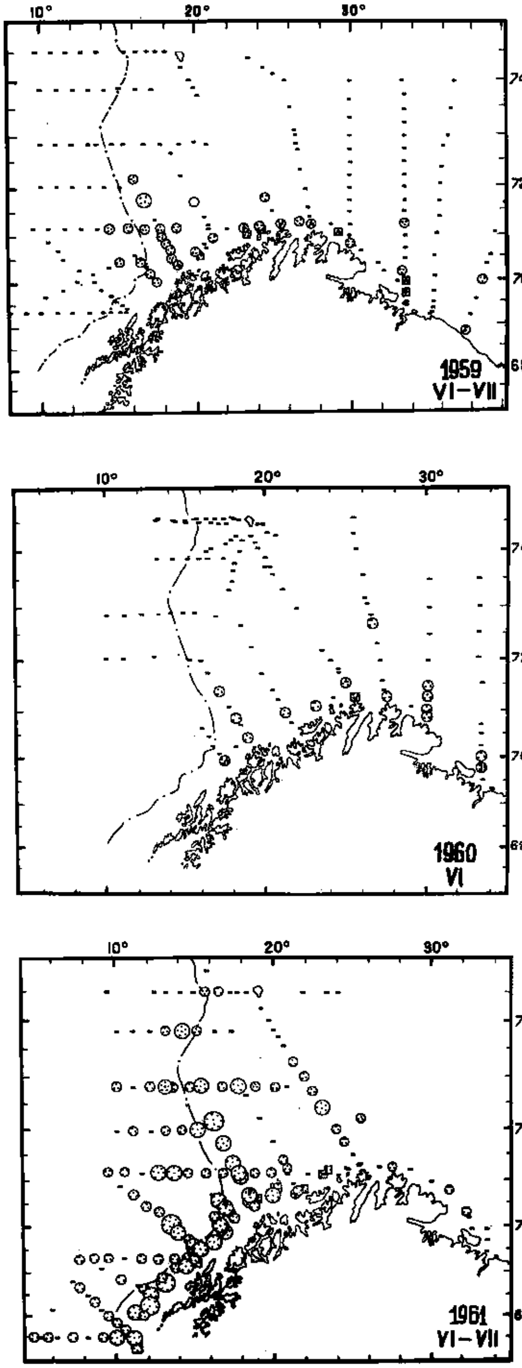


Fig. 4. Distribution of cod larvae of different sizes in June-July 1959-1961 based on catches taken with ring trawl. Circles and squares indicate the number of larvae per haul. Squares represent catches taken during second visit to the stations along the paths of the route. Sectors represent larvae sizes from 5 mm up (black) from 6 to 10 mm (shade), over 11 mm (points).

the drift of eggs and larvae were confirmed by the distribution and catch per hour of trawling of "demersal" fry of the 0-group in winter season (Figs. 5, 6, 7: Table 2).

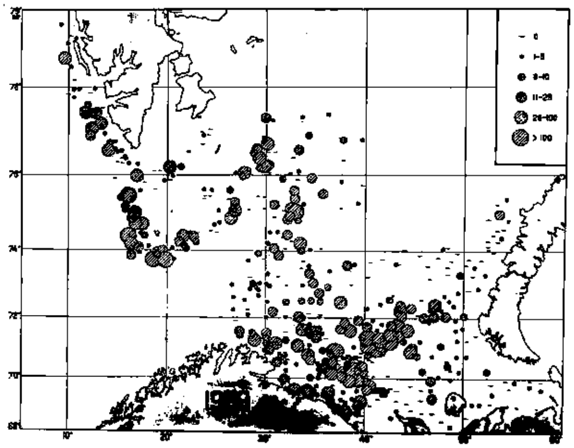


Fig.5. Distribution of the 0-group cod of the 1959 year-class. Sizes of circles indicate the number of specimens in catches per hour of trawling.

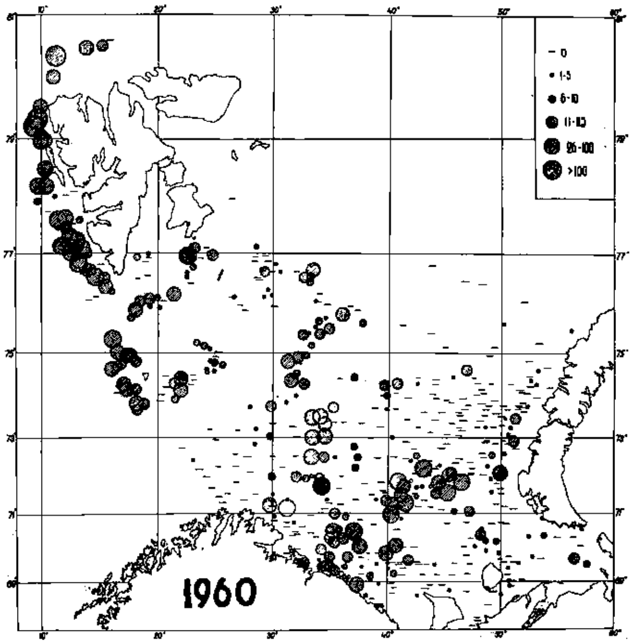


Fig. 6. Distribution of 0-group cod of 1960 year-class. Sizes of circles indicate the number of specimens taken per hour of trawling.

TABLE 2.

AVERAGE CATCHES OF 0-GROUP COD IN VARIOUS AREAS OF THE BARENTS SEA DURING THE WINTER (NUMBERS PER HOUR USING A BOTTOM TRAWL WITH COVER)

Areas	1961-1962		1960-1961		1959-1960	
	no. of hauls	no. of specimens	no. of hauls	no. of specimens	no. of hauls	no. of specimens
Southern part of the Barents Sea						
Central	111	4	108	9	168	18
West	132	2	84	10	247	8
Coastal	26	6	27	5	68	10
East	42	3	41	2	45	2
North-east	42	2	38	1	27	1
Central elevation	67	2	27	10	29	14
Total:	420	3	325	7	584	11
North-west areas of the Barents Sea						
Bear Island						
South slope	33	16	18	14	34	33
East slope	21	10	18	5	21	9
West slope	37	12	15	35	49	21
Total:	91	13	51	17	104	23
North Spitsbergen	17	141	5	39	-	-
West Spitsbergen	48	30	49	66	59	9
Zuyd Cape trench	32	7	37	14	30	30
Hope Island	23	7	19	1	27	8
Persues Elevation	44	7	14	6	17	4
Total:	255	22	175	29	137	16
West trench	-	-	-	-	11	4
Whole Sea	675	10	500	15	832	12

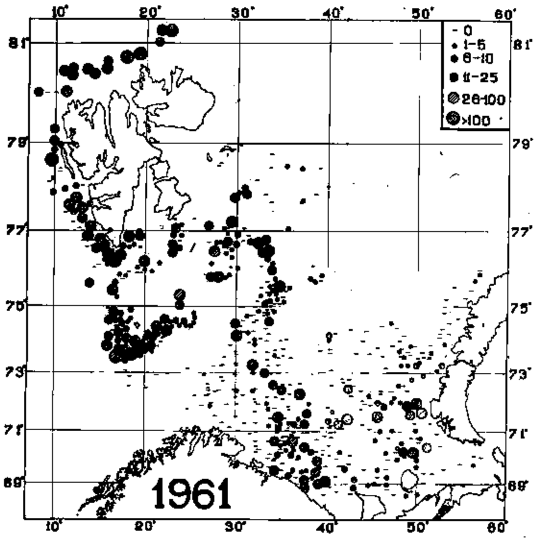


Fig.7. Distribution of 0-group cod of 1961 year-class. Sizes of circles indicate the number of specimens taken per hour of trawling.

ABUNDANCE OF EGGS, LARVAE AND "DEMERSAL" FRY OF COD

Table 3 shows average numbers of eggs and larvae per haul during the three years under review. The abundance of eggs and larvae in April-May does not correspond to that in June-July. The highest abundance of pelagic eggs and larvae in April-May was observed in 1959 (95.9 specimens per haul) and the lowest in 1960 (23 specimens). The greatest number of larvae in the period June-July was observed in 1961 (1.1 specimens per haul) and the least in 1959 (0.19 per haul). Also, the average number of eggs and larvae per haul did not correspond to the average catch of "demersal" fry per hour of trawling (Table 2). On the contrary, the number of eggs and larvae was the least in 1960 and the total number of "demersal" fry all over the Sea was the greatest (15 specimens per hour's trawling against 12 in 1959 and 10 in 1961). Such a discrepancy could be accounted for by a number of factors, particularly by different rates of survival of specimens in various years. But very likely it is to be explained by the fact that

TABLE 3.

AVERAGE NUMBERS OF COD EGGS AND LARVAE PER HAUL

Year		April-May						June - July		
		Egg net								
		Eggs			Larvae	Eggs + larvae		Larvae		
		Stages 1 and 2	Stages 3 and 4	Total		Stages 1 to 4 + larvae	Stages 3 and 4 + larvae	Egg net	Ring trawl	Egg net + Ring trawl
1961	Specimens	19.22	5.34	24.56	0.24	24.80	5.58	0.63	3.97	1.11
	%	78.30	21.70	100						
	No. of hauls	426	426	426	426	426	426	440	74	514
1960	Specimens	8.64	0.64	9.28	0.02	9.30	0 66	0.31	0.11	0.26
	%	93.10	6.90	100						
	No. of hauls	393	393	393	393	393	393	275	105	380
1959	Specimens	80.42	14.09	94.51	1.41	95.92	15.50	0.08	0.50	0.19
	%	85.09	14.91	100						
	No. of hauls	374	374	374	374	374	374	334	118	452

the area of distribution of eggs and larvae was not fully covered by our investigations. Wiborg (1961) found that the number of eggs and larvae in the coastal waters of Norway, in Westfjord, was higher in 1960 than in 1959 whereas on the outside of the Lofoten Islands, near Eggum, it was lower. According to our data, the number of eggs and larvae in the open part of the Sea, near the north-west coast of Norway, was also much higher in 1959 than in 1960. The difference in the numbers of eggs and larvae in coastal waters and in open areas of the Sea has been noticed previously in my own work (unpublished) on the 1948 and 1949 year-classes. According to Wiborg (1949), the number of larvae in the Westfjord was greater in 1949 than in 1948, whereas according to our data, the number of larvae on the outside of the Lofoten Islands in the high sea was greater in 1948 than in 1949.

The average catch of the 0-group varied during these years in different areas. In the southern part of the Sea and in the area of Bear Island, a decrease in the average catch of fry per hour of trawling was observed from 1959 to 1961, whereas the average catch of fry in the areas to the north of Bear Island was the highest in 1960 (29 specimens) and the lowest in 1959 (16 specimens).

According to the estimates of the young of various ages, the 1959 year-class can be evaluated as an average one. On the basis of total catches of the 0-group fry over the whole area, it can be assumed that the 1960 and 1961 year-classes also approximate to the average, with only this difference, that the 1960 year-class is somewhat more, and the 1961 year-class somewhat less, abundant than that in 1959.

The survival rate also varies by years. The ratio of the number of larvae caught during the second survey (in June-July) to the number of eggs and larvae caught during the first survey (April-May) may be expressed as a percentage: from this, the survival rate of eggs and larvae in the interval between the two surveys can be estimated. This ratio is shown in Table 4. On the left side of the table the eggs of all stages of development are presented: on the right side of the table, only the eggs of the third and fourth stages of development, when their identification as cod was undoubted. The stages of development of cod eggs are given according to Rass (1949). For 1959 the percentage is quite low. In this year, a high mortality rate during the early stages of development of eggs appeared to be due to weather conditions: in the spring of 1959 there were more stormy days than in 1960 and 1961.

TABLE 4.

PERCENTAGE RATIO OF COD LARVAE DURING JUNE-JULY TO EGGS AND LARVAE IN APRIL-MAY (BASED ON EGG NET SAMPLES IN BOTH PERIODS AND RING TRAWL SAMPLES IN JUNE AND JULY)

Year	To the eggs of all stages of development and to larvae			To the eggs of the 3rd and 4th stages of development and larvae		
	egg net	ring trawl	egg net + ring trawl	egg net	ring trawl	egg net + ring trawl
1961	2.54	16.00	4.47	11.29	71.15	19.89
1960	3.33	1.17	2.79	46.97	16.66	39.39
1959	0.08	0.52	0.19	0.52	3.23	1.22

In 1960 and 1961 the percentage of the number of larvae caught in June was higher than the percentage of the number of eggs and larvae caught in April-May, which indicates a higher survival rate. The high indices (3.33 and 46.97%) obtained with the egg net in 1960 (Table 4) can be explained by the presence of the second peak in mass spawning which resulted in the appearance of many eggs in early stages of development in April and May, and of small larvae which are easy to catch by egg net in June. The indices obtained for ring trawl catches reflect the changes in the number of larvae which took place during the first peak period of spawning. These indices evidently lie between those of 1959 and 1961. A great reduction in the abundance of the 1960 year-class in the southern part of the Sea took place, apparently, at an older age. This assumption is confirmed by the data published by Ponomarenko (this symposium) which indicate that a great number of the fry of the 1960 year-class had been eaten by young cod of the II and III age groups in the winter season of 1960-1961. Greater numbers of fry of this year-class than of the 1959 and 1961 year-classes were eaten.

