# THE PROCEEDINGS OF THE 

## SOVIET-NORWEGIAN SYMPOSIUM ON

## REPRODUCTION AND RECRUITMENT OF ARCTIC COD



# The proceedings of the Soviet-Norwegian symposium on: <br> REPRODUCTION AND RECRUITEMENT OF ARCTIC COD <br> Leningrad 26-30 September 1983 

Edited by
O.R. God $\phi$ and S. Tilseth
FOREWORD Page ..... 4
BACKGROUND : ..... 5
V.K. Zilanov ..... 5
The importance of the Barents Sea cod and haddock for the Soviet and Norwegian fisheries
SECTION I. Eggs and larvae ..... 13
G. Sætersdal and H. Loeng ..... 13
Ecological adaptation of reproduction in Arctic cod
S. Tilseth ..... 36
The distribution of cod larvae and prey org- anisms in the Lofoten area related to critical prey concentrations
H. Bjørke and S. Sundby ..... 72
Distribution and abundance of post larval northeast Arctic cod and haddock
SECTION II. Stock assessment ..... 99
O. Nakken ..... 99Acoustic estimates of spawning cod in the Lofotenarea in 1982 and 1983
S. Sundby and P. Solemdal ..... 113
The egg production of of Arcto-Norwegian cod (Gadus Morhua L.) in the Lofoten area estimated by egg surveys
V.P. Serebryakov, V.M. Borisov and V.K. Aldonov ..... 136
Population fecundity and abundance of year-classes of the Arcto-Norwegian cod
A. Hylen and C.J. Rørvik ..... 154
Estimating the maturity ogive for the northeast Arctic cod by a modified mesh assessment model
K. Randa Page ..... 189
Abundance and distribution of 0-group Arcto- Norwegian cod and haddock 1965-1982
I.Ya. Ponomarenko ..... 210
Survival of bottom-dwelling young cod in the Barents sea and the factors determining it
V.M. Borisov and V.V. Blinov ..... 227
The use of fishing effort, juvenile abundance and previous years' catch data for the forecast of Arcto-Norwegian cod catch
V.L. Tretyak ..... 238
A method of estimating the natural mortality rates of fish at different ages/exemplified by the Arcto-Norwegian cod stock
SECTION III. Population structure. ..... 272
K. Jørstad ..... 272Genetic studies on eggs, larvae and 0-group ofthe Arctic cod stock
O.R. God $\varnothing$ ..... 289Migration, mingling and homing of north-eastArctic cod from two separated spawning grounds

## FOREWORD

Nearly all of the rich fish resources of the Barents Sea are shared between the Soviet Union and Norway. It is therefore highly desirable that the two countries' scientific investigations on these fish stocks are well coordinated. To this end the principal institutions involved, the Polar Research Institute of Marine Fisheries and Oceanography (PINRO), Murmansk and the Institute of Marine Research, Bergen are developing, under the aegis of the Mixed Soviet-Norwegian Fisheries Commission, a programme of close cooperation. Under this programme a series of symposia have been planned dealing with important aspects of the fish resources of the Barents $S e a$ and their environment. This volume presents the contributions submitted to the first of these symposia held in Leningrad 26-30 September 1983 and which dealt with reproduction and recruitment of Arctic cod (northeast Arctic cod, Arcto-Norwegian cod are synonyms applied by different authors). In addition to this version in the English language the contributions will also appear in a version in the Russian language published by VNIRO, Moscow.

The editors of this version are responsible for some modest editorial changes in a few contributions in which it has not been possible to obtain the authors approval. We do not think, however, that this has resulted in any change of meaning or in loss of clarity. The editors are also indebted to miss Karin Pittman for correcting the English text.

Bergen, July 1984
The Editors

```
"There is no strength for work without cod".
(Russian popular saying)
'Skuld' Torsken os feile, hvad havde vi da?...
    Nei! Fisken i Vandet, det er vores Bröd
    Og mister vi hannem, da lider vi N\varnothingd."
(Petter Dass, Norwegian poet of the XVII century)
```

THE IMPORTANCE OF THE BARENTS SEA COD AND HADDOCK FOR THE SOVIET AND NORWEGIAN FISHERIES

by<br>Zilanov V.K.<br>Representative of the USSR Government in the Mixed Soviet-Norwegian Fisheries Commission

From the above Russian and Norwegian expressions it is clearly seen how important cod and haddock were for the Russian people inhabiting the coasts of the Barents and White Seas and for the Norwegian people of the Barents and Norwegian Sea coasts.

Cod and haddock are the final and most valuable products of the Barents Sea, living on plankton-eating fish such as capelin, small-sized herring, polar cod, plankton organisms and benthos. Being a significant component of the ecological complex of living resources of the Barents and Norwegian Seas, these two species have long been exploited by the Soviet and Norwegian fishermen.

The history of cod and haddock fisheries is characterized by fluctuations in catches, and changes in principal fishing methods and fishing areas. Studies of the main stock formation
processes resulted in fishery management aimed at maintaining the reproduction of the fish resources at a level which would provide a steady recruitment to maintain a rational fishery.

In the pre-war period the cod fishery was mainly concentrated off the north-west coast of Norway and in the southern Barents Sea, while the haddock fishery was principally conducted in the southern Barents Sea. Mean annual catches of cod and haddock in 1932-1938 were 504.2 and 141.8 thousand tons respectively (Tables 1-4). Approximately $70 \%$ of the total world catch of cod and haddock was taken by the Soviet Union and Norway, cod being caught more by Norway and haddock by the Soviet Union.

Table l. Mean annual catch of cod by some countries and total in the Barents and Norwegian Seas (according to the ICES data). Tonnes

| Period | Meas. unit | Total | including |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | USSR | Norway | Britain | FRG | Other Countries |
| 1932-1938 | t | 504234 | 77420 | 288452 | 90058 | $45715^{\text {x) }}$ | 3709 |
|  | \% | 100.0 | 15.3 | 57.1 | 17.8 | 9.1 | 0.7 |
| 1947-1950 | t | 798157 | 170265 | 277152 | 308897 | 32692 | 9152 |
|  | \% | 100.0 | 21.3 | 34.7 | 38.7 | 4.1 | 1.2 |
| 1951-1960 | t | 765865 | 335881 | 267986 | 186047 | 30108 | 45743 |
|  | \% | 100.0 | 38.8 | 30.9 | 21.5 | 3.5 | 5.3 |
| 1961-1970 | t | 761232 | 355108 | 240717 | 139038 | 4951 | 21418 |
|  | \% | 100.0 | 46.6 | 31.6 | 18.3 | 0.7 | 2.8 |
| 1971-1976 | t | 807710 | 309348 | 332548 | 83180 | 27133 | 55501 |
|  | \% | 100.0 | 38.3 | 41.2 | 10.3 | 3.4 | 6.8 |
| 1977-1982 | t | 531482 | 163561 | 307413 | 27075 | 4429 | 29004 |
|  | \% | 100.0 | 30.8 | 57.8 | 5.1 | 0.8 | 5.5 |

x) German catch

In those years fishing with trawls was developing and fishing vessels of new types were designed and built to taken cod and haddock from the entire area of their distribution. This process was interrupted by the Second World War.

In the post-war period, especially during the first few years, the food shortage rapidly intensified the development of cod and haddock fisheries in the Barents Sea. A definite share in catches appertained to Britain, West Germany and other countries. Compared to the pre-war years the distribution of catches by areas has undergone some changes, the southern Barents Sea becoming most important for trawl fishing (Tables 2 and 4). Mean annual catch during 1951-1960 was 865.7 thousand tons, i.e. 300 thousand tons over that of the pre-war period.

Table 2. Distribution of mean annual catches of cod by fishing area. (according to the ICES data) Tonnes.

| Year | Meas. unit | Total | Including |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | North-west coast of Norway | Bear Is.-Spitsbergen area | Southern <br> Barents Sea |
| 1932-1941 | t | 504234 | 251480 | 82630 | 170124 |
|  | \% | 100.0 | 49.9 | 16.4 | 33.7 |
| 1947-1950 | t | 798157 | 253611 | 146902 | 397644 |
|  | \% | 100.0 | 31.8 | 18.4 | 49.8 |
| 1951-1960 | t | 865765 | 182766 | 174521 | 508478 |
|  | \% | 100.0 | 21.1 | 20.2 | 58.7 |
| 1961-1970 | t | 761232 | 154013 | 157730 | 449489 |
|  | \% | 100.0 | 20.2 | 20.7 | 59.1 |
| 1971-1976 | t | 807710 | 224729 | 113962 | 469019 |
|  | \% | 100.0 | 27.8 | 14.1 | 58.1 |
| 1977-1982 | t | 531482 | 239498 | 32922 | 259063 |
|  | \% | 100.0 | 45.1 | 6.2 | 48.7 |

At the same time the mean annual catch of haddock remained at the same level as in the pre-war years - 142.5 thousand tons (Tables 1-3).

During the years which followed the Soviet Union and Norway maintained a firm lead in the cod and haddock fisheries due to the restoration of their fishing capacity though historically and geographically their fisheries are based on different components of the exploited part of the fish stocks. The Soviet fishery during the post-war period was mainly concentrated in the southern Barents Sea characterized by distributions of young and middle aged cod.