The survival rate of eggs, larvae and pelagic fry of the 1961 year-class was the highest of the three year groups studied. However, the number of "demersal" fry in almost all areas, except North Spitsbergen, was found to be the lowest. It can, therefore, be assumed, that a high mortality rate of this year-class took place in the pelagic stage before "settling" of fry or during their transition to the near-bottom way of life. "Demersal" fry in the southern part of the Sea during winter season were eaten by older young of cod in inconsiderable amounts which, in the opinion of Ponomarenko (this symposium), was due to their low abundance.

The effect, on the total abundance of the 1961 year-class, of extensive transportation of fry to such a distant area as North Spitsbergen will be studied further. The estimates of the young in the north-western part of the sea in autumn of 1962 showed a great reduction in catches of the young of the 1961 year-class per hour of trawling (less than one specimen on the average).

THE CONDITION OF DRIFT OF COD EGGS AND LARVAE

The years investigated were characterized by different temperature and salinity conditions, intensity of various branches of the warm current, periods of development and plankton biomass.

The year 1961 was characterized by an average temperature regime: 1959 was warmer and 1960 was the warmest of the three (abnormally warm for the Norwegian Sea). The average temperatures in the sections investigated in 1959-1961, and changes in temperature in these sections from year to year, (Kislyakov and Borovaja, 1963) are shown in Tables 5 and 6. As seen from the Tables, temperature conditions during a year and in different years changed in different ways in various parts of the area, on the routes of drift of eggs and larvae. The years 1959, and particularly, 1960 were characterized by an intensive inflow of Atlantic water into the Norwegian Sea. Beginning in the spring of 1961 a reduction in advection of heat by the current was observed in the Norwegian Sea (Alekseev *et al.*, 1963).

The intensity of the branches of warm currents varied: for example, the eastern branch of the Norwegian Current and the West Spitsbergen Current were the most intensive in 1960. Because of

TABLE 5.

AVERAGE TEMPERATURE IN THE 0-200 m LAYER AND IN STANDARD SECTIONS DURING APRIL-MAY OF 1959, 1960 AND 1961 (ACCORDING TO KISLYAKOV, 1963)

Sections	1959	1960	1961
7-c	6.38	7.12	6.79
8-c	6.20	6.27	6.44
9-c	6.34	6.26	5.95
72°00'	5.44	5.92	5.31
10-c	5.62	5.63	4.99
73°50'	-	5.30	4.93
1A	6.61	6.31	6.55
1B	6.87	6.45	6.05
1	6.15	6.96	6.01
2	6.10	6.34	5.81
2A	5.63	6.10	5.54
3	4.82	5.03	4.60
35	4.43	4.58	4.27
4	4.16	4.32	3.85
6	3.59	3.84	2.96

TABLE 6.

CHANGE IN AVERAGE TEMPERATURE BETWEEN YEARS IN SECTIONS OF THE 0-200 m LAYER DURING APRIL-MAY (ACCORDING TO KISLYAKOV, 1963)

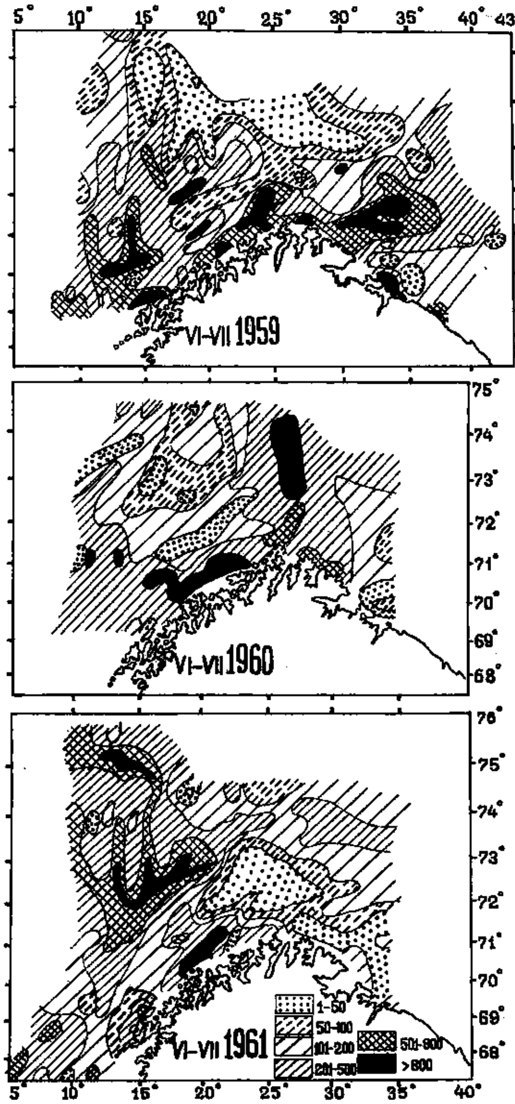
Sections	Change in temperature		
	from 1959 to 1960	from 1960 to 1961	from 1959 to 1961
7-C	+0.74	-0.33	+0.41
1A	-0.30	+0.24	-0.06
1B	-0.42	-0.40	-0.82
8C	+0.07	-0.17	+0.24
1	+0.75	-0.70	-0.14
9C	-0.08	-0.31	-0.39
72°N	+0.48	-0.61	-0.13
10C	+0.01	-0.64	-0.63
73°50'N	-	-0.37	-
2	+0.24	-0.53	-0.29
2A	+0.47	-0.56	-0.09
3	+0.21	-0.43	-0.22
35	+0.15	-0.31	-0.16
4	+0.16	-0.47	-0.31
6	+0.25	-0.88	-0.63

this, the temperature in the West Spitsbergen Current was higher in 1960 than in 1959 and 1961. In 1959 the intensities of the branch of the North Cape Current and of the branch of the Murmansk Coastal Current were higher than in 1960 and 1961. Throughout the year, positive temperature anomalies were observed in the Murmansk Coastal branch. Kondratsova (1961) is of the opinion that the year 1959 in the Coastal branch was one of the warmest in the period from 1953 to 1960.

The intensity of the main branch of the Murmansk Current in 1959 was low. The north branch of the North Cape Current was characterized by a lower intensity as compared with the Murmansk branch. In 1960 the intensity of the main branch of the Murmansk Current was high, and the intensity of the Murmansk Coastal Current was low (Kondratsova, 1962). In 1961 the north branch of the North Cape Current was characterized by a particularly high intensity of all the branches in the Barents Sea. In the second half of the year the temperature in this branch was abnormally high (Kislyakov and Borovaja, 1963).

The salinity of water masses in the area of the north-western and north coasts of Norway was highest in 1960, somewhat lower in 1959 and lowest in 1961. In 1961 the salinity in the east branch of the Norwegian Current was several hundredths of parts per mille lower than in 1960. The 35.2% isohaline extended 200 miles farther to the south as compared with 1960 (Kislyakov, 1963). The most distinctive feature of the year 1961 was the extension of coastal diluted waters from Fugloy and Sarö Islands far to the north and their mixing with the Bear Isle Current which was also greatly diluted by fresh water in 1961. As a result of this, waters with salinity over 35 °/oo could not penetrate into the surface layer of the Barents Sea. In the spring of 1959 and 1960 such a wide spreading of coastal waters was not observed. In June and July of 1961 there was further dilution of coastal waters flowing outwards from the area of the north-west coast of Norway towards the north and from the Bear-Spitsbergen region towards south-west. These distributions of waters influenced the distribution of cod larvae and plankton (Figs. 8, 9).

As a result, in that year, no close relation was observed between the distribution of larvae and the abundance of "settled" cod fry on the one hand, and the intensity of branches of the warm currents on the other. Such a relationship, between the distribution of larvae and the intensity of current branches, was quite obvious in 1959 and 1960 and was reported earlier by Kislyakov (1961) for the fry of the 1946-58 year-classes in the Arcto-Norwegian cod. The transport of a great number of fry into the Spitsbergen area in 1961, when the intensity of the West-Spitsbergen Current



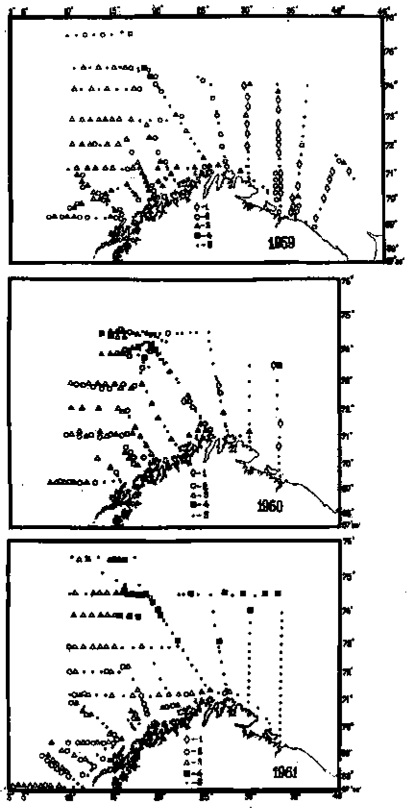


Fig. 9. Distribution of warm water (white) and cold water (black) organisms in June-July of 1959-61 (according to A.A. Degtjareva).

1 — *Physophora*
2 — *Limacina retroversa*
3 — *Collozoum*
4 — *Limacina helicina, Aeginopsis*
5 — not present in the catch

Fig. 8. Plankton biomass (in mg/m^3) in June-July of 1959-61 (according to A.A. Degtjareva).

1 — 1-50
2 — 51-100
3 — 101-200
4 — 201-500
5 — 501-800
6 — > 800

was reduced (as compared with 1960) can be explained, Kislyakov believes, by the presence in 1961 of a peculiar watershed in the area between the north coast of Norway and Bear Island. The appearance of this watershed was caused by a high water level in this part of the Sea, which obstructed penetration of the Antarctic waters into the Barents Sea and resulted in driving away a great number of eggs and larvae with freshened waters from the coastal zone of Norway into the high seas. The existence of such hydrological conditions in this area is considered by Adrov (1957) as quite normal. In May and June, northern and eastern winds predominate there: these impede the North Cape Current and carry away greatly freshened waters into the open Sea. Just such an intensive outflow of freshened waters from coastal areas was observed in 1961.

From the data obtained by A.A. Degtereva, who studied the plankton in these years, the biological spring (beginning of the *Calanus* spawning) off the north-west coast of Norway began earlier in 1960 (late March) than in 1959 and 1961 (the first ten-day period of April). The development of phytoplankton and the spawning of *Calanus* in the years 1959 and 1960 were observed earlier in the coastal zone, and somewhat later in deep water areas located outside the continental slope. In 1961, unlike the two previous years, spawning of *Calanus* off the coasts and in the high seas took place at the same time. As a result, the development of *Calanus* in the eastern branch of the Norwegian Current began earlier in 1961 than in 1959 and 1960. In 1961 the period of spawning of *Calanus* was more prolonged as was shown by the simultaneous presence in plankton samples of great quantities of eggs, nauplii and various copepodite stages of plankton. In 1959, and particularly in 1960, the period of *Calanus* spawning was considerably shorter. All this affected the abundance of plankton as well as its biomass. As a result the highest abundance for the spring season (late April-May) was observed in 1961, and the highest biomass in 1960 (Table 7). The high abundance of *Calanus* in 1961 has to be accounted for by the presence of great amounts of nauplii and early stages, whose proportion by weight was inconsiderable.

TABLE 7.

ABUNDANCE OF *Calanus* AND BIOMASS OF PLANKTON, 1959-1961.

Calanus IS SHOWN AS NUMBERS UNDER 1 m^2 IN THOUSANDS ALONG 4 SECTIONS (67°31'N, 71°10'N, NORTH CAPE TO BEAR ISLAND AND KOLA SECTION TO 33°30'E) BIOMASS IS EXPRESSED IN mg/m^3 IN THE WHOLE AREA OF THE INVESTIGATIONS

Year	Abundance of *Calanus*						Plankton biomass	
	April-May			June-July				
investigated	nauplii	copepods	total	nauplii	copepods	total	April-May	June-July
1961	62.6	32.2	94.8	1.8	14.9	16.7	182.1	255.3
1960	21.9	40.7	62.6	6.2	28.4	34.6	228.7	455.3
1959	24.3	34.3	58.6	7.2	46.5	53.7	112.7	443.9

In 1960, because of earlier spawning of *Calanus* in the coastal zone at the time when observations were made, they had reached later stages of development (III, IV and even V). Small crustaceans in these stages were comparatively scarce but, because of their size, they resulted in a very high biomass. The only exception was the North Cape - Bear Island section, where in 1960, due to delayed spawning of *Calanus*, the abundance and biomass of plankton were lower than in the years 1959 and 1961.

In the summer season (June-July) the bulk of plankton was represented by *Calanus finmarchicus* of copepodite stages IV and V, the so-called "Red *Calanus*". The most extensive spreading of Red *Calanus* towards the east in the coastal zone was observed in 1959 (Fig. 8), less extensive in 1960: in 1961 the border of the area of their distribution was found in the region of the North Cape-Bear Island section. In 1961 in the south-west part of the Barents Sea between the North Cape and the Kola sections, *Calanus* were almost absent, and the main components of zooplankton were represented by *Oithona similis* and *Oncaea borealis*. This distribution of *Calanus* resulted in an abrupt reduction of their abundance and biomass in the south-west part of the Barents Sea (Fig. 8), which affected the total biomass (Fig. 7). In the Eastern branch of the Norwegian Current, however, plankton biomass was rather high.

These data show the existence in the period reviewed of a close relationship between the distribution and direction of the drift of eggs, larvae and pelagic fry of cod, the plankton organisms and the movement of water masses. Annual changes are also clearly revealed by the data on distribution of warm water organisms (Fig. 9). The main drift of these organisms in June-July of 1961 took place in the eastern branch of the Norwegian Current, whereas their transport to the southern part of the Barents Sea was not observed.

Most interesting data on the life of larvae in various branches of current are reported by ysoeva and Degtereva in a paper presented to this symposium (see p. 412). A study of feeding f larvae and pelagic fry of cod by these authors showed that the distribution of the larvae was elated to the greatest concentrations of their main food - *Calanus finmarchicus*. Thus, better onditions for the feeding of larvae and pelagic fry existed in those branches of the currents here their main drift was observed. In the branches of the currents where the abundance of *'alanus* was not high, as in 1961 in the southern part of the Barents Sea, large larvae had to feed n other numerous, but smaller organisms (in particular, *Oithona similis* and *Evadne nordmani*), which nfluenced their weight.

SUMMARY

. As a result of the three years' investigations some peculiarities were found in formation of the Arcto-Norwegian tribe of cod of the 1959, 1960 and 1961 year-classes during the first year of life. These years differed in relation to the temperature and salinity of the water, the intensity of different branches of the currents, the periods of development and plankton biomass.

Variations were observed in the timing of the mass spawning and the total duration of cod spawning, in the distribution and abundance of eggs, larvae and "demersal" fry of cod and in the conditions for the feeding of larvae. For every year-class, there was a characteristic period when greatest decrease in abundance occurred.

. A close relationship was observed between the biological processes and the annual changes in the dynamics of water masses.

The main drift of eggs and larvae of cod, the highest biomass of plankton and the most favourable conditions for the feeding of cod larvae were found mainly in those branches of the currents which were more intensive in the given year.

. The distribution of cod larvae in the branches of the currents coincided with that of warm water plankton organisms. An absolute conformity was observed between the periods of spring development of plankton and spawning of cod.

. The investigations showed the complexity of the problem of revealing the factors determining the strength of individual year-classes of the Arcto-Norwegian tribe of cod.

REFERENCES

ADROV, N.N. 1957. "Hydrological investigations in the Kopytov area". *Trudy PINRO*, 10: 198-211, Fig. 12, Table 1.

ALEKSEEV, A.P. and B.V. ISTOSHIN. 1956. "Scheme of constant currents of the Norwegian and Greenland Seas". *Trudy PINRO*, 9: 62-68, Fig. 4.

ALEKSEEV, A.P., B.V. ISTOSHIN, and L.P. SHMARINA. 1963. Soviet Hydrological Investigations in the Norwegian and Greenland Seas in 1961. *Ann. biol. Copenhague*, 18 (1961): 24-26, Fig. 30-33.

CORLETT, J. 1958. Plankton in the western Barents Sea and the year-class strength of the Arcto-Norwegian Cod. *J. Cons.* 23 (3): 354-356.

HILL, H.W. and A.J. LEE, 1958. The effect of wind on water transport in the region of the Bear Island fishery. *Proc. roy. Soc. Edinb.* (B), 148: 104-116.

HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in light of biological research. *Rapp. Cons. Explor. Mer*, 20: 1-228.

KISLYAKOV, A.G. 1959. "Temperature conditions and yields of year-classes of the cod, spawning off the north-west coast of Norway". *Scientific and Technical Bulletin PINRO*, No. 1/9, p. 22-26, Fig. 3, Table 5.

KISLYAKOV, A.G., 1961. "The relation of hydrological conditions to fluctuations in the abundance of cod year-classes". Transactions of the meeting of the Ichthyological Commission of Academy of Sciences of the USSR, 13: 260-264, Fig. 3, Table 2.

1962. Hydrographic conditions in the Norwegian Current and the North Cape Current in the spring of 1960. *Annu. biol. Copenhague*, 29 (1960): p. 25, Fig. 2, Table 1.

1963. Hydrological Conditions in the north-eastern part of Norwegian Sea and the adjacent areas of the Barents Sea in April-June 1961. *Ann. biol. Copenhague*, 28 (1961): 26-29, Fig. 6, Table 2.

KISLYAKOV, A.G. and L.X. BOROVAJA, 1963. Hydrological Conditions in the Barents Sea in 1961. *Ann. biol. Copenhague*, 28 (1961): 29-33, Fig. 37-42, Table 3.

KONDRATSOVA, O.F. 1961. "The characteristics of temperature conditions of the Murmansk coastal waters in 1959". Transactions of the Murmansk marine biological institute (MMBI), 3/7, p. 5-14, Fig. 7, Table 4.

1962. "Heat conditions in the south part of the Barents Sea in 1960". Transactions of MMBI, 4/8, p. 3-10, Fig. 9, Table 1.

PONOMARENKO, I.Ja. 1964. "Comparative characteristics of some biological indices of the bottom stages of 0-group cod belonging to the 1956, 1958-1961 year-classes". *This symposium Contribution No. B-7.*

RASS, T.S. 1949. "Composition of ichthyofauna of the Barents Sea and systematical indications of fish eggs and larvae of this reservoir". Materials on fish reproduction and development in the North Seas. *Trudy VNIRO*, 27: 9-65, Fig. 32, Table 5, bibliography.

ROLLEFSEN, G. 1930. Observations on cod eggs. *Rapp. Cons. Explor. Mer*, 65: 31-34, Fig. 2.

SYSOEVA, T.K., and A.A. DEGTEREVA, 1964. "The Relation between the Feeding of Cod Larvae and Pelagic Fry and the Distribution and Abundance of their Principal Food Organisms". *This symposium Contribution No. B-16.*

TANTSURA, A.I. 1959. "Currents of the Barents Sea". *Trudy PINRO*, 11: 35-53, Fig. 7, Table 1, bibliography.

WIBORG, K.F. 1949. The occurrence of fish eggs and larvae along the coast of Northern Norway during April-June 1948 and 1949. *Ann. biol. Copenhague*, 6: 12-16, Fig. 15.

1957. Factors influencing the size of the year-classes in the Arcto-Norwegian tribe of cod. *Fiskeridir. Skr. Havundersøk.*, 11, No. 8.

1961. Forekomst av egg og yngel av fisk i vest of nordnorske kyst og bankfarvann våren 1960. *Fiskets Gang* No. 9, p. 190-195, Fig. 8, Table 4.

B-16

THE RELATION BETWEEN THE FEEDING OF COD LARVAE AND PELAGIC FRY AND THE DISTRIBUTION AND ABUNDANCE OF THEIR PRINCIPAL FOOD ORGANISMS

By

T.K. Sysoeva and A.A. Degtereva[1]

ABSTRACT

This paper summarizes 3 years' investigations (1959-1961) on the feeding of larvae and pelagic ry from the Arcto-Norwegian cod stock. .

The main food item of larvae and pelagic fry in the first three months of their life is *Calanus inmarchicus*. The larvae and fry feed on *C. finmarchicus* in different periods of life and at dif-erent stages of development, such as nauplii, younger and older copepodites. The close relation f the life of cod larvae and pelagic fry with that of *Calanus finmarchicus* is supported by the fact hat, in June of all the years studied, coincident quantitative occurrences of larvae and fry of cod d *C. finmarchicus* were observed in different branches of the currents.

Oithona similis, Pseudocalanus elongatus, Acartia cluasi, Evadne nordmanni and other species ich smaller than *Calanus finmarchicus* serve as secondary food for larvae and fry of cod. They ecome especially important when there is a lack of *Calanus finmarchicus* in the plankton. The mini-um abundance of *Calanus finmarchicus* in the plankton when the intensity of feeding of cod larvae d fry decreases is from 5,000 to 18,000 specimens under 1 m^2.

Investigations into the problem of the formation of rich and poor year-classes were carried t regularly from 1959 to 1961. The present paper deals with the analysis of the material relating the feeding conditions of larvae and pelagic fry of cod. The authors used the data on spawning, undance and distribution of eggs, larvae and fry which are published by Baranenkova (this sympo-ium). Some data on the food composition of larvae and pelagic fry of cod as well as on their se-ective ability were obtained previously by Wiborg (1948, 1960).

Our material permitted us to get a generalized picture of the regular changes in the feeding young cod during the three months of their life, from the moment when they begin to feed freely til they reach a length of 42 mm. This part of cod ontogenesis can be divided into four periods the basis of characteristics of the feeding and morphology of larvae and pelagic fry (Fig. 1).

FIRST PERIOD. The larvae, just beginning active feeding, feed on minute slow moving plankton, inly on nauplii of *Calanus finmarchicus*. Their length is 3.2-7.0 mm. A characteristic morpho-gical feature of larvae in this period is an undifferentiated fin fold.

SECOND PERIOD. The larvae gradually begin to take more active and, with increasing length, rger organisms, such as Copepoda in different copepodite stages. Nauplii and copepodites of *lanus finmarchicus* and *Oithona similis* prevail. The larvae are 7.0-19.0 mm in length. During is period paired and unpaired fins, stomach, pyloric caeca and barbel are formed. Thus, by the eginning of the third period the larvae are already transformed into the fry.

THIRD PERIOD. The fry consume comparatively large organisms, mainly *Calanus finmarchicus* at e IV - V copepodite stages ("red *Calanus*"). The length of fry ranges from 19.0 to 35 mm. They e gradually acquiring their characteristic "chess" pigmentation.

---

[1] Polar Research Institute for Marine Fisheries and Oceanography, Murmansk, USSR.

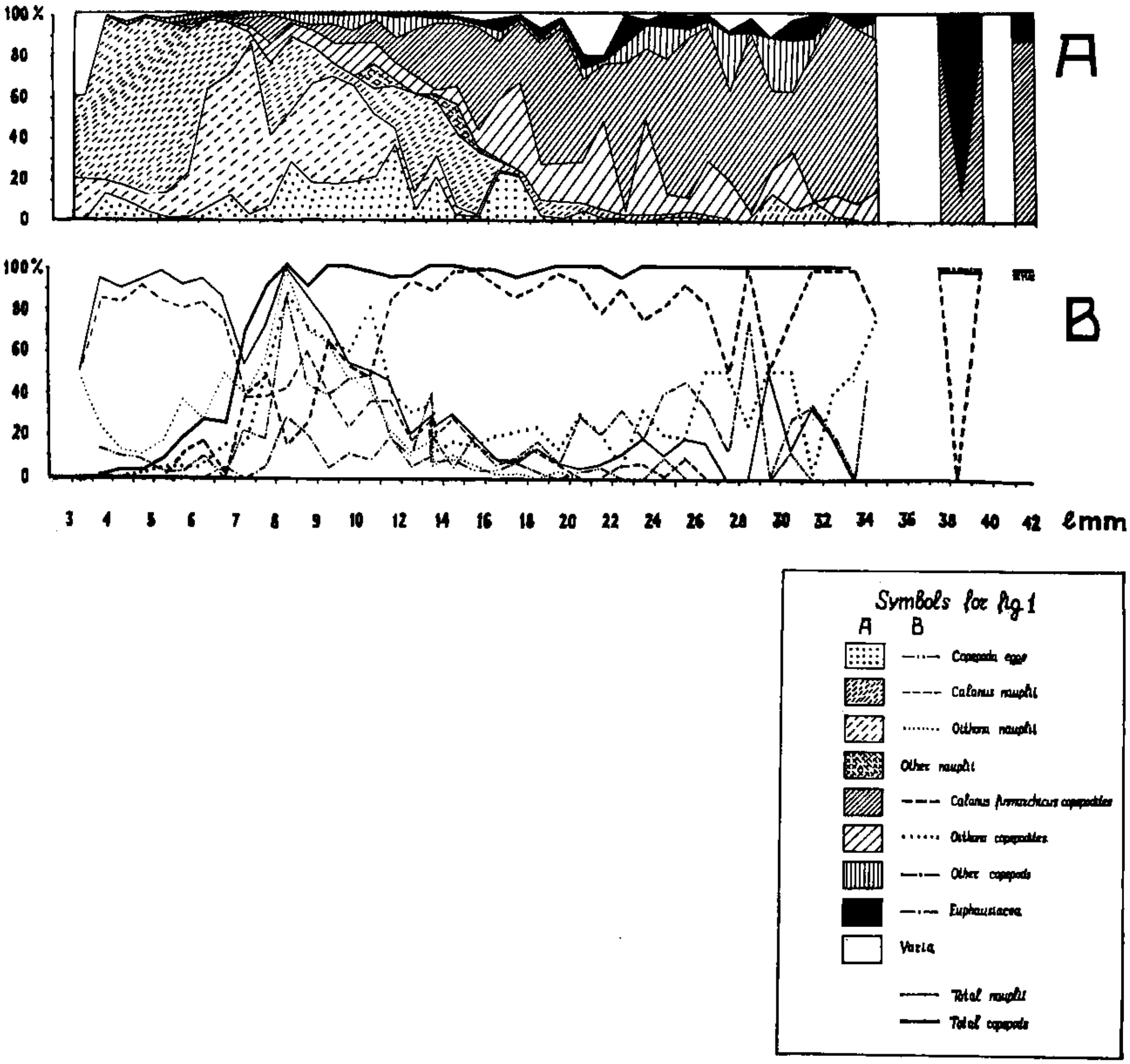


Fig. 1. Changes in the composition of the food of larvae and pelagic fry of cod with increasing length.
A. Importance of the main food organisms (numbers in %).
B. Occurrence of the main food objects (numbers of digestive tracts containing food in %).