Table 3. Mean annual catch of haddock by some countries and total in the Barents and Norwegian Seas (according to the ICES data) Tonnes.

| Period | Meas. <br> unit | Total | including |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | USSR | Norway | Britain | FRG | Other <br> Countries |
| 1932-1938 | t | 141875 | 75914 | 19418 | 22983 | $23296{ }^{\text {x }}$ ) | 264 |
|  | \% | 100.0 | 53.5 | 13.7 | 16.2 | 16.4 | 0.2 |
| 1947-1950 | t | 135762 | 27216 | 23235 | 74297 | 10002 | 1016 |
|  | \% | 100.0 | 19.9 | 17.1 | 54.9 | 7.4 | 0.7 |
| 1951-1960 | t | 142540 | 51962 | 41353 | 37758 | 11108 | 349 |
|  | \% | 100.0 | 36.5 | 29.0 | 26.5 | 7.8 | 0.2 |
| 1961-1970 | t | 144072 | 55912 | 57691 | 27561 | 2408 | 500 |
|  | \% | 100.0 | 38.8 | 40.0 | 19.1 | 1.7 | 0.4 |
| 1971-1976 | t | 199640 | 97431 | 58467 | 24871 | 11310 | 7561 |
|  | \% | 100.0 | 48.8 | 29.3 | 12.5 | 5.7 | 3.7 |
| 1977-1982 | t | 86916 | 26913 | 51514 | 4759 | 2215 | 1515 |
|  | \% | 100.0 | 31.0 | 59.3 | 5.5 | 2.5 | 1.7 |

x) German catch

In contrast the Norwegian cod fishery was principally conducted off the northwest coast of Norway where cod of middle and older year groups are distributed. In the former case, the fishery is based on the feeding grounds, whereas in the latter one on the spawning grounds. This suggests different fishing techniques: in the southern Barents Sea trawls of different designs (bottom, mid-water, twin) are used, while off the northwest coast of Norway hook-and-line fishing gear (long-lines, handlines), drift nets, seines of different designs and to a lesser degree trawls are used. Such a differentiated utilization of fishing gear is caused not only by historical factors, fishermen traditions and geographical conditions, but also by fish behaviour. As older cod are more

Table 4. Distribution of mean annual catches of haddock by fishing area. (according to the ICES data) Tonnes.

| Year | Meas. unit | Total | Including |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | North-west coast of Norway | Bear Is.-Spitsbergen area | Southern <br> Barents Sea |
| 1932-1941 | t | 141875 | 15996 | 7118 | 118761 |
|  | \% | 100.0 | 11.3 | 5.0 | 83.7 |
| 1947-50 | t | 135762 | 32252 | 8452 | 95058 |
|  | \% | 100.0 | 23.8 | 6.2 | 70.0 |
| 1951-1960 | t | 142540 | 27043 | 6083 | 109414 |
|  | \% | 100.0 | 19.0 | 4.3 | 76.7 |
| 1967-1970 | t | 144972 | 27896 | 1176 | 115000 |
|  | \% | 100.0 | 19.4 | 0.8 | 79.8 |
| 1971-76 | t | 199640 | 35970 | 7671 | 155999 |
|  | \% | 100.0 | 18.0 | 3.9 | 78.1 |
| 1977-1982 | t | 86916 | 33493 | 1944 | 51479 |
|  | \% | 100.0 | 38.5 | 2.3 | 59.2 |

active and cautious their strong feeding reflex is used to catch them. This suggests the application of baited hooks as the most active fishing technique.

The haddock fishery has also undergone some changes in the postwar years. Catches increased, among other things, off the northwest coast of Norway. As in the case of the pre-war years, the main fishing gear used here are trawls which take advantage of the biology and behaviour pattern of haddock. This species feeds mainly on bottom organisms and is found in the near-bottom layers during a major part of its life.

In the 1960 s and 1970 s catches reached their maximum values over 1 million tons of $\operatorname{cod}(1968,1969,1974)$ and more than 200 thousand tons of haddock (1972, 1973, 1974). As this took place, some pronounced fluctuations in catches occurred presenting severe problems primarily to the fishermen of coastal states of the Barents and Norwegian Seas. Low yields occurred in 1957-1960, 1964, 1965, 1966, 1971, 1972 and 1979-1983. It should be emphasized that fluctuations in catches frequently have an inverse tendency - a rise in catches in Norway corresponds to a fall in catches in the Soviet Union and vice versa. As mentioned above, we attribute that phenomenon to the fact that fisheries of these countries are based on different components of the commercial stock and are conducted in different fishing areas.

In the 1960 s and 1970, trawl fishing for cod and haddock was carried out in the Barents Sea by a number of countries. The largest catches were taken by Britain, France, West Germany, the Faroe Islands, Poland, East Germany, Portugal, Spain and others. The total mean annual catch of non-coastal states of this region amounted to 195.8 thousand tons in 1961-1970 and 209.5 thousand tons in 1971-1976. In some years cod and haddock catches were over 300 thousand tons.

The introduction of a 200 -mile economic fishing zones by the coastal states of the Northeast Atlantic offered strong possi-
bilities for a better utilization of the cod and haddock stocks by the Soviet Union and Norway, as almost the entire range of distribution of these species falls within the zones declared by the countries. The initial period after introduction of the 200 mile zones coincided with the occurrence of a number of poor yearclasses of cod and haddock in the Barents Sea. Besides, cooling of the water masses in those years was responsible for a redistribution of the commercial fish concentrations of middle and older age-groups towards western areas of the Barents Sea. As a result, the southern Barents Sea became commercially less important (Tables 2, 4), while the availability of cod off the northwest coast of Norway increased. This was responsible for an increase in Norwegian catches and a decline in Soviet catches (Tables 1,3 ).

Utilization of cod and haddock as food by the two coastal states also presents some difficulties. In the Soviet Union the fish is basically consumed by the Soviet population, while in Norway it is primarily exported to different countries in America, Africa and Europe.

The fluctuations in cod and haddock catches and their impact upon the economic position of fishermen of coastal states strongly demand further development and systematization of investigations. Of primary importance is the relative influence of reproduction and recruitment upon the formation of the commercial part of cod and haddock stocks, as well as the elaboration of fishery management which is based on the scientific data of all components of the fish populations.

It should be emphasized that a number of measures directed towards the reproduction and conservation of cod and haddock stocks are already under way. They have been developed in the last few years within the framework of the Mixed Soviet-Norwegian Fisheries Commission created in conformity with the Intergovernmental Agreement between the USSR and Norway on the Cooperation in Fisheries of April II, 1975. Since then, total allowable catches of cod and haddock were introduced and national quotas of the species were allocated (1976); fishing
efforts were redistributed from the eastern to the western parts of the Barents Sea (1978); a number of fishing grounds in the eastern and northwestern areas of the Barents Sea were closed for fishing with the aim of protecting immature fish; a change to 125 mm meshed trawls made of cotton, hemp, polyamid or polystyrene filament or to 135 meshed trawls made of other materials took place on January 1, 1981; new commercial minimum sizes were adopted for cod ( 42 cm ) and haddock ( 39 cm ), and other measures. Nevertheless, the analysis of these arrangements has shown that in some cases they are based on assumptions which disregard changed fishing conditions, such as a shift in fishing pressure from the recruiting to the spawning part of stocks and other changes.

Proceeding from the above facts, and on the initiative of Soviet and Norwegian scientists it was decided at the lith session of the Mixed Soviet-Norwegian Fisheries Commission to hold a specialized symposium on the reproduction and recruitment of cod and haddock stocks.

There can be no doubt that the data presented in this collection of papars, and further intensification of studies in this field will contribute to further development of rational management arrangements for the cod and haddock fisheries in the Barents Sea within the framework of the Mixed Fisheries Commission.

SECTION I
Eggs and larvae

ECOLOGICAL ADAPTATION OF REPRODUCTION IN ARCTIC COD

By

GUNNAR SÆTERSDAL and HARALD LOENG
Institute of Marine Research

## ABSTRACT

A recent period (1977-1982) of cold climate in the Barents Sea resulted in a greatly reduced feeding area available for the Arctic cod and in consistent low recruitment. With the start of a warmer period in 1982/83 the area and potential for production of cod biomass expands and recruitment has increased. An hypothesis is presented that through evolutionary processes the reproduction of the Arctic cod is adjusted to the variations in the feeding area caused by climatic fluctuations. Historical data on sea temperature and ice cover are used to describe the climatic fluctuations for the period 1900-1983 and these are compared with data on fluctuations in yearclass strength. It is concluded that conditions favouring high survival rates of cod larvae must be related to the occurrence of high temperatures in the Atlantic component of the Norwegian current. The processes and/or phenomena must have a large time- and space scale. This is also confirmed by the high incidence of temporal similarity in survival success of the stocks of cod, haddock and herring in this area.

## INTRODUCTION

Through evolutionary processes fish populations must have been adapted to a varying environment in a way which ensures their survival in unfavourable periods and an optimum use of favourable periods. There may be considerable interests in trying to find the ways in which these adaptions function.

The cod as a species belongs in the northern temperate and boreal regions, but reaches into sub-arctic areas where conditions are suitable, e.g. S.E. and S.W. Greenland and Barents Sea - W. Svalbard. In these populations which live close to the northern limits of distribution of the species, periodical fluctuations in stock size have been described (Rollefsen, 1954; Ottestad 1942). It has been partly assumed and partly demonstrated that these are in some ways related to climatic shifts occurring in the stock environments.

The feeding area of the Arctic cod in which the main production of the stocks biomass occurs is subject to large fluctuations related to changes in the ocean climate especially in the eastern and central Barents Sea. Although cod can survive in temperatures below $0^{\circ} \mathrm{C}$, it is seldom found in abundance in waters of less than $2-3^{\circ} \mathrm{C}$. The physiological significance of the temperature relationship is probably its direct effect on the capacity for growth of the cod. A more indirect effect relating cod distribution and climate is that also the distribution of one of the principal food organisms of the cod, the capelin demonstrate large scale shifts with climatic changes.

Maslov (1968) describes changes in the distribution of cod and haddock in the Barents Sea which he relates to changing climatic conditions. And the effects on the distributions of these two large fish stocks of the onset of a period of cold climate in the Barents Sea in 1978-1981 have been described by Loeng, Nakken and Raknes (1983) and Midttun, Nakken and Raknes (1981). The last mentioned paper demonstrate a clear westward shift of the distribution of young cod and haddock in this period result-
ing in an occurrence of these species limited to the western half of the Barents Sea. A simultaneous similar change took place in the distribution of the fisheries. Recruitment to these stocks was at a low level in this period particularly in the eastern Barents Sea. During these cold years with extreme southern ice limits migrating herds of harp seals reached the Finnmark coast where also the white whale was commonly observed. With the change of climate which took place in 1982 and 1983 a marked eastward shift of capelin distribution has been observed and the 0-group recruitment indices for both cod and haddock have increased to relatively high levels.

Thanks to the joint international survey systems operated by USSR and Norway, these large scale and dramatic events in the stocks can now be followed more or less "on line". Simpler observations on stocks and environment are, however, available for a considerable time period and it would be of interest to analyse these in a search for general ecological relationships. The following working hypothesis was formulated:


#### Abstract

In periods of "cold climate" the feeding areas of the cod in the Barents sea are restricted and there is a similar restricted need for recruitment. Production of rich yearclasses in such periods would be a waste. From a survival strategy point of view it would be an advantage in such periods to send a larger part of the recruits to the west Svalbard region where the environmental conditions seem to be less variable. The history of the fishery indicate that periods of high and low recruitment to Svalbard have occurred, but these fluctuations will not be further examined in this paper.


After a shift from a "cold" to a "warm" period the capelin with its short life cycle will repopulate the eastern areas in the cause of l-2 years and with the increase of temperature, conditions will soon be favourable for production of cod in a greatly expanded area of the eastern and central Barents Sea. In order to utilize this potential both in
space and time, there is a need for high recruitment during the first few years of a new "warm period".

We will in this paper examine to what extent such a strategy can be demonstrated in the data on stock biology and the physical environment. The available time series of data are unusually long and takes us back to the turn of the century. The nature and quality of the data are varying and they must therefore be carefully examined.

## VARIATIONS IN RECRUITMENT

THE DATA

The available data which can be used for assessing the variations in yearclass abundance comprise age data on various parts of the stock and, in later years, surveys of the relative abundance of 0 -group and juvenile fish. The following series have been used: (Indices listed in Table 3).

Yearclasses 1902-1919 in the skrei stock.

The data are based on early scale-readings by Oscar Sund and on the yield of the skrei fisheries. This aging method has later been shown to be lacking in reliability, especially on higher age groups and the sampling was inadequate. The main findings were, however, corroborated by a large programme of length sampling where the periodical recruitment of abundant yearclasses can be identified. The age distributions of Lofoten skrei 1913-1928 from Sund (1920, 1926 and 1936) were combined with the yield of the total skrei fisheries in numbers and the yield in numbers of each yearclass was expressed as a ratio of the average yield of the corresponding age groups for the whole period.

Some early survey data from the Barents Sea and Bear Island grounds 1905, 1907 and 1913 also support the main findings from the early periode of Sund's skrei-anaIysis, see Hjort, (1914, p. 111 and p. 130).

## Yearclasses 1917-1945 in the skrei stack

G. Rollefsen introduced otolith age readings of skrei and on this basis calculated an index of each yearclass's contribution to the stock. His data cover the yearclasses 1917-1943 (Rollefsen, 1952). Further observations include the yearclasses 1944 and 1945 (Rollefsen, 1954).

Yearclasses 1946-1952 in the stock of young cod

This series from Sætersdal and Hylen (1959) gives indices of relative abundance based on observations of age and yield in the fisheries for young cod 1950-1959. These observations are important because of the great increase in fishing mortality in the total stock in this period.

Virtual population analysis

This gives estimates of abundance at age 3 of the yearclasses 1946-1977 (Anon. 1979 and 1982).

USSR young fish surveys

This provides a trawl survey index of abundance at age 3 for the yearclasses 1957-1979 (Anon. 1982).

0-group surveys

The data derive from the international 0-group surveys in the Barents Sea which cover the period 1965-1983. Use is made of the logarithmic index estimated by Randa (1983).
2.2 Analysis of the data on yearclass abundance

The frequency distributions of the 6 series of observations on yearclass abundance are shown in Table 1 . In order to obtain a rough comparison of the range and distribution of the series, the total range of variance was grouped into three subranges and the

Table l. Frequency distributions of series on yearclass abundance of Arctic cod, 1902-1983. For explanations see text.

| Yearclasses 1902-1920 <br> "Skrei" stock <br> o. Sund |  |  | Yearclasses 1917-43 <br> "Skrei" stock <br> Rollefsen |  |  | Yearciasses 1946-52 <br> Young cod <br> Satersdal \& Hylen |  |  | ```Yearclasses 1946-77 VPA-estimate total stock``` |  |  | Yearclasses 1957-79 <br> III-group <br> Barents Sea <br> USSR-trawl survey |  |  | ```Yearclasses 1965-83 0-group Barents Sea``` |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| I |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| . 2 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| . 3 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 0.4 | 2 |  |  |  |  |  |  |  | 0.1 | 1 |  | 0 | 8 |  |  |  |  |
| . 5 | 3 |  | . 2 | 4 |  |  |  |  | . 2 | 6 |  | 5 | 4 |  | 1-20 | 7 |  |
| . 6 | 2 |  | . 4 | 3 |  | . 2 | 1 | 4 | . 3 | 2 | 29 | 10 | 2 | 17 | 21-40 | 4 | 15 |
| . 7 |  | 11 | . 6 | 2 | 19 | . 4 | 1 | $\mathrm{m}_{1}=0.55$ | . 4 | 3 | $\mathrm{m}_{1}=0.36$ | 15 | 2 | $\mathrm{m}_{1}=7$ | 41-60 | 2 | $m_{2}=29$ |
| . 8 | 2 | $m_{1}=0.63$ | . 8 | 2 | $\mathrm{m}_{1}=0.7$ | . 6 | 2 |  | 0.5 | 4 |  | 20 | 1 |  | 61-80 | 2 |  |
| . 9 | 1 |  | 1.0 | 5 |  | . 8 |  |  | . 6 |  |  | 25 |  |  | 81-100 | 1 |  |
| 1.0 | 1 |  | . 2 | 2 |  | 1.0 | 1 | 2 | . 7 | 3 |  | 30 |  |  | 101-120 |  |  |
| . 1 | 3 |  | . 4 | 1 |  | . 2 | 1 | $\mathrm{m}_{2}=1.2$ | . 8 | 4 | 11 | 35 | 1 |  | 121-140 |  | - 2 |
| . 2 |  |  | . 6 | 2 |  | -4 |  | 2 | . 9 | 1 | $\mathrm{m}_{2}=0.84$ | 40 |  |  | 141-160 | 1 | $\mathrm{m}_{2}=120$ |
| . 3 | 1 |  | . 8 | 1 |  | . 6 |  |  | 1.0 | 1 |  | 45 | 1 | 3 | 161-180 | 1 |  |
| . 4 |  |  | 2.0 |  | 5 | . 8 |  |  | . 1 | 1 |  | 50 | 1 | $m_{2}=45$ | 181-200 |  |  |
| 1.5 |  | 6 | . 2 | 2 | $\mathrm{m}_{2}=1.9$ | 2.0 |  | 1 | . 2 | 1 |  | 55 |  |  | 201-220 |  |  |
| . 6 |  | $m_{2}=1.33$ | . 4 |  |  | -2 | 1 | $\mathrm{m}_{3}=2.3$ | . 3 |  |  | 60 |  |  | 221-240 |  | 2 |
| . 7 | 2 |  | . 6 |  |  |  | 7 |  | . 4 |  | - | 65 |  |  | 241-260 |  | $\mathrm{m}_{3}=210$ |
| . 8 |  |  | . 8 |  |  |  |  |  | 1.5 | 1 | 3 | 70 | 2 | 3 |  | 19 |  |
| . 9 |  |  | 3.0 | 2 |  |  |  |  | . 6 | 1 | $m_{3}=1.63$ | 75 |  | $\mathrm{m}_{3}=79$ |  |  |  |
| 2.0 |  |  | . 2 |  |  |  |  |  | . 7 |  |  | 80 |  |  |  |  |  |
| . 1 |  |  | . 4 |  | 3 |  |  |  | . 8 |  |  | 85 |  |  |  |  |  |
| . 2 |  |  | . 6 |  | $\mathrm{m}_{3}=3.4$ |  |  |  |  | 33 |  | 90 |  |  |  |  |  |
| . 3 |  |  | . 8 |  |  |  |  |  |  |  |  |  | 23 |  |  |  |  |
| . 4 |  |  | 4.0 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 2.5 | 1 | 2 | . 2 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| . 6 |  | $\mathrm{m}_{3}=2.75$ |  | 27 |  |  |  |  |  |  |  |  |  |  |  |  |  |
| . $7 \quad 3$ |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| . 8 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| . 8 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 3.0 | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  | 19 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

frequencies and mean values within each sub-range calculated. Table 2 lists these frequencies and the ratios of the mean of the highest sub-range over that of the lowest, and similarly for the middle sub-range. This represents an estimate of the average abundance of rich and medium yearclasses measured in units of the abundance of poor broods.

Table 2. Frequency distribution of yearclasses of low, medium and high abundance in the various data-series and the ratios of mean yearclass strength.

| Abundance | o. Sund Yearcl. |  | G. Rollefsen |  | Sætersdal \& Eylen |  | VPA 3 year |  | USSR <br> Trawl <br> estimate |  | 0-group survey |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | \% |  | \% |  | $\%$ |  | \% |  | \% |  | \% |
| Low | 11 | 58 | 19 | 70 | 4 | 57 | 19 | 58 | 17 | 74 | 15 | 79.0 |
| Medium | 6 | 31 | 5 | 19 | 2 | 29 | 11 | 33 | 3 | 13 | 2 | 10.5 |
| High | 2 | 11. | 3 | 11 | 1 | 14 | 3 | 9 | 3 | 13 | 2 | 10.5 |
|  | 19 |  | 27 |  | 7 |  | 33 |  | 23 |  | 19 |  |
| $\frac{m_{3}}{m_{1}}=$ | 4.4 |  | 4.9 |  | 4.2 |  | 4.5 |  | 11.3 |  | 7.2 |  |
| $\frac{\mathrm{m}_{2}}{\mathrm{~m}_{1}}=$ | 2.1 |  | 2.7 |  | 2.2 |  | 2.3 |  | 6.4 |  | 4.1 |  |

A comparison of the frequencies and ratios of abundance for the six data sets shows the following: the four series based on age determination of commercial fish are characterized by a ratio of highest to lowest sub-range of 4.2 to 4.9 with a mean of 4.5 . The ratio middle to lowest is $2.1-2.7$ with a mean of 2.3 . The corresponding ratios for the two survey data sets are considerably higher, 11.3 and 7.2 for the highest and 6.4 and 4.1 for the middle range. Also the frequencies of occurrence of the various ranges show a consistent difference with higher frequencies of middle-range yearclasses for the data series based on older fish. It seems reasonable to assume that these differences between the two sets of data are real: the variation in yearclass abundance is considerably higher when observed directly as juveniles than the apparent variation in the adult stock. There may be a number of factors contributing to this phenomenon: differential natural and fishing mortalities, incorrect age readings and landing statistics. Comparisons of VPA and survey data covering the same series of yearclasses show the same discrepancy. Whatever the causes, we will for the purposes of this analysis assume that the survey data provides the best estimates of the true variations in recruitment, and for the whole period the yearclasses in the highest sub-range will be presented as being 10 times as abundant as those in the lowest range, the middle range 5 times. If yearclasses of low, medium and high abundance occur with frequencies of about $75 \%$, $12 \%$ and $12 \%$ as is indicated by the survey data this means that about 70 per cent of all recruitment derive from the broods of high and medium abundance. Their occurrence is therefore of a similarly high significance for the survival of the stock.

Fig. 1 and Table 3 presents the assessment of yearclass abundance in three categories: low, medium and high abundance corresponding to the subranges into which each series were grouped. Our general view is that the 0-group surveys provide the most reliable and least biased estimate of zero group recruitment. There is a fair degree of correspondence between the three different estimates for the yearclasses 1965-1979, but with one important exception. The yearclass 1969 appears in the VPA-series with an abundance in





Fig. 1. Assessment of yearclass abundance in three categories: low (L), medium (M) and high (H) abundance for the period 1902-1983.
the upper "medium" range, while both of the survey data sets present this yearclass in the lower "low" range. It seems likely that this discrepancy is caused by an "overspill" in the VPA data from the rich 1970-yearclass caused by aging problems. If this is so, the same effect may have caused biased estimates of yearclasses adjacent to those of high abundance also in the earlier VPA data, e.g. Yearclasses 1962, 1957, 1947-49.