FOURTH PERIOD. This period is characterized by a transition of fry to the consumption of young Euphausiacea. According to Wiborg (1960) and Ponomarenko (this symposium), Euphausiacea become the main food of cod fry and, as was observed by Ponomarenko, influence the indices of fullness, fatness and nutritional condition of fingerlings.

Each period consists of several stages characterized by changes in feeding and morphology. These stages cannot be discussed in this short paper. The size limits of these stages are designated in Fig. 2(B).

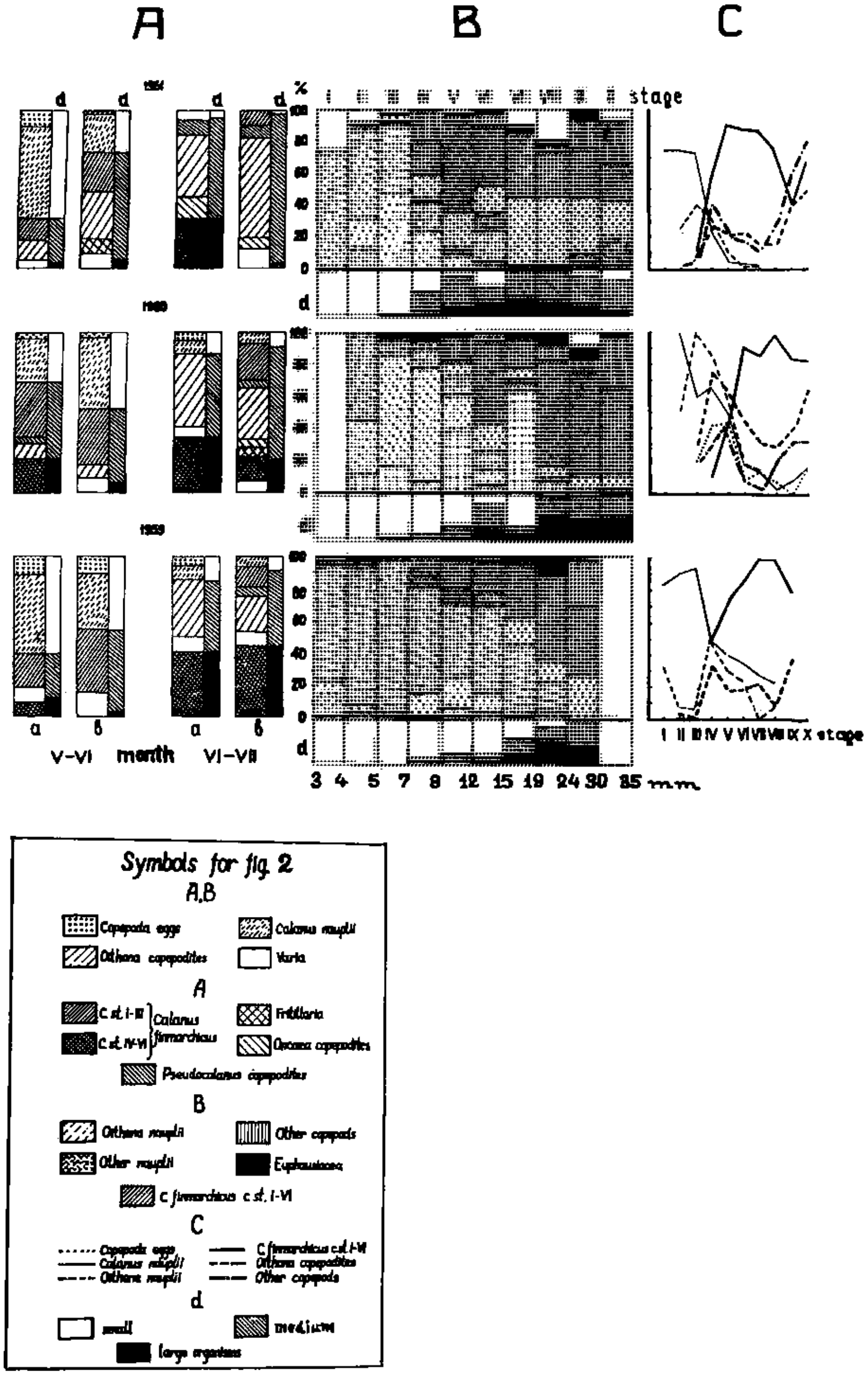


Fig. 2. Plankton composition in the sea (A) and composition of food of larvae and pelagic fry of cod (B,C) in different years.

A. Number of organisms as a percentage of the total. (a — Norwegian Sea; b — Barents Sea.)

B. Number of organisms as a percentage of the total.

C. Percentage occurrence.

D. Importance of small, medium and large organisms in plankton and in the food of larvae and pelagic fry (number of organisms in %).

It is clear from the above summary, that the life of cod larvae and fry is closely related to the life cycle of *C. finmarchicus*, the most numerous zooplankter in the Barents and Norwegian Seas. In the second half of April, when active feeding of cod larvae starts, nauplii of *C. finmarchicus*, the basic food of larvae at the first stages of development, occur in the plankton in great quantities. In late May, the larvae become more active (second period) and can take more active food organisms, namely *Calanus finmarchicus* of the I-III copepodite stages, which appear by this time in the plankton. In June, most of the larvae reach a length of about 20 mm and feed on "red *Calanus*" which develops at this time over a large sea area.

In June, a coincidence of the quantitative distribution of cod larvae with that of *C. finmarchicus* was observed in separate branches of the currents in all the 3 years investigated. In 1959, the main mass of larvae was carried into the southern part of the Barents Sea. The abundance of *C. finmarchicus* in 1959 was also higher in the southern part of the Barents Sea where great biomasses of this organism were recorded over large areas (Fig. 2A and Fig. 8 in the paper by Baranenkova, this symposium). In 1961, most of the larvae drifted into the area of Bear Island and Spitsbergen where greater abundance and biomass of *C. finmarchicus* was observed (Fig. 2A and Fig. 8 in the paper by Baranenkova, this symposium). The year 1960 was intermediate in respect to the abundance of larvae and distribution of plankton biomass in June in the area investigated. Such a coincidence of the quantitative distribution of *C. finmarchicus* with that of the larvae and fry of cod is evidently the consequence of the general factors influencing the distribution both of the food organism and of its consumer. A similar phenomenon was recorded by Ponomarenko (this symposium) for demersal fry of 0-group cod in the southern part of the Barents Sea, feeding on Euphausiacea: the fewer fry in the southern part of the Barents Sea, the more scarce was their food. The larvae and pelagic fry of the 1961 year-class, being the least numerous in the southern part of the Barents Sea, could not feed on *C. finmarchicus* (their main food item) due to its scarcity. In 1959, however, the larvae and fry were transported mainly into the southern part of the Barents Sea and fed there freely on *C. finmarchicus*.

Oithona similis took second place in the food of larvae and pelagic fry (Fig. 1). It was more often encountered in the food of cod larvae in June, in the period of its mass appearance in the plankton, and provided the food for recently hatched cod larvae. In 1960, the spawning of cod had two peaks. The food of larvae appearing in April consisted mainly of nauplii of *C. finmarchicus*. The more numerous larvae of the second peak, which reached a length of 6-12 mm in early June, fed mainly on nauplii of *Oithona* in the coastal zone in 69°20'N (Fig. 2B and C). Due to the early spawning in that year, *Calanus finmarchicus* reached copepodite stages IV and V in the coastal zone in early June, too large to be eaten by such small larvae. In the area beyond the continental slope, the larvae lived on nauplii of *Oithona* and eggs and nauplii of *Calanus finmarchicus* which were available in those waters.

Copepodites of *O. similis* are important in the food of fry and large larvae when *C. finmarchicus* occurs in small numbers. For instance, in 1961, when *C. finmarchicus* was very scarce in the southern part of the Barents Sea (Table I, Fig. 2A), *Oithona similis* was most important in the food of larvae and fry of 15-35 mm (Fig. 2B, C, Table 2). Together with *O. similis*, the importance of other planktonic organisms (such as *Evadne nordmanni*, *Pseudocalanus elongatus*, *Acartia clausi*) also increased, although, because of the predominance of *C. finmarchicus* in the plankton, the importance of these species in the diet of larvae and pelagic fry is quite insignificant.

TABLE 1. THE ABUNDANCE OF *Calanus finmarchicus* (COPEPODITE STAGES) UNDER 1 m^2 IN THE UPPER 50 m, JUNE-JULY, IN THOUSANDS OF SPECIMENS.

Year	Section 69°20'N	Section 71°10'N	Section North Cape Bear Island	Section along the Kola Meridian
1959	31.6	25.8	53.1	75.3
1960	9.6	15.6	83.8	4.4
1961	20.3*	18.8	18.0	2.6

* This figure represents the abundance of *Calanus* on the section 67°30'N.

The food objects were grouped by sizes: (1) small organisms (eggs and nauplii of Copepoda), (2) medium organisms (small copepoda including *O. similis* and *C. finmarchicus* at the I-III copepodite stages) and (3) large organisms (*C. finmarchicus* at the IV-V copepodite stages, Euphausiacea, Tunicata, fish larvae). The importance of each group both in the diet of larvae and in the plankton is shown in Fig. 2d.

As is evident from Fig. 2B, C, d, the larvae of cod up to the VI-VII stages, belonging to the 1959 and 1960 year-classes, lived for a relatively long period of time on small organisms: nauplii of *C. finmarchicus* in 1959 and nauplii of *Oithona* in 1960. In 1961, the larvae as early as the IV stage ate medium and even large organisms. In 1959 and 1960, the pelagic fry fed on large organisms (*C. finmarchicus* in the IV-V copepodite stages), whereas in 1961, medium-sized organisms prevailed in their food (*O. similis*, other Copepoda, *Evadne nordmanni*).

It was found that the qualitative composition of food influences the increment in weight. To illustrate this, we present diagrams showing the changes in the body weight of larvae and fry in different years (Fig. 3). Larvae and fry up to 29 mm of the 1959 and 1960 year-classes, living for a long time on small organisms when in the larval phase, had a lower body weight than larvae and fry of the same length in the 1961 year-class which started feeding on medium and large organisms earlier. Fry of over 29 mm in the 1959 and 1960 year-classes, feeding freely on *C. finmarchicus* in the IV-V copepodite stages, had a higher body weight than the fry of the 1961 year-class of the same length feeding on the great quantities of *O. similis* and *E. nordmanni*.

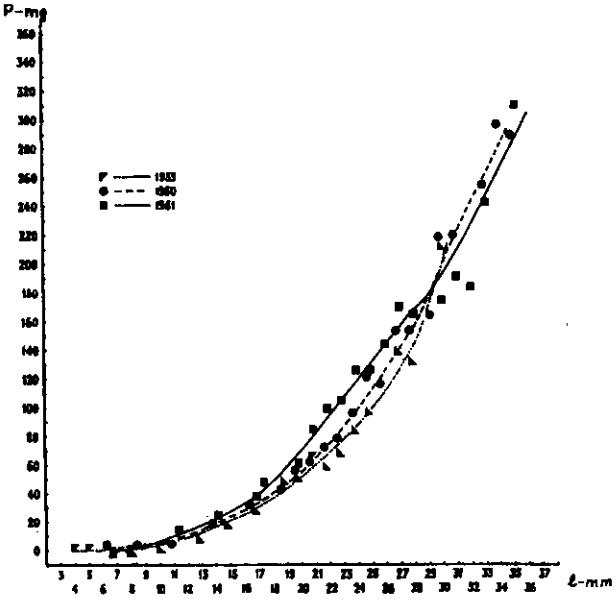


Fig. 3. Change of the weight of larvae and pelagic fry with linear growth.

The material on the feeding of pelagic fry in the southern part of the Barents Sea enabled us to judge at what concentration of *C. finmarchicus* fry start living on the secondary food organisms. It can be seen from the material for 1961 (Table 1) that the abundance of *C. finmarchicus* of 2,600 specimens under 1 m^2 in the 50 m surface layer, observed on the section along the Kola Meridian, was not sufficient for fry feeding. This is evidenced by the data on the food consumption of cod fry in the area eastwards of the section North Cape-Bear Island (Table 2). The abundance of *C. finmarchicus* of 4,400 specimens under 1 m^2, observed on the section along the Kola Meridian in 1960, seemed to be very low too: the stomachs of fry, 17 and 27 mm long, caught on this section contained no *Calanus*. As in 1961, the food of fry consisted of *O. similis, E. nordmanni* and *Fritillaria* which

TABLE 2. IMPORTANCE OF THE MAIN COMPONENTS IN THE FOOD OF LARVAE AND PELAGIC FRY IN 1961 IN DIFFERENT PARTS OF THE AREA (NUMBER OF SPECIMENS AS PERCENTAGES OF THE TOTAL NUMBER).

Region	Food components	Stage VII. 15.0 to 19.0 mm	Stage VIII. 19.0 to 24.0 mm
Southern part of the Barents Sea to the east of the Section North Cape-Bear Island	*Calanus finmarchicus*	2.4	
	Oithona similis	76.3	65.7
	Other Copepoda	1.2	3.5
	Evadne nordmanni	17.5	30.6
Southern part of the Barents Sea, Inshore Station.	*Calanus finmarchicus*		1.8
	Oithona similis	63.6	12.5
	Other Copepoda		30.4
Section North Cape Bear Island	*Calanus finmarchicus*	68.9	77.8
	Oithona similis	6.7	
	Other Copepoda	22.2	7.4
Section 72°50'N.	*Calanus finmarchicus*	100	85.4
	Oithona similis		
	Other Copepoda		3.7

were abundant in this area. The abundance of *C. finmarchicus* of about 18,000 specimens under 1 m^2 provides sufficient food supply for cod fry, as is seen from the data for 1961 obtained on the section North Cape-Bear Island (Tables 1 and 2).

REFERENCES

BARANENKOVA, A.S. 1964. Notes on the Condition of Formation of the Arcto-Norwegian Tribe of Cod of the 1959-1961 Year-Classes During the First Year of Life. *This symposium, Contribution No. B-15.*

PONOMARENKO, I.Ja., 1964. Comparative Characteristics of Some Biological Indices of the bottom Stages of 0-Group Cod Belonging to the 1956, 1958, 1959, 1960 and 1961 Year-Classes. *This symposium, Contribution No. B-7.*

WIBORG, K.F. 1948. Investigations on cod larvae in the coastal waters of northern Norway. *Fiskeridir. Skr. Havundersøk.*, 9 (3): 1-27.

1960. Investigations on pelagic fry of cod and haddock in coastal and offshore areas of northern Norway in July - August, 1957. *Fiskeridir. Skr. Havundersøk.*, 12 (8): 1-18.

B-17

THE BREEDING AND LARVAL DISTRIBUTION OF REDFISH IN RELATION TO WATER TEMPERATURE

By

A. Kotthaus[1]

ABSTRACT

This paper deals with the larval redfish material collected on board the R/V *Anton Dohrn* on the occasion of a joint Icelandic-German survey in the central North Atlantic carried out in April-May 1961. Reference is made to the results of a similar survey during the ICNAF Environmental Survey (NORWESTLAND 2) in 1963.

Larval redfish distribution along with the water temperature conditions are considered, and the "breeding" places of the redfish are located from the occurrence of new born larvae. The question of the depths at which redfish larvae are liberated is discussed.

INTRODUCTION

Tåning (1949) summarized the known facts about the distribution of redfish larvae in the North Atlantic. His paper, however, left some questions unanswered. Tåning considered that the area in which larvae were found corresponded to the breeding area. We know, however, that there are strong currents in the North Atlantic which may displace the larvae for considerable distances from the breeding areas within a relatively short time. We may also assume that the larvae were no longer at the original spawning places at the time when most of the Danish investigations were carried out (at the end of June and the beginning of July). It would seem, therefore, that Tåning's views are not necessarily correct.

From the hydrographic conditions at the time of the investigations, Tåning concluded that the liberation of larvae occurs at temperatures of 3° to 5°C and at depths between 300 and 500 m. When the larvae ascend to the upper layers, they need a temperature of 8° to 9°. Consequently the question remains as to whether or not these temperatures occur at the time of the main spawning, *i.e.*, in April and May, because the hydrographic conditions may change very quickly.

Tåning gives no details of geographical variation in the size of larvae. It is necessary to know this in order to discover the location of the breeding areas; the smaller the larvae are, the nearer the breeding places will be.

To study these problems, Iceland and Germany decided to make a special survey of redfish larvae together with hydrographic observations. It was not possible, of course, for these two nations to survey the whole distributional area of redfish larvae shown by Tåning. Therefore, the first investigations were restricted to the central North Atlantic, including the Irminger Sea and the Denmark Strait. This area was chosen because it seemed to be the most important breeding area of the oceanic stocks of redfish and may perhaps be important in studies of the Icelandic and Greenlandic stocks.

The Icelandic-German survey was carried out from the end of April to the beginning of June, 1961. Icelandic scientists aboard the R.V. *Aegir* investigated Denmark Strait and the Irminger Sea north of 60° N. lat., and German scientists aboard the R.V. *Anton Dohrn* investigated the southern and eastern parts between the longitude of 42°W and the Iceland-Faroe Ridge and southwards to the northern border of the Gulf Stream. The results of these two cruises were submitted separately as preliminary reports to the ICES Meetings in 1961 (by A. Kotthaus) and 1962 (by J. Magnusson).

---

[1] Biologische Anstalt Helgoland Abteilung Fischereibiologie, 2 Hamburg-Altona 1, Federal Republic of Germany.

GEAR AND METHODS

The Nansen closing net was used for vertical hauls. Horizontal tows were made using three Icelandic High Speed samplers (IHSS), at different depths, on a few occasions when the sea conditions were too bad to use the Nansen net. Fish larvae were separated from the whole catch, and not, as is usually done in bigger plankton catches, from a part of it. The water temperature was measured at every station by a hydrographic series to 500 m or by the bathythermograph from the surface to 270 m.

RESULTS AND DISCUSSION

a) The distribution of redfish larvae.

Figure 1 shows that redfish larvae were found over most of the area (square symbols) with the exception of the relatively warm waters of the Gulf Stream. Two main areas of distribution, separated by some stations without redfish larvae (open circles), may be distinguished (apart from a third in the south of Iceland, which shall not be considered here): a) a small area to the south-south-east of Cape Farewell, which probably extends farther westwards, and b) a very extended area on both sides of the Middle Atlantic-Ridge (MAR), which continues to the north and north-east along the Reykjanes Ridge as indicated by Magnusson's (1962) simultaneous investigations. These areas are characterized by distinct water temperatures at a depth of 30 m: in the western area the temperature ranged from 4° to 5.5°C, and in the central area along the MAR, from 6° to 8°C (south of Iceland in the eastern area we found still higher temperatures of 8° to 9.5°C). No larvae were found in waters with temperatures higher than 9.5°, *i.e.*, in Gulf Stream waters. These areas of distribution correspond well with Henderson's (1961) distribution chart, although the areas in his charts are not so well defined, probably because of the combination of material from several months.

b) Abundance of redfish larvae.

The abundance of redfish larvae may be seen from Fig. 1 which shows the total number caught at each station. The highest density of larvae, more than 10 specimens per sample, was found along the western slope of the MAR. Somewhat smaller concentrations, 6 - 10 specimens, were encountered in the western area south-south-east of Cape Farewell. In all other regions the number per station was less than 6.

As indicated by divided vertical hauls with the Nansen closing net and by catches with the IHSS, larval redfish prefer the upper layers between 15 and 50 m in depth. No larvae were found below 60 m or in the upper recorder of the IHSS which was fishing at 5 m.

c) Breeding places of the redfish.

In order to find out where the redfish larvae were born, all larvae were measured. From measuring pre-extrusion larvae, we know that these range from about 5 to 7 mm in length; in only a few cases were there larvae measuring up to 7.5 mm. Such small and doubtless new-born larvae with the remains of the yolksacks still visible were found only at very restricted places. These correspond with the highest concentrations of larvae along the western slope of the MAR and south-south-east of Cape Farewell. Outside these areas the new-born fish were extremely scarce.

We must conclude from this that the hatching of larvae is restricted to special areas, although some redfish may occasionally spawn (if this expression may be allowed for the ovo-viparous redfish) outside these areas. These observations show that the area of occurrence of redfish larvae is not at all identical with the breeding area of the adult fish.

Figure 2, which is based on the Icelandic material (Magnusson, 1962) as well as the German samples (Kotthaus, 1961 and 1962), shows the spawning areas in the central North Atlantic. The intensity of spawning in the area west of Iceland slowly decreases to the south and ends at about 52°N. The spawning area to the south-south-east of Cape Farewell, is clearly separated from the central area but is of no significance when compared with this.

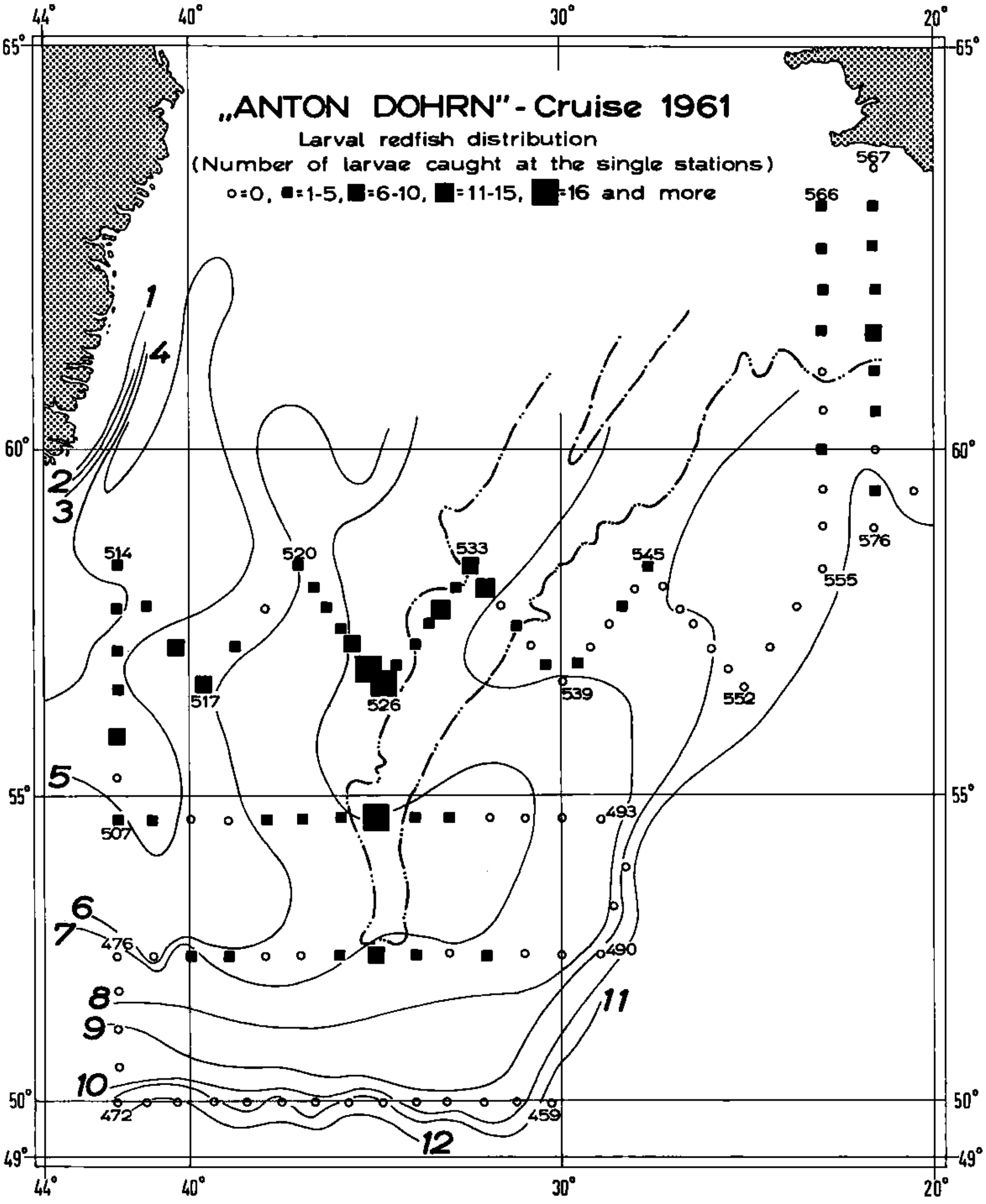


Fig. 1. The abundance of redfish larvae at each station during the cruise of the *Anton Dohrn* in 1961 (see key above). The position of the Middle Atlantic Ridge and the Reykjanes Ridge are indicated by the 1,000 m and 2,000 m depth contours. The isotherms are based on observations at 30 m depth. Small figures show station numbers.