Table 3. Indices and assessment of yearclass abundance 1902-1983.


In the cases where estimates differ for the same yearclasses the choise is based on the following arguments: For the yearclass 1918 Rollefsens assessment of "high" abundance was chosen rather than Sund's "low" on the assumption that the otolith readings were more reliable. For the 1947-yearclass also the VPA estimate is close to "low". The 1957-59 yearclasses all appear as "low" in the USSR trawl survey data. In the "USSR assessment" (Anon. 1982 and Anon. 1967) which is based on the appearance of the yearclasses in the USSR trawl fishery mainly on young cod, these yearclasses are estimated as -Average,+Average and +Average respectively. The trawl fisheries in Division I, Barents Sea which are based mainly on 3-5 year old cod showed a marked increase both of c.p.u.e. and total yield in 1962 and 1963 which is also consistent with relatively high abundance of the yearclasses 1958 and 1959 (Anon, 1967). Finally Mankevich (1965) describes the 1958-yearclass as "above average" and the 1959-yearclass as "rich". The USSR trawl survey during these first years were thus probably not representative. The 1962 -yearclass has a low index in the III-group trawl survey. It is estimated as "poor" in the USSR assessment and the VPA "medium" value is probably a result of an "overspill" from the rich 1963 and 1964 yearclasses.

The "USSR Assessment" gives both the 1963 and the 1964 yearclasses as "rich". In the few cases where the estimates differ in the years after 1965 the 0-group estimate has been relied on.

One must note that this analysis of a number of independent series of estimates cannot reveal any possible long-term trends in yearclass abundance.

## CLIMATIC VARIATIONS

THE HYDROGRAPHIC DATA

With exception of two periods, 1906-20 and 1941-1944, regular observations of temperature in the Kola section (along $33^{\circ} 30^{\prime} E$ ) have been carried out since 1900. Monthly mean temperature for the depth layer $0-200 \mathrm{~m}$ (between $70^{\circ} 30^{\prime} \mathrm{N}-72^{\circ} 30^{\prime} \mathrm{N}$ ) have been made available to the Institute of Marine Research by the Knipowich Polar Research Institute of Marine Fisheries and Oceanography, Murmansk. Midttun, Nakken and Raknes (1981) have calculated monthly mean temperatures for the period 1921-80. Anomalies from these mean values have been calculated for the whole observation period.

During the period l900-1925 we have used sea surface temperature data from the meteorological station Gjesvær. This station, located at $71^{\circ} 06^{\prime} N, 25^{\circ} 22^{\prime} \mathrm{E}$, was operated in the period $1881-$ 1925. Based on monthly temperature means presented by FROGNER (1948), anomalies for the quarter April-June have been prepared. During this quarter the water masses are relatively well vertically mixed, and the surface data should therefore reflect temperature changes in most of the water column. It is also shown by Blindheim, Loeng and Sætre (1981) that there is a fair interrelationship between the trends from the meteorological stations and those in the upper 200 m of the Kola section. However, the anomalies can not be directly compared with each other.

Data on the ice conditions in the Barents Sea since 1900 have been taken from several sources. Table 4 lists the different periods, for which there exist data on the ice conditions.

Table 4. The different sources used in order to make an ice index for the Barents Sea.

| Period | Data source (References) | Classification made by | Period of the year | Area |
| :---: | :---: | :---: | :---: | :---: |
| 1900-31 | The Danish Meteorological Institute, Copenhagen | Kissler (1934) | April-Auqust | Spitsbergen-Novaya Zemlya |
| 1932-38 | The Danish Meteorological Institute, Copenhagen | The authors | April-August | Spitsbergen-Novaya Zemlya |
| 1946-63 | Institute of Polar Research, Oslo | Lunde (1965) | February-September | West of about $40^{\circ} \mathrm{E}$ |
| 1964-70 | Meteorological Office, Bracknell | The authors | February-September | Spitsbergen-Novaya Zemlya |
| 1971- | The Norwegian Meteorological Institute, Oslo | Loeng (1979) | January-October | Spitsbergen-Novaya Zemlya |

The classification of the ice conditions made for some of these periods could not directly be compared with each other. Therefore we found it convenient to use a common scale for the whole period. We have chosen a scale ranging from -2 to 2 where -2 characterize a year with extremely large ice covered areas and 2 is a year with extremely little ice. A normal ice year is indicated by 0 while -1 and 1 indicate a year with ice conditions between normal and extreme.

The first author who gave an index for ice covered areas for a longer period in the Barents Sea was Kissler (1934). He used ice charts from The Danish Meteorological Institute for the months April-August and classified each year according to a scale from 1 to 5. His results therefore could easily be transferred to our scale.

Det Danske Meteorologiske Institut (1926) published mean ice borders for the period 1898-1922. On the basis of this mean we
have characterized the years 1932-1938 in the same way as described above. We also classified some years before 1932 in order to get our classification consistent with Kissler (1934). It should be mentioned here that the ice charts from The Danish Meteorological Institute cannot be relied upon in detail as there exist very few observations from the areas considered. Nevertheless, since there are no better data available, these ice data are used.

For the years 1939-1945 no ice data have been available. From 1946 to 1963 Lunde (1965) has given an ice index for the western Barents Sea, i.e. the area west of about $40^{\circ} \mathrm{E}$. He gave each month from February to September a value, characterizing the ice coverage. The sum for all months then characterized the period February-September. His scale has been divided in 5 parts in order to get the same classification as for the earlier years.

From February 1960 the Meteorological office, Bracknell (1960-) started to present regular monthly ice charts. These have been used in order to characterize the years 19.64-70. The years 1960-1963 were used to compare our index with the one given by Lunde (1965) in order to get the indices fairly consistent.

An ice index for the Barents Sea based on ice-charts from The Norwegian Meteorological Institute up to 1978 is published by Loeng (1979). The years 1979-83 have been treated in the same way. We have also transformed this index to the one used here.

It is obvious that our ice inđex is not any absolute measure of the ice condition during the period 1900-1981. However, the main intention is to show the relative changes in the ice condition. That purpose is, in our opinion, satisfied by the index.

## ANALYSIS OF THE CLIMATIC DATA

Temperature anomalies from the Kola-section and Gjesvær are shown in Fig. 2 together with the ice index for the Barents Sea. There is a fairly good accordance between the temperature anomalies and variations in the ice coverage for most of the period.


There may be different reasons for this accordance. Novitskiy (1961) was of opinion that the ice conditions are determined by the heat content of the Atlantic influx to the Barents Sea, while Bochkov (1976) claim that both temperature and ice conditions depend on the 11 years solar activity cycle. However, we will not discuss this further in this paper.

Almost the whole period before 1920 was cold with more ice than normal. However, for the two years 1918-19 there is some discrepancies with the ice condition characteristics given by Kissler (1934). Our analysis of the data from the Danish Meteorological Institute indicates that these years should be given the index 0 , i.e. normal ice conditions. At the same time there was a marked rise in the temperature at Gjesvar, confirming a change in climate already in 1918.

According to the classical works of Zubov (1943, 1948) the amount of ice in the Barents Sea for the years 1920-33 was in average 15 per cent less than for the period 1900-19. Even if there was little ice during the first half of the 1920's, the temperature was normal or slightly below normal. During the second half of the l920's the temperature climate is characterized as cold.

The longest period of a warm regime was between l930-40. Here we also found the year with least ice, 1937. In order to do justice to the year, 3 should have been used in the index.

The years after 1945 are characterized by fluctuations of duration of 3-5 years. During the period 1946-63 there is some discrepancy between the ice index given by Lunde (1965) and the temperature anomalies in the Kola section. One possible explanation of this discrepancy is that Lunde (1965) did not take the ice conditions in the eastern Barents Sea under consideration. The ice conditions in the western and eastern Barents Sea some years vary differently (Loeng 1979).

Table 5. Periods of different climatic regime and yearclass of high and medium abundance.

| Period | Climatic regime | Yearclass abundance |  |
| :---: | :---: | :---: | :---: |
|  |  | High | Medium |
| 1900-1903 | Cold |  |  |
| 1904-1908 | Medium | 1904 | 1905. 1906 |
| 1909-1917 | cold |  | 1912, 1915, 1917 |
| 1918-1922 | Medium | 1918, 1919 |  |
| 1923-1929 | Cold |  | 1929 |
| 1930-1936 | marm |  | 1930 |
| 1937-1939 | Extra warm | 1937 |  |
| 1940-1944 | Unknown |  | 1942, 1943 |
| 1945-1949 | Medium |  | 1948, 1949 |
| 1950-1955 | Warm | 1950 | 1954 |
| 1956-1958 | Cold |  | 1958 |
| 1959-1962 | Warm |  | 1959 |
| 1963 | Cold | 1963 |  |
| 1964 | Medium | 1964 |  |
| 1965-1969 | Cold |  |  |
| 1970-1976 | Warm | 1970 | 1973, 1975 |
| 1977-1982 | Cold |  |  |
| 1983- | Warm | 1983 |  |

When the ice conditions for the whole Barents sea are taken into consideration, as after 1964, the variations in the ice conditions is in fairly good accordance with temperature anomalies in the Kola section. The different periods of climatic regimes are summarized in Table 5.

THE PERIOD 1970-1983

In Table 5 the years 1970-1976 are characterized as "warm" while the years 1977-1982 are "cold". The latter period was very cold and in addition the longest cold period on record, in any case since 1920. For the whole period 1970-1983 we have plotted the ice index made by Loeng (1979) together with the temperature anomalies from the Kola section (Fig. 3). The accordance between the two parameters is very good, and it gives reason to believe that the distribution of ice to a great extent depends on the oceanic climate.

From the beginning of 1982 the temperature started to rise, and at the end of the year the temperature was above normal. Data


Fig. 3. The period 1970-1983: Logarithmic index estimated by Randa (1983) (upper) and temperature anomalies in the Kola section (continuous line) together with the ice index (broken line) calculated by the method described by Loeng (1979) (lower).
from the month January-March 1983 showed a positive anomaly of $0.5-0.8^{\circ} \mathrm{C}$, while the results obtained during the international $0-g r o u p$ survey in August-September 1983 gave a positive anomaly of about $I^{\circ} \mathrm{C}$ Anon (1983). The ice conditions started also to improve during 1982, and during the winter 1983 ice was rarely observed south of $76^{\circ} \mathrm{N}$ in the western and central Barents Sea. Also in the eastern Barents Sea ice conditions have been less severe than during the previous years.