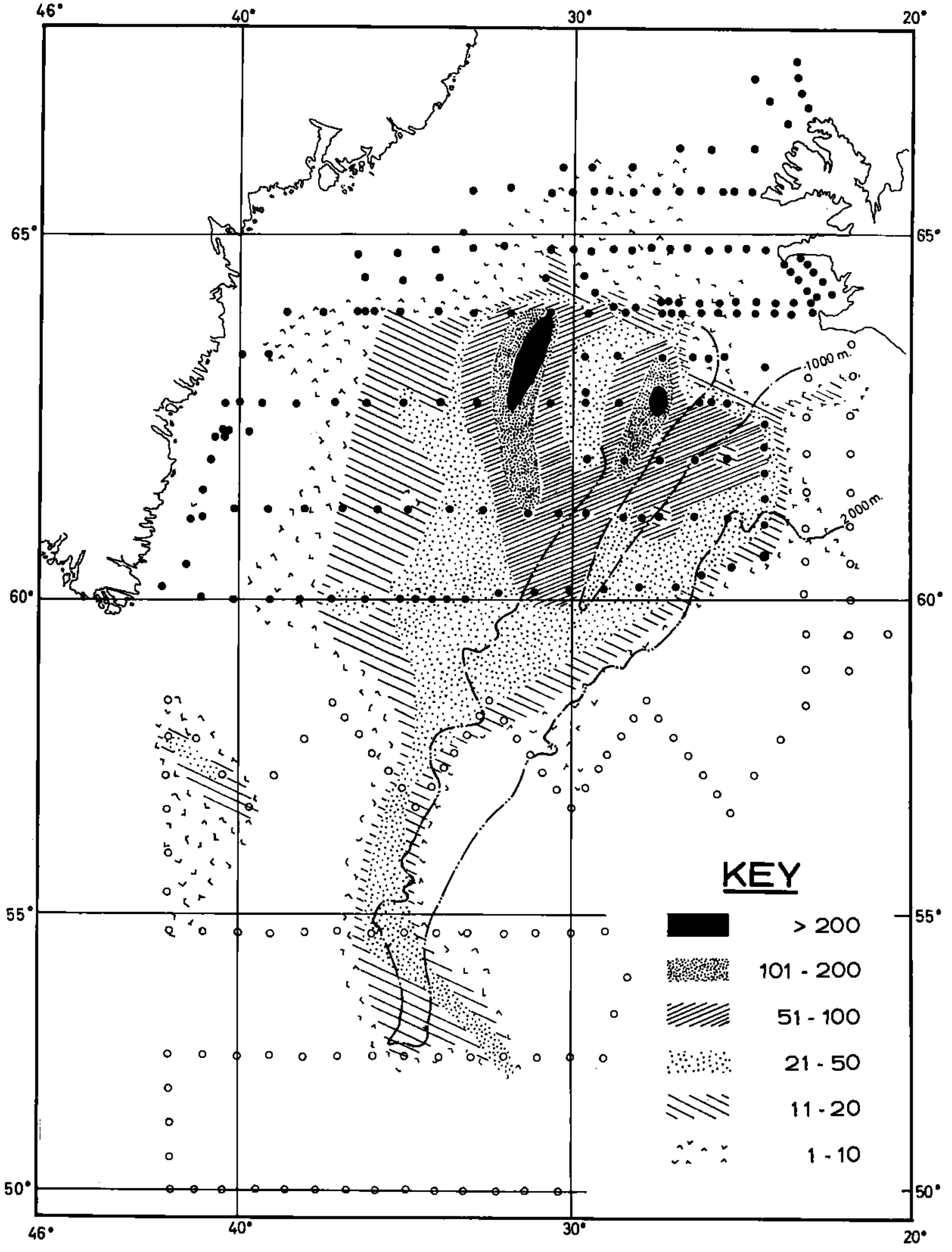


Fig. 2. Spawning areas of the redfish; based on the German *Anton Dohrn* and Icelandic *Aegir* cruises in 1961. The key shows numbers of redfish larvae of less than 7 mm length. The positions of the Middle Atlantic Ridge and the Reykjanes Ridge are indicated by the 1,000 m and 2,000 m depth contours.

d) Spawning depth of the redfish.

The depths at which redfish larvae are extruded have been uncertain until now. Einarsson (1960) doubts whether redfish fry are born at depths of 200-500 m as Tåning and others had supposed. He believes that the young hatch at depths of between 500 and 800 m, and he has evidence to show that temperature conditions at these depths, at least to the west of Iceland, are not necessarily in opposition to Tåning's hypothesis that the redfish require a temperature of 3° to 5°C in order to spawn.

Our observations in 1961 tend to agree with those of Einarsson. The fishing we did in the open ocean at depths of up to 450 m by longline and floating trawls as well as echo soundings never indicated the presence of pelagic redfish in the area. From these observations it is easy to believe that the ripe redfish females are living in much deeper water at spawning time.

The fact that adult redfish have been caught at different localities in the open ocean at depths of less than 300 m does not conflict with the possibility of spawning in deep water. We have never heard, so far, that running females have been caught at these depths. It could well be that these fish caught by line are either spent fish (having ascended from the deep spawning places to the upper layers and are migrating, using the currents at these depths, to their feeding places on the Icelandic slope) or else they are fish belonging to an oceanic stock of redfish generally living in these levels, whose breeding places, however, are far deeper. That males were also caught leads us to suggest this probability. This problem might be solved by racial investigations.

The question now arises as to whether or not the temperature conditions at these depths of 500 - 800 m fulfil the temperature requirements of 3° to 5°C for spawning. Einarsson (1960) states that, in the areas west of Iceland which he believed to be breeding grounds, the temperatures at depths of 500 - 800 m were within the range of 4° to 6°C.

The hydrographic measurements carried out on our cruise only cover depths down to 500 m. However, we may conclude from the trends of the isotherms (Fig. 3) that at least along the MAR the required temperatures must exist at depths of more than 500 m. Our diagrams show this fact clearly: water masses of relative high temperature of 4° to 6°C push down in a wedge-like form to remarkable depths. In the northernmost section the 5°-isotherm dipped below the 500 metre-line at one point. This downward sweep of warm water masses seems to be common in that season along the Reykjanes Ridge and the MAR as indicated in the diagrams of Tåning (*loc. cit.*, p. 89, Fig. 2) and from the investigations on *Anton Dohrn* during the IGY in 1958 and later (Dietrich, 1960, p. 14, 20, 26 and 32). It is easy to believe that the ripe female redfish are carried by the relatively small and deep-reaching wedge of warm water running from the south-west coast of Iceland to their breeding places along the submarine ridges. This supposition is supported by the observations in April of several years that ripe female redfish are concentrated in considerable numbers off the south-west coast of Iceland in depths of 450 m and more at the base of the Reykjanes Ridge. (This is the *marinus* type redfish, which lives at other times at depths of no more than 350 m). If the hypothesis of deep-sea spawning of the redfish should prove to be correct, the larvae would be able to ascend to the surface in more or less isothermal waters.

In 1963, as part of the NORWESTLANT survey, the *Anton Dohrn* made a cruise off south-east Greenland from 24 May to 30 June. Detailed results will be published in ICNAF Special Publication No. 7, as part of the NORWESTLANT series of papers, but a brief summary is given here.

The area covered by the NORWESTLANT survey in 1963 overlapped partly with the 1961 cruise but lay further to the north-west, extending to the coast of Greenland. In general the NORWESTLANT survey provided confirmation of the results based on the earlier cruise. There were three areas in which redfish larvae were found, two of these corresponding to those found previously (the central area, west of the MAR, and the region south-south-east of Cape Farewell). The other region was an area along the east coast of Greenland with temperatures of 5° to 6.3°C. The smaller larvae were found in the south-west and western parts of the survey and there was an irregular gradient of increasing sizes to the east and north-east. It is assumed that this pattern resulted from the current systems carrying the larvae from their birth places and towards the Icelandic shelf where they can descend to the bottom.

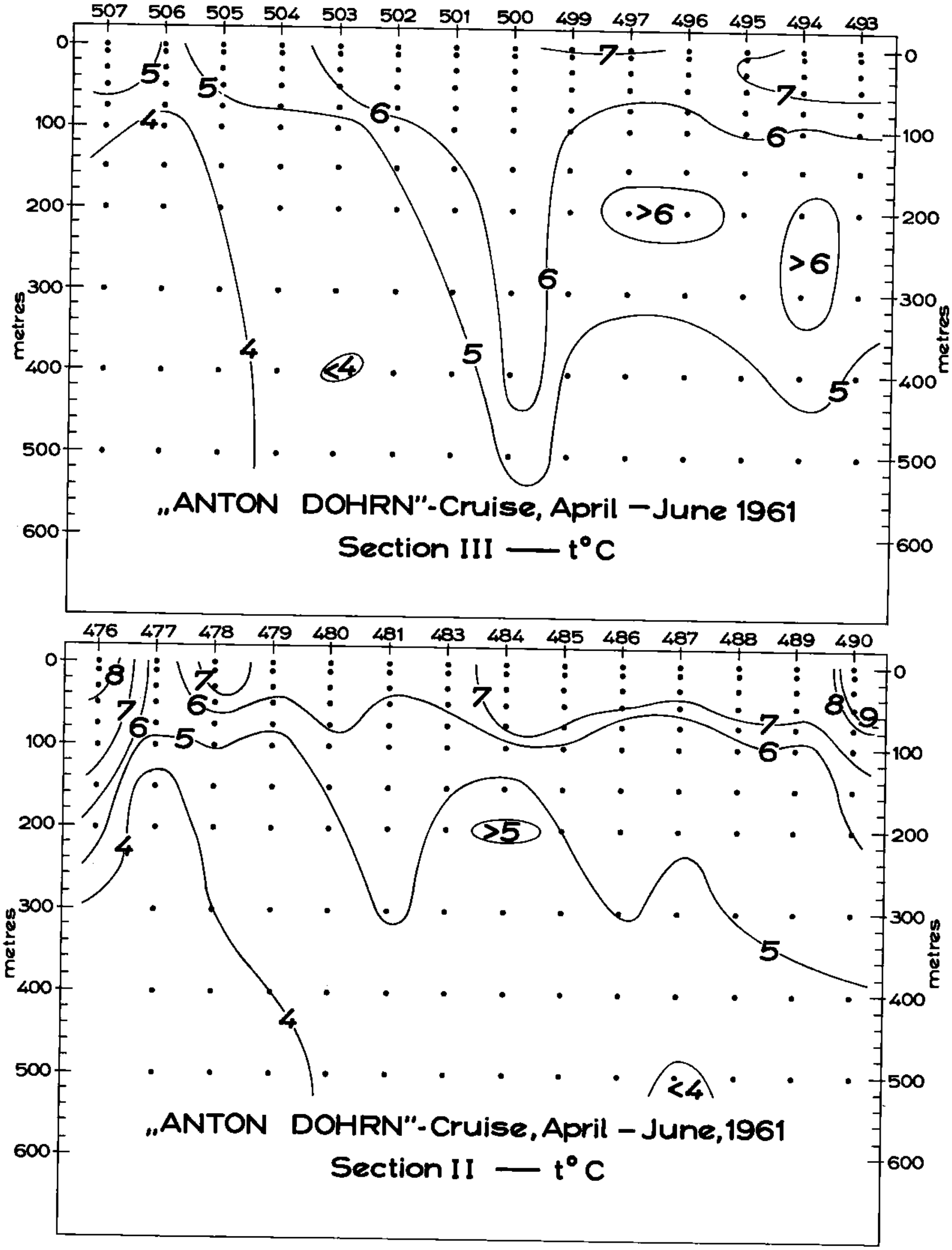


Fig. 3. The vertical distribution of temperature in two sections of the 1961 cruise. Station numbers are indicated above the sections as in Fig. 1.

Above —— 50°40'N : 42°00'W to 29°00'W

Below —— 52°30'N : 42°00'W to 29°00'W

One difference between the surveys in 1961 and 1963 was noticed in the vertical temperature distributions. The downward sweep of the isotherms which was a feature of the 1961 results (Fig.3) was not apparent in 1963. From our hypothesis on breeding conditions, it would seem likely that the conditions were unfavourable for breeding in June 1963. Only at the southern part of the MAR did we find a slight hint of the downward sweep of the isotherms and it was only in this region that we found young larvae.

SUMMARY

Though our investigations are preliminary, we feel there is evidence for the following statements:

1) There are three main areas of occurrence of redfish larvae in the central North Atlantic covered by the *Anton Dohrn* cruises of 1961 and 1963 each showing different thermal conditions; these are:

a) a central area along the Middle Atlantic Ridge having temperatures of about 6° to 8°C (at 30 m depth).

b) a western area south-south-east of Cape Farewell with temperatures of about 4° to 5.5°C.

c) an area along the east coast of Greenland with temperatures of 5° to 6.3°C.

2) The main spawning area in the waters surveyed by *Anton Dohrn* runs along the western slope of the Middle Atlantic Ridge, only extending to the eastern slope in the south. Some spawning of less importance also occurs in the other two areas.

3) The spawning of the redfish probably occurs at depths of more than 500 m and at water temperatures of between 4° and 6°C. This, however, concerns only the main spawning area. In the others the breeding conditions may differ from these.

4) Since the spawning areas were found to be restricted, the area of occurrence of redfish larvae cannot be considered to correspond with the breeding places of the adult fish.

REFERENCES

DIETRICH, G. 1960. Temperatur-, Salzgehalts- und Sauerstoffverteilung auf Schnitten von FFS *Anton Dohrn* und VFS *Gauss* im Internationalen Geophysikalischen Jahr 1957/58. *Dtsh. Hydrogr. Z.*, Ergänzungsheft Reihe B, 4.

EINARSSON, H. 1960. The fry of *Sebastes* in Icelandic waters and adjacent seas. *Rit Fiskid.* 2 (7): 1-67.

HENDERSON, G.T.D. 1961. Continuous plankton records: The distribution of young *Sebastes marinus*(L). *Bull. Mar. Ecol.*, 5, 46: 173-193.

KOTTHAUS, A. 1961. Redfish larvae investigations in the central North Atlantic in 1961 (preliminary report). ICES-C.M., 1961, paper no. 4.

1962. Rotbarschbrut im zentralen Nordatlantik. *Inform. Fischw.*, 1/2: 7-14.

MAGNUSSON, J. 1962. Redfish larvae in the Irminger Sea in May, 1961. ICES-C.M.,1962, paper no. 90.