Already Helland-Hansen and Nansen (1909) suggested that temperature variations of some duration in the Barents Sea probably are of advective nature. The temperature is determined mainly by the conditions in the Atlantic inflow to the Barents Sea. Therefore, changes in the climate will first be observed in the western Barents Sea. Temperature changes in the eastern part will most often occur about one year later (Loeng, Nakken and Raknes, 1983). The same delay was indicated between Lofoten and the Kola section by Helland-Hansen and Nansen (1909).

## RELATIONSHIP BETWEEN CLIMATIC PERIODS AND RECRUITMENT

Various methods of smoothing the temperature and ice-cover data shown in Fig. 2 were attempted. These brought out more clearly the periodicity of the system, but tended to dislocate the times of the shifts of the regimes which we think are of special interest. From Table 5 six cold periods can be identified ranging from 3 to 9 years duration with an average of abt. 6 years, and 7 warm/medium periods ranging from 4 to 7 years with an average of 5.5 years. In addition an extra warm period of 3 years occurred during 1937-39 (the years 1963 and 1964 are not included in this grouping).

As can be seen from the listing of yearclasses of high and medium abundance in Table 5 the shift from a "cold" to a "warm" or "medium" period was related in time to the occurrence of yearclasses of high abundance in 1904, 1918/19, 1970 and 1983 and to yearclasses of medium high abundance in 1929/30 and 1958/59. Yearclasses of high abundance also occurred when the regime changed from "warm" to "extra warm" in 1937 and from "medium" to "warm" in 1950.

The yearclasses 1963 and 1964 both of high abundance do not fit into this picture of high recruitment with a regime of increasing temperature. They occurred after the end of a warm period when a relatively "cold" year was followed by a "medium" year.

It seems, however, fair to conclude from this comparison that the major part of the yearclasses of high and medium abundance
are either associated directly with positive temperature anomalies in the early part of a warm period or they occur immediately prior to a shift to a warmer regime (1918, 1929, 1948, 1958). It would thus seem that the hypothesis of an adjustment of the recruitment to a fluctuating potential for stock biomass production is confirmed by this analysis of historic data.

The actual interrelationship has of course not been revealed by this study. Since the maturity age of the Arctic cod of 7-9 years is well within the range of variation of a total climatic period ("warm" + "cold"), fluctuations of the stock size started and influenced by the changing climate could result in variations in recruitment if a close relationship existed between the spawning stock size and recruitment. Such a relationship does, however, not seem to exist. At the levels of intermediate size of the spawning stock, it is thought that the survival rate of the larvae and the resulting abundance of the 0-group stage is determined by conditions of the environment to which the eggs and larva are exposed in an early period. The nature of the conditions favouring survival are the subject of intensive research.

Another possible linkage between the extent of the feeding areas available to the cod in the Barents Sea and the level of recruitment exists in the system of ocean currents in the region. As is shown by the close relationship between the extent of ice cover of the Barents Sea and the temperature of the Kola Section for the period 1970-82 (Fig. 3), the width of the cods production area seems largely to be determined by, the heat transport of the Atlantic water flowing into the southern and central Barents Sea. The variations of temperature observed here can in a general way be predicted from observations up-stream along the Norwegian coast including the parts which form the main spawning areas of the cod. Some special conditions of the Atlantic water of the Norwegian current related to high temperature and/or increased velocity could result in favourable conditions for larval survival. At the far end in the Barents Sea the increase of temperature tends to extend feeding areas. As mentioned under
2.3 above there will be a time lag of about one year between the increase of temperature at Lofoten and that of the central/eastern Barents Sea. The existence of such a time lag could explain the cases where increased recruitment occurs just before the shift from a colder to a warmer period in the Barents Sea.

If the special conditions of the environment which favour high larval survival are related to major changes in the dynamics or temperature regime of the Norwegian current the phenomen or processes must have a large scale both in time and space. One would then expect that also other stocks which reproduce in this ecosystem would be similarly affected. Dragesund 1971) compared yearclass strength of some stocks spawning at the Norwegian coast for the period 1950-65 and found that there was "a clear tendency towards rich yearclasses of several species". Without going into a detailed comparative analysis the following list of years of common high recruitment in cod, haddock and herring is a convincing demonstration of close temporal relationship in conditions for larval survival:

| Cod | 1950 | $1958 / 59$ | $1963 / 64$ | 1970 | 1975 | 1983 |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| Haddock | 1950 |  |  | $1969 / 70$ | 1975 | $1982 / 83$ |
| Herring | 1950 | 1959 | $1963 / 64$ | S.tock. depleted | 1983 |  |

Systematic comparisons of prior data are not known, except for the outstanding yearclasses of cod and herring from the year 1904 which through Hjort's work belong in the history of fishery science!

Our analysis for cod as well as the degree of co-variance of several stocks thus indicate that the environmental conditions resulting in yearclasses of high abundance are related to processes or phenomena of the oceanographical environment which must be of a large scale both in space and in time. It is also indicated that they are directly or indirectly related to in-
creased heat transport in the Atlantic component of the Norwegian current.

It is hoped that these indications may point towards a fruitful approach for further studies.

## REFERENCES

Anon. 1967. North East Arctic Fisheries Working Group. Report of the Meeting at Copenhagen, December 4-14th 1967.

Anon. 1979. Report of the Arctic Fisheries Working Group. C.M. 1979.

Anon. 1982. Report of the Arctic Fisheries Working Group. C.M. 1982/Assess: 2.

Anon. 1983. Preliminary report of the international 0-group fish survey in the Barents sea and adjacent waters in August-September 1983. Coun. Meet. int. Coun. Explor. Sea, 1983 ( $\mathrm{G}: 35$ ) : I-28. (Mimeo.)

Blindheim, J., Loeng, H. and Sætre, R. 1981. Long-term temperature trends in Norwegian Coastal Waters. Coun. Meet. Int. Coun. Explor. Sea, 1981 ( $\mathrm{C}: 19$ ) : I-13.

Bochkov, Yu.A. 1976. On the effect of solar activity of various periodicity on the thermal regime of the Barents Sea. Coun. Meet. int. Coun. Explor. Sea, 1976 (C:2): 1-19.

Det Danske Meteorologiske Institut (1901-1940). Isforholdene i de Arktiske Have 1900-1938. Tillæg til Naut.-met. Aarb. 1900-1938, 1901-1940.

Dragesund, O. 1971. Comparative analysis of yearclass strength among fish stocks in the North Atlantic. FiskDir. Skr. Ser. HavUnders., 16: 49-64.

Helland-Hansen, B. and Nansen, F. 1909. The Norwegian Sea. FiskDir. Skr. Ser. HavUnders., 2(2): l-360.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. Viewed in light of biological research. Rapp. Proc. Verbs. Cons. Int. Expl. Mer. 20: l-228.

Kissler, F. 1934. Eisgrenzen und Eisverschibungen in der Arktis swischen $50^{\circ}$ west und $105^{\circ}$ Ost im 34-jährigen Zeitraum 1898-1931. Beitr. Geophys., $42(1): 12-55$.

Loeng, H. 1979. A review of the sea ice conditions of the Barents Sea and the area west of Spitsbergen. Fisken Hav., 1979 (2): 29-75. (In Norwegian, abstract in English.)

Loeng, H., Nakken, O. and Raknes, A. 1983. The distribution of capelin in the Barents Sea in relation to the water temperature in the period 1974-1982. Fisken Hav., 1983(1): l-17. (In Norwegian with English abstract.)

Lunde, T. 1965. Ice conditions at Svalbard 1946-1963. Norsk Polarinst. Årb. 1963: 6I-80.

Mankevich, E.M. 1965. Some investigations on Age and Length Compositions of Cod in the Barents sea in 1963. Ann. Biol. vol. XX: 126-127.

Meteorological Office. Monthly ice charts 1960-. Brachnell, England.

Midttun, L., Nakken, O. and Raknes, A. 1981. Variations in the geographical distribution of cod in the Barents Sea in the period 1977-1981. Fisken Hav., 1981(4): l-16. (In Norwegian, abstract in English).

Maslov, N.A. 1968. The influence of natural factors and fishing upon the age composition, abundance and distribution of the Barents Sea bottom fishes. Proceedings of the Polar Research Institute of Marine Fisheries and Oceanography, Murmansk, 23: 86-103. (Canadian translation, 1975).

Novitskiy, V.P. 196I. Permanent currents of the Northern Barents Sea. Trudy gos. okeanogr. Inst. 64: l-32. (U.S. Naval Oceanographic Office, Transl. 349 1967): 1-39.

Ottestad, P. 1942. On periodical variations in the yield of the Great Sea Fisheries and the possibility of establishing yield prognoses. FiskDir. Skr. Ser. HavUnders., 7 (5): 1-ll.

Randa, K. 1983. Abundance and distribution of O-group ArctoNorwegian cod and haddock 1965-1982. Contribution to the PINRO/HI-symposium in Leningrad, September 1983.

Rollefsen, G. 1952. Beretning 1950-52 fra Fiskeridirektoratets Havforskningsinstitutt. Årsberetn. Norg. Fisk. 1952 (6): 1-108.

Rollefsen, G. 1954. Observations on the Cod and Cod Fisheries of Lofoten. Rapp. et Proc. Verb. Cons. Int. Expl. Mer. Vol. 136: 40-47.

Sund, O. 1920. Unders $\varnothing$ kelser over torskefiskene. Årsberetn. Norg. Fisk. 1920 (1): 46-50.

Sund, O. 1926. Torskebestanden i 1926. Arsberetn. Norg. Fisk. 1926(1): 113-121.

Sund, O. 1936. The fluctuations in the European stocks of cod. Rapp. et Proc. Verb. Cons. Int. Expl. Mer. Vol. CI (3): 1-21.

Sætersdal, G. and Hylen, A. 1959. Skreiundersøkelsene og skreifisket i 1959. Fisken Hav. 1959(1): l-20.

Zubov, N.N. 1943. Arctic Ice. Moscow 1943. (Translated by U.S. Naval Oceanographic Office and Meteorological Society, 1963: 1-491.)

Zubov, N.N. 1948. In the center of the Arctic. Moscow-Leningrad 1948. (Ch. VI: Arctic ice, ch. VII: The warming of the Arctic. Translation $T$ l4R. Defence Scientific Information Service. Defence Research Board, Ottawa, Canada 1950, 54 p.).

# THE DISTRIBUTION OF COD LARVAE AND PREY ORGANISMS IN THE LOFOTEN AREA RELATED TO CRITICAL PREY CONCENTRATIONS 

## by

## S. Tilseth

Institute of Marine Research

## ABSTRACT

The distribution of cod larvae and their main prey organisms in the first feeding areas off the Lofoten islands have been studied in sheltered and exposed areas in relation to feeding conditions. These findings are discussed in relation to laboratory studies on larval feeding dynamics and food density required to meet metabolic demands. It was found that the cod larvae are sporadic feeders having intervals of digestion between feeding periods.