TÅNING, Å.V. 1949. On the breeding places and abundance of the redfish (*Sebastes*) in the North Atlantic. *J. Cons.*, 16: 85-95.

B-18

SOME RESULTS OF SOVIET RESEARCH WORK ON ICHTHYOPLANKTON IN THE NORTHWEST ATLANTIC: EGGS AND LARVAE OF COD

By

V.P. Serebryakov[1]

ABSTRACT

The distribution and abundance of cod eggs and larvae are considered in relation to the surace water temperatures and current systems off the Labrador and Newfoundland regions. Spawning n the spring months started at very low, and sometimes negative, temperatures. It is shown that emperature, through its effect on the rate of development of larvae, determines the length of time hat larvae are transported by the currents and, therefore, the subsequent distribution of the oung cod.

In 1959-62 the Soviet research and scouting vessels collected ichthyoplankton in the northwest art of the Atlantic Ocean. The samples were taken with conical egg nets with a diameter at the pening of 80 cm and gauze 140) in 15-20 min oblique hauls; 1,674 samples were taken. Collections overed the waters of Labrador (ICNAF Subarea 2), Newfoundland (Subarea 3), Nova Scotia (Subarea 4) nd Georges Bank (Subarea 5). Cruises were conducted during the spring and summer, from March to ugust. The material included eggs and larvae of 37 fish species belonging to 18 families (Appendix). ost numerous were the eggs and larvae of gadoids, *Pleuronectes*, scorpionfishes, and *Ammodytes*. Preiminary data have been published previously (Serebryakov, 1962 and 1963). The present paper conains the results of investigations of cod only.

The distribution of eggs and larvae of cod in the waters of Nova Scotia, Gulf of Maine, Georges ank, Saint Pierre and Green Bank was given in the works of Dannevig (1918), Bigelow and Schroeder 1953). In addition, our investigations cover the more northern areas, which had not been invesigated earlier.

In March, ichthyoplankton was collected only in the waters of Flemish Cap, on the slopes of rand Newfoundland Bank (GNB) and in the area to the east of the Avalon Peninsula (Fig. 1A). Indiidual cod eggs were observed over the oceanic depths to the east of Flemish Cap Bank, on the northast and southwest slopes of the Grand Bank over the depths of 150-375 m; and in somewhat greater uantities (up to 11 specimens per vertical haul) in the area of the Grand Bank east of the Avalon eninsula over depths of 74 to 160 m (Fig. 1A). In March the surface layer temperature in these reas was as follows: 0.35°C near Avalon Peninsula along the section 47°00N; 1.8°C in the Flemish ap area; and 0.52°C on the southeast slope of the Grand Newfoundland Bank. In all cases 90% of he eggs were at the first stage of development, according to the stages defined by Rass (1949). he scarcity of eggs and the predominance, amongst them, of eggs in the first stage of development, oupled with the small numbers of post-spawners amongst the adult fish (Table 1), suggest that spawing began in March when only occasional individuals were spawning.

In April and May collections were made in almost all the investigated areas. The distribution f cod eggs during the spring period in the Labrador area is most interesting.

From 14th to 18th April, 1962 large quantities of eggs were found on the boundary between cenral and north Labrador waters on the slope of the shelf over depths from 380 to 450 m; more than ,000 eggs were hauled at two stations (Fig. 1B). More than 600 eggs were also caught on 24 April t two stations in the area of South Labrador. The catch composition of eggs of North and South abrador differed with respect to the ratio of development stages (Table 2).

All-Union Research Institute for Marine Fisheries and Oceanography, Moscow, USSR.

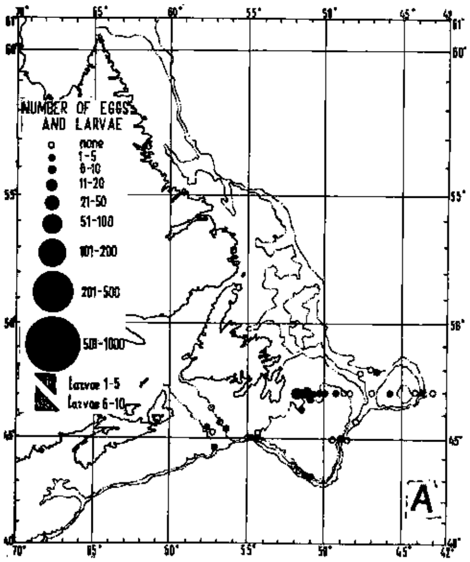


Fig. 1A. Distribution of eggs (circles) and larvae (triangles) of cod (*Gadus m. morhua*): A — in March.

TABLE 1. MATURITY OF GONADS OF ADULT SPAWNERS CAUGHT IN MARCH DURING 1957-61 IN THE WATERS OF GRAND NEWFOUNDLAND BANK (30 AND 3N) (AS PERCENTAGES OF THE NUMBER OF DISSECTED FISH).

Areas	Gonad maturation stages							
	II	III	IV	IV-V	V	VI	VI-II	Total number of dissected fish
3N	34.3	12.0	46.0	0.4	0.4		6.9	525
30	50.0	12.0	29.0	5.0	4.0			565

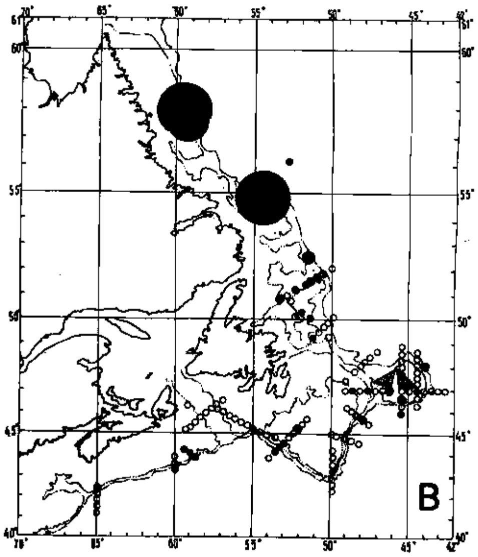


Fig. 1B. Distribution of eggs (circles) and larvae (triangles) of cod (*Gadus m. morhua*) : B — in April.

TABLE 2. COMPOSITION OF EGG CATCHES IN THE LABRADOR AREA BY THE STAGES OF DEVELOPMENT APRIL 1962, AS PERCENTAGES OF THE TOTAL CATCH OF EGGS IN THE AREA.

	Stages of egg development				
Areas	I	II	III	IV	Total number of eggs
North Labrador	76	33	0	0	1020
South Labrador	26	57	13	4	650

Gonad maturation stages of adult fishes in these areas were also different (Table 3).

TABLE 3. GONAD MATURATION STAGES OF COD CAUGHT IN THE LABRADOR AREA IN APRIL 1962, AS PERCENTAGES OF THE NUMBER OF DISSECTED FISH IN THE AREA.

Areas	Stages of maturity					Total number of dissected fish
	IV	IV-V	V	VI	VI-II	
North Labrador			20	80		180 specimens
South Labrador	26		10	19	45	726 specimens

In May the material was collected in the waters off North and Central Labrador as well as to the north of Hamilton Bank, on the boundary of Central and South Labrador. Catches of cod eggs during this period were considerably poorer than in April: at two stations in the North Labrador area only 6 eggs were caught at the temperature -1.0°, whereas in the Central Labrador area 88 specimens were caught at the temperature -0.1°, and at the boundary of Central and South Labrador Area - 129 eggs at the temperature + 0.9°. The proportions of the development stages of eggs in the samples off Central Labrador are different from that in samples from the northern part of Hamilton Bank (Table 4).

TABLE 4. COMPOSITION OF EGG CATCHES IN THE LABRADOR AREA BY THE DEVELOPMENT STAGES IN MAY 1962, AS PERCENTAGES OF THE TOTAL CATCH OF EGGS IN THE AREA.

	Stage s of egg's development				Total number of eggs
Areas	I	II	III	IV	
Central Labrador	95	0	2.5	2.5	88
Boundary of Central part of Southern Labrador	1	14	28	57	129

Almost all the adult cod caught in these areas were post-spawners, only a few specimens having gonads at the fifth stage of maturity. The first larvae were taken in May, when larvae, 3.5 mm and 3.6 mm long, were found on the boundary of Central and South Labrador.

At the end of June there were very few eggs in the area of South Labrador (Fig. 1C); no samples were taken from the north. Only a few eggs were caught (not more than 10 per egg net haul). A total of 12 larvae of 4.5 - 5.7 mm long was encountered in the area of South Labrador and to the north of the Newfoundland Bank.

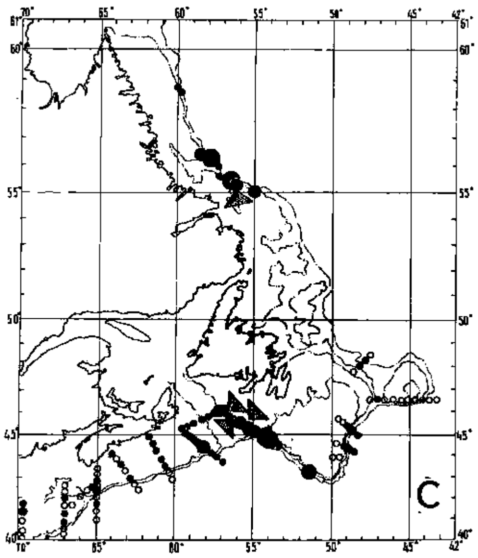


Fig. 1C. Distribution of eggs (circles) and larvae (triangles) of cod (*Gadus m. morhua*): C — in May.

The analysis of the distribution of cod eggs and larvae and the condition of gonads of adult spawners during spring months in the waters of Labrador allows us to describe some of the characteristics of cod reproduction in these areas. The presence of a large number of eggs and spawning cod in the areas of North, Central and South Labrador is a clear indication that the spawning of cod on the slopes of the Labrador Shelf takes place in April-May. However, the character of spawning in the areas of North and South Labrador is different. In the waters of North Labrador the spawning period is shorter and proceeds on a larger scale than in the waters of South Labrador. This is confirmed by the fact that in April adult cod off North Labrador were represented only by spawners, while off South Labrador spawners make up only about 30% (Table 3). Spawning off North Labrador takes place in April and in the first ten-day period of May, whereas in mid-May only post-spawners are found in the area. Off South Labrador spawning is extended from April to July: spawning cod and eggs of the first stages of development are encountered there in April, May, late June and July.

The presence of eggs in the first stages of development (I and III) as well as the absence in the samples of cod in the late stages in the North Labrador area in April (Table 2) is explained by the fact that the extruded eggs in this area are driven away from the spawning areas to the areas of Central and South Labrador by the Labrador Current where they reach later stages of development during the drift (Table 2 and Table 4).

In April the temperature of the surface layer where eggs were distributed was very low: -1.5°C off North Labrador, and -0.1°C off South Labrador; in May the temperature was -0.1°C in the Central Labrador area and +0.9°C in South Labrador. Low temperatures of the surface layer of about 100 m thick and deeper are characteristic of the Labrador Current (Buzdalin, Elizarov, 1962). Development of cod eggs in the Labrador areas takes place at very low temperatures, sometimes negative, influencing both the rate of development and duration of drift of eggs and larvae. Thus, at a temperature 0.0°C, the period of egg development from fertilization to hatching takes about 43 days, and at a temperature -1.0°C about 50 days (Apstein, 1909). Within this time the eggs would be driven about 280-300 miles away from the spawning grounds by the Labrador Current, its velocity being 10 cm/sec off North and Central Labrador and 14-20 cm/sec off South Labrador (Kilerich,1943), *i.e.* they would cover the distance equal to the distance from North to South Labrador. If the actual pattern of drift and development of eggs corresponds to the described one, then the larvae hatched from the eggs spawned near North Labrador would be expected to appear in Central and South Labrador only 40-50 days after the commencement of spawning, *i.e.* in mid-May (the beginning of spawning falling on late March-early April). It was in mid-May when the larvae of cod, 3.5 to 3.6 mm long, were discovered on the boundary of Central and South Labrador.

The larvae hatched from the eggs in Central Labrador are likely to drift further to the south, to the areas of South Labrador and northern Newfoundland Bank. This is shown by the increasing size of larvae as they move to the south. Thus, in May the length of larvae in the Central Labrador area was 3.5 to 3.6 mm; in June in the South Labrador area, 4.2 to 5.7 mm; in July in the northern Newfoundland Bank, 9.0 mm; in August in the northern Newfoundland Bank and southern Labrador, 12.7 to 13.9 mm.

In the more southern areas the number of cod eggs was considerably smaller. Only individual eggs were observed in the egg-net catches in the northern Newfoundland Bank. In April, the eggs were found on the northeast, south and southwest slopes of the Flemish Cap Bank, over depths of 290-450 m. In the area southwest of Flemish Cap, some eggs at the first stages of development were found over a depth of 2,200 m. Individual specimens of cod eggs were observed in the central part of the bank over depths less than 100 m (Fig. 1B). In May only a small number of cod eggs were observed in the area: only on the west slope of the Bank, five eggs at the first stages of development were found. In April larvae of cod (17 specimens) were found in this area in the central part of the Bank over a depth of 150-255 mm where the temperature of the surface layer was +4.35°C; the length of the larvae was from 4.0 to 5.5 mm.