The maximum gut filling of first feeding cod larvae was close to 3 prey/larval gut when nauplii were the dominant food organism. The larval gut evacuation processes were dependent on the volume and state of digestion of the gut content. The critical prey density for first feeding cod larvae varied between 21 nauplii/l and 190 nauplii/l depending on larval swimming speed and feeding success.

The highest concentrations of both cod larvae and its main prey organism, copepod nauplii, were found in the Austnesfjord, $H \varnothing 11 a, H e n n i n g s v æ r$ and the Vesteråsfjord area. Patches of nauplii in densities between $50-100$ per liter were found in
these areas. From larval cod gut content analysis good agreement was found between feeding conditions and food density distribution. The effect of increased wind forces created a homogenous vertical distribution of both cod larvae and prey organisms causing reduced accessibility of food to the cod larvae.

## INTRODUCTION

In 1914 Hjort suggested in his hypothesis that the fluctuation in the year class strength of fish varied in magnitude according to the availability of food in the early larval stages. He proposed the "critical period" concept, stating that lack of food at the time of yolk absorption was the predominant factor causing high mortality. Several field studies have been accomplished during recent years to test this hypothesis. May (1974) concludes from a review of 11 investigations that no conclusions could be drawn due to the inadequacy of the sampling gear. Because of the difficulties involved in obtaining adequate data from field investigations a lot of effort have been devoted during the last decade to assess the relationship between prey density and larval fish growth and survival from laboratory experiments (Rosenthal and Hempel, 1970; Lasker et al., 1970; Wyatt, 1972; Hunter and Thomas, 1974; Laurence, 1974, 1977; Lasker and Zweifel, 1978; Houde, 1978, and Werner and Blaxter, 1981). A review of this data (Hunter, 1981) shows that there is a disparity between the required densities of prey for first feeding fish larvae and densities found in the sea. The search model of Vlymen (1977) demonstrates, however, that the average fish larvae could only survive if food organisms were distributed in dense patches. From these findings Hunter (1981) suggests that samples should be taken relevant to larval searching behaviour to obtain a better understanding of the relationship between estimates of food densities required by fish larvae and densities found in the sea. This involves an enormous number of discrete plankton samples both in space and time. This has, however, been accomplished by an in situ particle counter system described by Tilseth and Ellertsen, (1984a) able to count and size particles most frequently
captured by cod larvae. They found small-scale patches with high density of nauplii in the larval cod first feeding areas of Lofoten (Northern Norway). Synoptic observations have been made in the Lofoten area, on the effect of wind forces on the static stability of the upper surface layers and the vertical distribution cod larvae and copepod nauplii (Tilseth and Ellertsen, 1984a and Ellertsen et al., 1984).

The larval cod selection of prey species and sizes have been described in several field investigations (Wiborg, 1948; Marak, 1960; Last, 1978 and Ellertsen et al., 1977). The larval feeding rate, gut evacuation rate and digestion time of the main larval cod prey organisms have been studied in laboratory experiments (Tilseth and Ellertsen, 1984b) and these findings have been applied to define criteria for larval gut content analysis. Laboratory experiments have been performed to estimate critical prey densities for first feeding cod larvae (Solberg and Tilseth, 1984). The objectives of the present paper are to review some of these laboratory findings and compare these findings with the results from a series of field investigations reported by Ellertsen et al. (1984) on the distribution of cod larvae and nauplii in the Lofoten area. The materials and methods applied by these authors as well as their results will also be described.

## MATERIAL AND METHODS

LABORATORY STUDIES

Feeding.

Cod eggs were artificially fertilized and incubated according to the method described by Tilseth and Ellertsen (1984b).

A homogenous age group of larvae were made during hatching by removing all larvae hatched during the first 24 hours and all unhatched eggs 48 hours later. The cod larvae start exogenous feeding at day 5 post-hatching, and according to Ellertsen et al. (1980) the most active feeding occurs at day 7. In the
present investigations all feeding experiments were performed with cod larvae at age 7 days post-hatching. The larvae were fed natural plankton sampled by an automatic pump system described by Tilseth et al. (1984). Due to the filters of the system the size range of the prey varied within $90 \mu \mathrm{~m}-500 \mu \mathrm{~m}$.

The experiments were performed under constant temperature $\left(5^{\circ} \mathrm{C}\right)$, salinity $\left(34.5^{\circ} / 00\right)$, light ( 100 lux ) and prey den- sity conditions ( 0.5 prey/ml) in 51 black-walled aquaria. Just prior to the experiments these aquaria were stocked with prey organisms. Cod larvae were sampled every 15 minutes for 1 hour followed by 1 hour intervals. The experiments were terminated after 5 hours. The cod larvae were preserved in $4 \%$ formaline in $10^{\circ} / 00$ sea water for gut content analysis.

The larval cod digestion time of prey organisms was studied in vitro. Cod larvae, visually observed when capturing prey, were transferred to a small aquarium (Fig. 1) where the gut content of the transparent larvae could be observed by a binocular microscope. The prey was dissected out of the larval gut when it became transparent and stained with $1 \%$ toluidine blue in $1 \%$ borax.


Fig. 1. Cod larvae in vitro observation aquarium ( $10 \mathrm{~cm} \times 10$ $\mathrm{cm} \times 2 \mathrm{~cm}$ ). The aquarium was submerged in a glass thermostatically controlled waterbath $\left(5^{\circ} \mathrm{C}\right)$ during observation.

The larval cod gut passage time was studied by feeding the larvae for 1 hour ( 0.5 prey/ml) and transfer these larvae to filtered sea water. Twenty larvae were sampled for gut content analysis every 30 minutes for 2 hours and thereafter every 1 hour for 2 hours.

Five hundred cod larvae were fed for 24 hours ( 0.1 prey/ml) in a 701 black walled aquarium. Twenty larva were sampled every hour through the 24 hour cycle. The light intensity was kept at 100-200 lux during daytime and reduced to 0.5 lux from 1900 h to 2400 h and increased again to 100 lux at 0500 h .

Feeding Success, Perceptive Field.

The larval cod rate of success in capturing prey organisms and the larval perceptive field were measured during the first four days of exogenous feeding (day 5 to day 8 post-hatching). Temperature ( $5^{\circ} \mathrm{C}$ ) salinity ( $34^{\circ} / 00$ ) light intensity (100 lux) and prey density ( $0.5 / \mathrm{ml}$ ) were kept constant during the observations. These were made visually in a 101 black-walled, white-bottomed aquarium. Five larvae were transferred from the incubator, and the first larva showing food searching behaviour was observed for 15 minutes, while the remaining four were disregarded. The number of attacks were recorded concomitantly with the estimation of reactive distance, (e.g. distance from the larval eye to prey, when the larvae shows that it has perceived the prey by changing swimming pattern (see Ellertsen et .al., 1980), relative to the larval standard length. The larva was preserved in $4 \%$ formaline in $10^{\circ} \% 0$ sea water for gut content analysis. Ten larvae were observed each day.

Swimming Speed.

The swimming speed of cod larvae was measured daily from day 2 to day 13 post-hatching. Larvae from two different female fish were measured. The swimming speed of 20 larvae was measured each day in a light-proof box where the artificial light intensity were adjusted to 100 lux by neutral filter. The light


Fig.2. Outline of the observation system for recording of cod larval swimming speed $a=s w i m m i n g ~ a q u a r i u m, ~ b=~ t h e r m o s t a t ~$ controlled water bath, $c=T V$ camera, $d=$ light source, $e=$ monitor, $f=$ video recorder $g=$ light proof box.
source was placed at a $45^{\circ}$ angle to the observation aquarium. This aquarium was 30 cm in diameter and 5 cm deep placed in a thermostatically controlled water bath at $5^{\circ} \mathrm{C}$ (Fig. 2). The position of the larva relative to the surface or bottom could be estimated by measuring the distance between the larva and its shadow. The larvae were given an adaption period of 30 minutes prior to recording. The larval swimming speed was recorded for 15 minutes on videotape by a TV camera. The swimming speed of each larvae was calculated by measuring the swimming distance directly on the TV-monitor by playback of the video-tape. Swimming speed was not measured when the larvae were at the surface or the bottom of the aquarium.

FIELD STUDIES

The distribution of cod larvae in the Lofoten area was studied by Juday net ( $80 \mathrm{~cm}, 375 \mu \mathrm{~m}$ mesh) and modified plankton nets ( $160 \mathrm{~cm}, 375 \mu \mathrm{~m}$, Ellertsen et $\mathrm{al} ., 1984$ ) and sampled by vertical hauls from 50-0 m. The investigations were carried out during the first 3 weeks in May from 1979 to 1983. A map of the Lofoten area is presented in Fig. 3. To investigate the


Fig. 3. Map of the Lofoten area with the main cod spawning area, spawning period and main drift route of eggs (from Ellertsen et al., 1984).
vertical distribution of cod larvae, samples were taken at 5 , $10,15,20,25,30$ and 35 m depths by submersible electric pumps as described by Solemdal and Ellertsen, (1984). Fifteen $\mathrm{m}^{3}$ of sea water was sampled at each depth. The diel vertical distribution of cod larvae was investigated both in the sheltered Austnesfjord (in 1980) and the open ocean bay of the Vesterålsfjord (in 1982). Cod larvae were preserved in $4 \%$ formaline in $10^{\circ}$ /oo sea water solutions for morphometric measurements, dry weights and gut content analysis.

The distribution of larval cod prey organisms in the Lofoten area was investigated by a small submersible electric pump (Flygt 2051, 250 1/min). Samples were pumped on deck through a

50 m long by 5 cm in diameter hose. Samples were taken at 0 , $2.5,5,7.5,10,12.5,15,20,25,30$ and 40 m depths. The sea water was collected in calibrated tanks (23.7 1) and zooplankton was filtered through $90 \mu \mathrm{~m}$ mesh plankton nets. The whole zooplankton sample was countered and identified by microscope. The small-scale distribution of zooplankton patches was studied by an in situ particle counter system described by Tilseth and Ellertsen (1984a). Zooplankton samples were taken on every second station on each section and during 24 -hour stations (the Austnesfjord and the Vesterålsfjord) every second hour.

Temperature and salinity were measured by a CTD sonde. The static stability of the water masses during diurnal stations is expressed in the squared Brunt-Väisälä frequency (Phillips, 1977) computed for 5 m intervals.

## LABORATORY STUDIES

## Feeding.

Ninety-seven percent of the prey organisms identified in the gut content analysis were copepod nauplii, $1.6 \%$ could not be identified and $1.4 \%$ were bivalve veliger larvae, rotifers and copepod eggs.