The presence of larvae in the central part of the Bank is most probably explained by the drift of eggs and larvae from the south and southwestern slopes, where cod spawn in March (Mankevitch and Prochorov, 1962) with cyclic currents or rather with their branches flowing from the slopes to the central part of the Bank (Buzdalin and Elizarov, 1962). It is possible that larvae of cod could be brought from the Northern Newfoundland Bank or from the northeast slope of the Great Newfoundland Bank. However, in this case larvae would have probably been larger owing to the longer duration of the drift.

In April very few cod eggs were found in the areas of the Grand Newfoundland Bank. Only a few eggs were observed in the northeast and southwest areas of the Bank (Fig. 1B). In May, cod eggs appeared on the northeast and southeast slopes, but in very small numbers; not over 5-6 specimens per vertical haul. In May, considerably more eggs were found on the southwest slope of the Grand Bank as well as in the areas of Saint-Pierre and Green Banks - up to about 50 specimens of cod eggs per vertical haul. All stages of development were represented in the catches of egg-nets with the first stage dominating (Table 5).

TABLE 5. COMPOSITION OF CATCHES OF COD EGGS IN THE AREAS OF SAINT-PIERRE BANK, GREEN BANK AND SOUTHWEST SLOPE OF THE GRAND NEWFOUNDLAND BANK BY THE DEVELOPMENT STAGES AS PERCENTAGES OF THE TOTAL CATCH OF EGGS IN THESE AREAS.

Stages of development				Number of eggs
I	II	III	IV	
55	19.5	19.5	6	325

Larvae of cod, 4.0 to 5.5 mm long occurred in these areas in May. The temperature of the surface water layer in these areas was from 1.8 to 2.8°C. Of the cod caught by trawl in these areas, 70% consisted of spawners or postspawners (see Table 6).

TABLE 6. MATURITY OF GONADS OF COD CAUGHT IN THE AREAS OF SAINT-PIERRE BANK, GREEN BANK AND SOUTHWEST SLOPES OF THE GRAND NEWFOUNDLAND BANK AS PERCENTAGES OF THE TOTAL NUMBER OF DISSECTED FISH.

Stages of maturity						Total number of dissected fish
II	III	IV	V	VI	VI - II	
22	0.1	7.2	33.9	20.2	16.4	670

Distribution of cod eggs and adult spawners shows that spawning of cod in these areas takes place during the first ten days of May. However, the abundance of spawning concentration was not so great, as the cod catches by trawl with vertical opening 8.5 m did not exceed 100 kg per one hour of hauling. This fact can, probably, explain the small number of eggs in plankton samples.

In April and May there were very few cod eggs in the areas of Nova Scotia and Georges Bank (Fig. 1C).

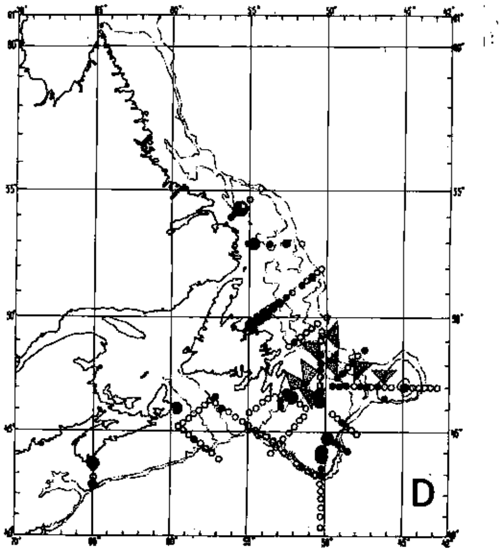


Fig. 1D. Distribution of eggs (circles) and larvae (triangles) of cod (*Gadus m. morhua*): D — in July-August.

In July-August, eggs of cod were distributed over lesser depths than during spring months. The main mass of eggs was discovered close to the coast or in the shallow areas of the banks (Fig. 1D). In August, eggs were distributed close to the coast over depths of about 150 m and at a temperature of +2.8°C, and in the shelf area at the latitude of Belle-Isle. In the area of the Northern Newfoundland Bank, eggs were also distributed mainly in the coastal waters. The main mass of the eggs in the waters of Grand Newfoundland Bank was distributed near the shores of Newfoundland Island over depths 48-150 m; in the northeastern part of the Bank over the depths 150-190 m; in the central part of the Bank and in the shallow waters of the southern part of the Bank. Individual eggs are driven away from the slopes of the Bank to the areas of oceanic depths. Individual eggs were found in the central part and on the southwest slopes of the Flemish Cap Bank. In August larvae of cod were distributed both near Avalon coast in the northern, northeastern and central parts of the Grand Newfoundland Bank. The larvae were 4.0-9.5 mm long. Only single larvae were found in the catches of egg-nets.

In August, eggs of cod were encountered over small depths in the area of Nova Scotia Shelf and the Great Newfoundland Bank. In July-August, the temperatures of waters where eggs and larvae of cod were distributed were, naturally, much higher than in April-May. If in April surface layer temperature near Labrador was 1.5 to 1.0°C, on the east and southeast slopes of GNB +0.50°C, on the south slope of GNB +4.0°C, on Flemish Cap Bank +4.38°C, Saint-Pierre and Green Banks +1.8 to +2.8°C, then in July-August the temperature of the surface layer near Labrador was +2.98° to +4.6°C, on the north and northeast slopes of GNB +7.70° to +8.78°C in the south of GNB +8.37° to +10.40°C and near the Newfoundland coast +7.0°C. In July-August the development rate of cod embryos owing to the higher temperatures, was considerably faster than during the spring months. In the area of South Labrador the duration of development from fertilization to the hatching stage at the temperature +2.88 - +4.60°C was about 18-23 days (Apstein, 1909), *i.e.* less than half what it was in April-May. In other areas the period of development in July-August was about 11-14 days. Owing to the increased rate of development, the time of pelagic life during the summer season is reduced, so it is possible to suppose that the duration of drift both with regard to time and distance must be much shorter in the summer period than in April-May.

CONCLUSIONS

1. Ichthyoplankton of the investigated areas is represented by eggs and larvae of 37 fish species from 18 families.

2. In April-May spawning of cod takes place in the waters of Labrador (Northern, Central and Southern parts). In Northern Labrador, spawning was observed to begin in April and end in the first ten days of May. In the waters off South Labrador spawning is more extended, in April, May, June and early August.

3. Development of cod eggs and larvae in the areas of Labrador in the spring months was observed at very low, sometimes negative temperatures, so the rate of development was very slow. This extends the period of passive pelagic life which is directly related to the duration of drift migration.

4. In the areas of Labrador drift of eggs and larvae was observed from the spawning grounds. Direction and velocity of the drift is determined by the Labrador Current. Eggs from North Labrador drift from Central to South Labrador. In May larvae appeared in the Central Labrador area and drifted to the south towards South Labrador and North Newfoundland Bank.

5. Drift of cod eggs and larvae was observed within the area of Flemish Cap. It was directed rom the south and southwest slopes towards the central part of the Bank, where the spawning grounds f cod were situated (Mankevitch and Prochorov, 1962). Direction of drift is determined by the cir- ular current which is directed from the southwest slope to the centre of the Bank in this area.

6. General trends of spawning of commercial fish species of Labrador and Newfoundland make it ossible to conclude that the extrusion of cod eggs takes place on the slope of the continental helf in the near-bottom slope waters with positive temperatures, *i.e.* in those waters which are ormed by the Irminger Current. But, their drift takes place in the waters of Labrador Current with hich the eggs and larvae are driven from their spawning grounds to the areas of banks located much ore to the south from the spawning grounds. So, it is possible to suppose that the formation of tocks of commercial fishes in these areas is largely determined by the character and conditions of he drift migrations during the period of early stages of development.

REFERENCES

APSTEIN, C. 1909. Die Bestimmung des Alters pelagisch lebende Fischeier. Mitteilungen des Deutschen Seefischerei-vereins. Bd. XXV, p. 364-373.

BIGELOW, H.B. and Wm. C. SCHROEDER. 1953. Fishes of the Gulf of Maine. *U.S. Fish and Wildl. Serv., Fishery Bull.* 74, 53: 577 p.

BUZDALIN, Ju. I. and A.A. ELIZAROV. 1962. Hydrological conditions in the areas of Newfoundland Banks and Labrador, 1960. *Soviet Fisheries Investigations in the North-West Atlantic. VNIRO-PINRO,* p. 155-171.

DANNEVIG, A. 1918. Canadian fish-eggs and larvae. Canadian fishery Expedition, 1914-1915. Ottawa.

KIILERICH, A. 1943. The hydrography of the West Greenland Fishing banks. *Medelelser fra Kommissionen for Danmarks Fiskeri og Havundersøgelser, Serie: Hydrogr.III, No.3,* p. 3-15.

MANKEVICH, E.M. and V.S. PROCHOROV. 1962. Size-age composition and spawning of cod on the southwest slope of Flemish-Cap Bank. *Soviet Fisheries Investigations in the North-West Atlantic. VNIRO-PINRO,* p. 355-360.

RASS, T.S. 1949. Composition of ichthyofauna and taxanomic classification of eggs and larvae of fishes of the Barents Sea. *Trudy VNIRO,* 17: 9-65.

SEREBRYAKOV, V.P. 1962. Some aspects of the ichthyoplankton studies in the areas of Labrador and Newfoundland. *Soviet Fisheries Research in the Northwest Atlantic Ocean. VNIRO-PINRO,* p. 227-234.

1963. Distribution of pelagic eggs and larvae of commercial fishes in the Northwest Atlantic area. *Annu. Meet. int. Comm. Northw. Atlant. Fish. 1963.* Doc. No. 56, Serial No. 1107 (mimeographed).

APPENDIX

SPECIAL COMPOSITION OF ICHTHYOPLANKTON IN THE AREAS OF LABRADOR (2), NEWFOUNDLAND (3), NOVA SCOTIA (4), GEORGES BANK (5).

	Areas				Total number	
Species	2	3	4	5	eggs	larvae
I. Clupeidae						
1. *Clupea harengus harengus* Linné	-	-	-	+	-	52
II. Osmeridae						
2. *Mallotus villosus villosus* (Müller)	-	+	-	-	-	162

Species	Areas				Total number	
	2	3	4	5	eggs	larvae
III. Bathylagidae						
3. *Bathylagus* sp.	-	+	-	-	-	4
IV. Myctophidae						
4. *Benthosema glaciale* (Reinhardt)	+	+	+	+	-	14
5. Genus sp.	+	+	+	+	-	176
V. Gadidae						
6. *Brosme brosme* (Muller)	-	-	+	+	426	-
7. *Enchelyopus cimbrius* (Linné)	-	+	-	-	5	7
8. *Urophycis* sp.	-	-	+	+	11	5
9. *Molva molva* (Linne)	-	-	+	-	4	-
10. *Merluccius bilinearis* (Mitchill)	-	+	+	+	467	20
11. *Pollachius virens* (Linné)	-	+	-	-	2	12
12. *Melanogrammus aeglefinus* (Linné)	-	+	+	+	390	6
13. *Gadus morhua morhua* (Linné)	+	+	+	+	11759	110
VI. Macruridae						
14. Macrurus sp.	-	-	-	+	-	1
VII. Syngnathidae						
15. Genus sp.	-	-	+	-	-	1
VIII. Anarhichadidae	-	+	+	-	-	3
16. *Anarhichas lupus* (Linné)						
17. *Anarhicas minor* (Olafson)	-	+	+	-	-	1
IX. Stichaeidae						
18. *Chirolophis ascanii* (Walb.)	-	-	+	+	-	57
X. Lumpenidae						
19. *Leptoclinus maculatus* (Fries)		+	-	-	-	1

	Areas				Total number	
Species	2	3	4	5	eggs	larvae
XI. Annodytidae						
20. *Ammodytes americanus* DeKay	-	+	+	-	-	12500
XII. Scombridae						
21. *Scomber* sp.	-	-	-	+	-	2
22. *Scomber scombrus* Linné	-	-	+	+	-	1
XIII. Thunnidae						
23. Genus sp.	-	-	-	+	-	2
24. *Katsuwonus pelamis* (Linné)	-	-	-	+	-	2
XIV. Scorpaenidae						
25. *Sebastes* sp. (*S. mentella* Travin)	+	+	+	+	-	2725
XV. Cottidae						
26. Genus sp.	-	-	+	-	-	24
27. *Mioxocephalus octodecim spinosus* (Mitchill)	-	+	+	-	-	1
XVI. Agonidae						
28. *Leptagonus decagonus* (Bloch et Schneider)	-	+	+	-	-	6
29. *Aspidophoroides monopterygius* (Bloch)	-	-	+	-	-	3
30. *Ulcina olriki* (Lutken)	-	-	+	+	-	3
XVII. Liparidae						
31. *Neoliparis atlanticus* (Jordan et Everman)	-	-	+	-	-	51
32. Genus sp.	-	-	+	-	-	1
XVII. Pleuronectidae						
33. *Hippoglossus hippoglossus hippoglossus* (Linné)	-	-	+	-	10	18
34. *Hippoglossoides platessoides limandoides* (Bloch)	+	+	+	+	2090	18
35. *Limanda ferruginea* (Storer)	-	+	+	+	1250	3
36. *Microstomus microcephalus* (Donovan)	-	+	+	-	74	-
37. *Glyptocephalus cynoglossus* (Linné)	-	+	+	-	405	10