The results of the gut content analysis are given as larval cod feeding incidence and feeding ratio (Fig. 4). The larval cod feeding incidence is defined as the percentage of cod larvae with gut content in the sample. Fig. 4(A) shows the increase in feeding incidence during the 5 hour feeding experiment, showing a rapid increase from $0 \%$ to $90 \%$ during the first 2 hours of feeding, varying between $80 \%$ and $93 \%$ during the next 3 hours. About $7 \%-10 \%$ of this larval population did not feed.

The cod larval feeding ratio is defined as the ratio between the number of prey found in the gut content to the number of larvae examined in the sample. Fig. 4(B) shows the larval feeding ratio against time during the feeding experiment. The



Fig. 4. Cod larval feeding incidence (\% larvae with gut content) and feeding ratio (no of prey/larval gut) during a 5 hour feeding experiment (from Tilseth and Ellertsen, 1984b).
feeding ratio increased during the first few hours, reaching a maximum level of 3.2 nauplii/larval gut after 4 hours. This seems to be the maximum gut filling, when the volume of the nauplii is still unchanged by digestion. The volume of the average nauplius captured by first feeding cod larvae was estimated to $91 \mu \mathrm{l}$. The mean volume of a distended gut of a 4.5 mm standard length cod larva was estimated to $329 \mu \mathrm{l}$. This gives a maximum filling of 3.5 nauplii/larval gut. The larval feeding rates are estimated for the time period of increasing feeding ratio. A linear regression analysis of these data gave feeding a rate of 0.94 nauplii/larvae gut per hour ( $y=0.18+$ $0.76 x, r^{2}=0.96$ ).

The larval cod digestion time for prey is defined as the time for the gut content to become transparent. The results from the visual observations showed that a $220 \mu \mathrm{~m}$ (carapace length) nauplius became transparent within 30 minutes, smaller nauplii becoming transparent after approximately 15-20 minutes. Fig. 5 shows a photo of 3 nauplii stained with toluidine blue all dissected out of 7 days old cod larvae, which had fed for 30 minutes. Nauplius A is negligibly affected by the process of digestion (defined as digestion category 1 , (dcl)). Nauplius B has most of the soft parts dissolved (dc2) and in nauplius $C$


Fig. 5. Nauplii dissected from a 7 days old larvae after a 30 minutes feeding period. The nauplii are coloured with $1 \%$ toluidine blue in $1 \%$ borax prior to photographing (from Tilseth and Ellertsen, 1984b).
only the excuviae is left (dc3). The excuviae were never observed to be affected by the digestive enzymes, but often collapsed and lost appendages after a longer period of peristaltic action.

The results from the larval cod gut passage experiments are shown in Fig. 6. This experiment was run in two steps, a 1 hour feeding period followed by a 4 hour period in filtered sea water. In Fig. 6A the larval cod feeding incidence is presented, which showed a level of $56 \%$ at the start of the starvation period. This dropped to $30 \%$ within the first hour with very little variation in the following 3 hours. Fig. 6(B) shows the larval cod feeding ratio (a) (only estimated for larvae with gut content), and the volume of the digestible organic material of the prey (b) (given in arbitary units based on the above described digestion categories, where dcl is given the value 1.0 , dc2 0.5 and dc3 0.1). Fig. 6(B) shows that the number of prey of the gut content was reduced from 2.4 nauplii/larvae gut to 1.3 nauplii/larvae gut within 2 hours, with no further reduction during the next 2 hours. The volume of the digestable organic material decreases from 0.55 to 0.13 within 90 minutes, with no further reduction. This means that only the excuviae are left.


Fig. 6. Cod larval feeding incidence (A) and feeding ratio ( Ba ) and the volume of digestable organic material in prey (b, arbitary units) during a 4 hour larval gut evacuation experiment (from Tilseth and Ellertsen, 1984b).

Bivalve veliger larvae (62\%) and copepod nauplii (35\%) dominated as prey organisms in the continuous feeding experiment, only a few rotifers, copepod eggs and phytoplankters (Peridinium sp) (3\%) were present. The results from the larval cod gut content analysis from this experiment are presented in Fig. 7. The feeding incidence (Fig. 7A) increased to $87 \%$ in 3 hour, and varied between $80 \%$ and $93 \%$ during the next 6 hours. A reduction occurred concomitantly with the reduction in light intensity to $40 \%$ at 2330 h , showing that about $50 \%$ of the fed larval population evacuated their guts. The feeding incidence increased after midnight with increasing light intensity reaching $90 \%$ at 0530 h , varying between $77 \%$ and $90 \%$ during the next 6 hours to 1130 h when the experiment was terminated.

The larval cod feeding ratio is presented in Fig. 7B as the total number of prey (a), number of bivalve veliger (b) and number of nauplii (c) per larval gut. The feeding ratio increased from 0 prey/larval gut to 4.0 prey/larval gut in 3 hours, giving a feeding rate of 1.3 prey/larval gut per hour, more bivalve veliger were captured (2.2/larval gut) than


Fig. 7A. Percentage of cod larvae with stomach content (feeding incidence) during a 24 hour feeding experiment. B. Average number of prey items in the cod gut (feeding ratio) (a), the number of bivalve veligers/larval gut (b), and the number of nauplii/larval gut (c) (from Tilseth and Ellertsen, 1984b).
nauplii (1.9/larval gut). The feeding ratio dropped to 3.0 prey/larval gut in the next 3 hours, followed by an active feeding period when the feeding ratio increased to 5.1 prey/larval gut at 1930 h . More than $95 \%$ of the nauplii were completely digested and the excuviae collapsed. The bivalve veliger were with a few exceptions undigested, but were stacked like plates such that the larval gut content were filled with
undigestable prey and excuviae. The feeding ratio decreased at 1930 h to 1.6 prey/larvae gut at 0030 h , and increased to at 0530 h a peak of 3.5 prey/larval gut. The feeding ratio dropped to 2.9 prey/larvae gut at 0730 h and increased again during the next 4 hours to 5.1 prey/larval gut by 1130 h when the experiment was terminated. More bivalve veliger larvae were found in the larval gut content than copepod nauplii in samples after midnight.

Feeding Success, Perceptive Field.

The results of the larval cod feeding success experiments are presented in Table 1 , showing an increase in feeding success from age 5 days post-hatching of $11.2 \%$ to $23.1 \%$ feeding success at age 7 days. The feeding success decreased to $14 \%$ with the resorption of the yolk sac at age 8 days post-hatching.

The larval cod perceptive distance increased with larval length from 3.36 mm to 3.48 mm (Table 1 ). No correlation could be made between the larval perceptive distance and the size of the prey. The larvae did, however, react to prey in all directions both above and below the horizontal axis of the larval body.

Table l. Cod larval feeding success during the first days of exogenous feeding. FS; mean percent feeding success, SD; standard deviation, SL; mean larval standard length (mm), $P D$; mean perceptive distance (mm) and $N$; number of larvae.

| Age | Feeding <br> FS | success <br> SD | SL (mm) | PD (mm) | N |
| :---: | :---: | :---: | :---: | :---: | ---: |
|  |  | 11.2 | 1.4 | 4.48 | 3.36 |
| 5 | 13.5 | 5.1 | 4.52 | 3.39 | 10 |
| 7 | 22.2 | 6.5 | 4.60 | 3.45 | 8 |
| 8 | 14.0 | 4.4 | 4.64 | 3.48 | 9 |



Fig. 8. Swimming speed of group $A$ and $B$ cod larvae (from Solberg and Tilseth, 1984).

Swimming Speed.

Fig. 8 shows the estimations of the larval cod swimming speed. These measurements were made on two different larval groups. The mean swimming speed (Fig. 8, solid line) increased in both groups from the start of the experiments to day 6 post-hatching, reaching a mean level of $12.2 \mathrm{~cm} /$ minute in group A larvae and $13.4 \mathrm{~cm} /$ minute in group $B$. The swimming speed decreased in both groups after day 6 to $8.2 \mathrm{~cm} /$ minute in group A larvae and $3.3 \mathrm{~cm} /$ minute in group B.

Table 2. The mean voiume of water searched by the cod larvae (in liters per 24 hours) during the first 4 days of exogenous feeding, calculated from the observed variation in reactive perceptive distance and variation in swimming speed, expressed by the mean swimming speed and the standard deviations.

| Age | $\begin{array}{c}\text { Search } \\ \overline{\mathrm{X}}\end{array}$ |  | $\begin{array}{c}\text { volume } \\ +\mathrm{SD}\end{array}$ |
| :---: | :---: | :---: | :---: | \(\left.\begin{array}{c}1 / 24 hour <br>

-\mathrm{SD}\end{array}\right]\)|  | 5.6 | 8.2 | 3.1 |
| :---: | :---: | :---: | :---: |
| 6 | 6.7 | 8.8 | 4.7 |
| 7 | 6.5 | 9.2 | 3.8 |
| 8 | 5.5 | 7.7 | 3.3 |

The volume of water searched by the cod larvae was calculated from the observations of larval reactive perceptive distance and swimming speed. The results are presented in Table 2.

Prey Density.

The food density requirements in the early stages of larval fish can be estimated from the behavioural search model outlined by Ivlev (1960), which in its simplest form requires an estimate of larval search volume, feeding success and ration:

$$
N=\frac{E L \cdot F}{\mathrm{En} \cdot \mathrm{~A} \cdot \mathrm{~S} \cdot \mathrm{FS}}
$$

where:
$\mathrm{N}=$ density of copepod nauplii/1;
EL = larval cod energy consumption rate, cal/larva per 24 hour;

F = increased metabolism for food processing and larval growth (4.5);
En $=$ energy ration of a $250 \mu \mathrm{~m}$ Calanus finmarchicus nauplius (1.3 $\cdot 10^{-3} \mathrm{cal}$ );

A = proportion of energy available to the predator (0.7),
S = larval search volume (1/24 hour), and
FS = larval feeding success.

The larval cod energy requirements have been measured by Solberg and Tilseth (1984). These measurements were made on unfed larvae and have been corrected for increased metabolism for food processing and growth according to Lasker (1963, 1970). The energy content of prey has been calculated from Tande's (1979) data and the available energy content of the prey for larval metabolism was set to 0.7 according to Winberg (1956) and Muiir and Niimi (1972).

The larval cod food density required to meet metabolic demands has been calculated for the first feeding period (Fig. 9) defined as the period from the first opportunity of exogenous feeding (day 5 post-hatching according to Ellertsen et al., 1980) to the first signs of starvation if food is not encoun-


Fig. 9. Larval cod food density requirements to meet metabolic demands at the outset of exogenous feeding (day 5) to the end of yolk-sac stage (EYS). - larvae showing mean swimming speed and feeding success, $\Delta-\Delta$ minimum sustained swimming speed and lower feeding success, o-o maximum sustained swimming speed and highest feeding success (from Tilseth and Solberg, 1983).
tered (day 8 post-hatching according to Solberg and Tilseth, 1984). The time available for visual feeding has been set to 24 hours according to Gjøsæter and Tilseth (1982). They found the light intensity to be above the treshold for feeding in the upper 38 m of the water column during 24 hours in Lofoten in mid May.

Three different levels have been calculated according to the variation in larval swimming speed (Fig. 8) and feeding success (Table 1). The larvae with the smallest search volume and lowest feeding success require 190 nauplii/l, the fastest swimmers with highest feeding success require 52 nauplii/l, while the average larvae require 89 nauplii/l at the onset of
exogenous feeding. The requirement for food density decreases through day 6 and 7 when the larvae are most successful in capturing prey organisms and show the fastest swimming speeds. The larval cod food density requirements vary at day 7 between 21 nauplii/l to 94 nauplii/l with an average food density requirement of 40 nauplii/l to meet metabolic demands. The food density requirement increases at day 8 post-hatching due to the decrease in both larval feeding success and swimming speed, varying between 39 nauplii/l to 175 nauplii/l with an average of 72 nauplii/1.

## FIELD STUDIES

The distribution of cod larvae in the Lofoten area during the first weeks of May in 1979, 1982 and 1983 is presented in Fig. 10. The occurrence of cod larvae during the same period in 1980 and 1981 was low, and larvae were only found in a few Juday net hauls. Dịstinctive for all three years was a similar pattern of distribution in the coastal current close to the shore with the highest concentrations of cod larvae in the Austnesfjord, Henningsvær-H申lla area and Gimsфy-Vesterålsfjord area. The amount of cod larvae found in the Lofoten area in 1983 was one order of magnitude higher than in previous years.

The distribution of copepod nauplii in the Lofoten area was investigated in $1980,-81$ and -82 . The results are presented Fig. 11 as the mean density of nauplii/l in the upper 40 meters of the water column. The density of naupiii varied between years, but the features of the distribution were similar to that of cod larvae in the coastal current with the highest concentrations in the Austnesfjord, Hфlla-Henningsvær and Gimsøy-Vesterålsfjord area.

The vertical distribution of nauplii in the Lofoten area was investigated in detail by Tilseth and Ellertsen (1984a) in 1981. They found patches of nauplii with high densities both off the Lofoten islands (west side), in the open ocean bay of the Vesterålsfjord (Fig. 12) and in the Austnesfjord-H申lla area (Fig. 13). As shown in Fig. 12 and 13 high density nauplii


Fig. 10. The distribution of cod larvae (no. per $\mathrm{m}^{2}$ surface) in the Lofoten area during the first 2 weeks in May in 1979, -82 and -83 .
patches were more frequently found in the sheltered Austnes-fjord-H $\phi 11$ a area than the more exposed areas west of the Lofoten islands.

Cod larvae would most probably experience different feeding conditions in these different areas. To study this aspect,


Fig. 11. The distribution of copepod nauplii (mean number per liter in the upper 40 m of the water column) in the Lofoten area during the first 2 weeks in May in 1980,81 and 82.
samples of cod larvae from four different localities from the 1982 investigation were selected for gut content analysis. The


Fig. 12. The particle ( $150 \mu \mathrm{~m}-500 \mu \mathrm{~m}$ ) distribution (per liter) on a section west off the Lofoten islands (A) and in the Vesterålsfjord (B) (from Tilseth and Ellertsen, 1984a).
cod larvae were categorized according to the yolk-sac staging system described by Ellertsen et al. (1984) (see Fig. 14). The gut content analyses of cod larvae of the same stages from different areas were compared. The yolk-sac stages representing cod larvae in the first exogenous feeding stages (5 and 6) were pooled, and as well as the larval stages assumed to be in the most critical stages (7, 8 and 9).


Fig. 13. The particle $(150 \mu \mathrm{~m}-500 \mu \mathrm{~m})$ distribution (per liter) on a section from the head to the mouth of the Austnesfjord (from Tilseth and Ellertsen, 1984a).

Samples from the following areas were analysed: the Austnesfjord, the inner part of the open ocean bay of the Vesteralsfjord, the western and eastern side of the Lofoten islands (see


Fig. 14. The cod larval yolk-sac stages. Stage $6=$ remains of the yolk is present in the yolk sac; stage $7=$ yolk sac empty; stage $8=$ the membranes of the yolk sac redused to a string; stage $9=$ the yolk sac membrane string partly resorbed; $10=$ the yolk sac membrane completely resorbed (from Ellertsen et al., 1984).

Fig. 1). Samples were analysed from several time periods for the different areas. The results are presented in Fig. 15 as the larval cod feeding incidence and feeding ratio. Since the cod larvae were sampled in vertical Juday net hauls the densities of nauplii in the different areas are given as the mean nauplii density in the upper 40 meters of the water column during the time period when the samples were taken.

The Austnesfjord showed the highest average food density (5-20 nauplii/l), and the larval cod feeding incidence varied between $87 \%$ and $98 \%$ for the oldest larvae (stage 7-9) whereas the youngest larvae examined (stages 5 and 6) showed a feeding incidence between $41 \%$ to $45 \%$. The feeding incidence of the oldest larvae from the Vesteralsfjord varied between $82 \%$ to $88 \%$, whereas that of the youngest larvae was only between $10 \%$ to $30 \%$. The average nauplii density in the area varied between


Fig. 15. Gut content analysis of cod larvae presented as feeding incidence (A) and feeding ratio (B) from four different localities in the Lofoten area (from Ellertsen et al., 1984).

5-10 nauplii/l. One sample from the east side of the Lofoten islands showed $78 \%$ feeding incidence for the older larvae and $11 \%$ for the youngest larvae The gut content analysis of cod larvae from the west side of the Lofoten islands showed a feeding incidence between $30 \%$ and $57 \%$. The youngest larvae in these samples had not been able to capture nauplii at all except for larvae in one sample from 9 May when $23 \%$ of the youngest larvae were found with gut content. The average nauplii density in this area varied between 1-5 nauplii/1.

The larval cod feeding ratio has been calculated only for the oldest larvae from the different areas. The results are presented in Fig. 15(B) showing a larval feeding ratio between 2.5 nauplii/larval gut and 4.2 nauplii/larval gut in samples from the Austnesfjord, between 2.4 nauplii/larval gut and 3.2 nauplii/larval gut in the Vesterålsfjord, 1.6 nauplii/larval


Fig. 16. The dry weight of cod larvae in stages 6,7 and 8 , from four different localities in the Lofoten area.
gut in samples from Lofoten east side and varying between 0.9 nauplii/larval gut to 1.0 nauplii/larval gut in samples from the west side of the Lofoten islands.

The dry weights of larval cod stages 6-8 are compared from the four different areas. The results are presented in Fig. 16, indicating a better growth for the larvae in the Austnesfjord and the Vesteralsfjord. The mean dry weight of stage 8 larvae was $72 \mu \mathrm{~g}$ and $75 \mu \mathrm{~g}$ respectively in these areas compared to $59 \mu \mathrm{~g}$ in samples from Lofoten east side and $56 \mu \mathrm{~g}$ from Lofoten west side, which was significantly lower ( $p=0.05$, t-test) than for larvae from the Austnesfjord and Vesteralfjord. The variation in dry weight was smallest in larvae sampled from the east side of the Lofoten islands.

The effect of wind velocity $\left(\mathrm{m}^{2} \mathrm{~s}^{-2}\right)$ on the static stability of the water masses (squared Brunt-Väisälä frequencies) and the vertical distribution of nauplii (no/l) and cod larvae (no/l), were studied during 24 -hour stations. These observations were


Fig. 17. Wind velocity $\left(\mathrm{m}^{2} \cdot \mathrm{~S}^{-2}\right) \mathrm{A}$, static water stability, (squared Brunt-Väisälä frequency) $B$, consentration of nauplii (per liter) $C$ and the concentration of cod larvae $D$ during a 24 hour station in the Austnesfjord in May 1980 (from Ellertsen et al., 1984).
made in the Austnesfjord in 1980 (data from Tilseth and Ellertsen, 1984a) and in the Vesterålsfjord in 1982 (data from Ellertsen et al., 1984). The results are presented in Fig. 17 and 18.


Fig. 18. Wind velocity $\left(\mathrm{m}^{2} \cdot \mathrm{~S}^{-2}\right) \mathrm{A}$, water static stability (squared Brunt-Väisälä frequency) $B$, concentration of nauplii (per liter) $C$ and the concentration of cod larvae D during a 24 hour station in the Vesteràlsfjord in May 1982 (from Ellertsen et al., 1984).

The wind was blowing up the fjord with varying velocities during the observations in May 1980 in the Austnesfjord (Fig. 17A). The surface water became completely mixed within 24 hours, demonstrated by the sudden decrease in squared BruntVäisälä frequencies at 1800 h (Fig 16B). Prior to this event nauplii were found in patches with densities $>60$ nauplii/l.


Fig. 19. Cod larval feeding incidence ( $\nabla-\nabla$ ) and feeding ratio ( $0-0$ ) during the 24 hour station the Austnesfjord in May 1980 (from Ellertsen et al., 1984).

The mixing of the upper layer broke up the nauplii patches and the distribution became more or less homogenous varying between 10 nauplii/l to 20 nauplii/l (Fig. 17C). No diel vertical migration could be observed, neither of nauplii nor of cod larvae (Fig. 17D).

The wind velocity was too low during the 24 -hour station in the Vesterålsfjord (Fig. 18A) to disrupt the static stability of the upper layer (Fig. 18B). Diel vertical migrations were observed both in the distribution of nauplii (Fig. 17C) and the larval cod distribution (Fig. 17D). Both the cod larvae and their main prey organisms showed vertical migration towards the surface at midnight.

The results from the gut content analysis of cod larvae from the 24 -hour station in the Austnesfjord are presented in Fig. 19 as larval feeding incidence and feeding ratio. The feeding incidence varied between $73 \%$ and $100 \%$ in samples taken before vertical mixing (1700 h to 300 h , see Fig. 17B); larval feeding ratio was $\geqq 1$ prey/larvae gut in all of these samples, $\geqq 2$ prey/larval gut in $71 \%$ of the samples and $\geqq 3$ prey/larval gut in $14 \%$ of the samples. The feeding incidence varied between $4 \%$ and $92 \%$ in samples taken after the mixing of the surface layers. The feeding ratio was $<1$ prey/larval gut in all samples taken at 0200 h and $<2$ prey/larval gut in all samples


Fig. 20. Cod larval feeding incidence ( $\nabla-\nabla$ ) and feeding ratio (o-o) during the 24 hour station in the Vesteråsfjord in May 1982 (from Ellertsen et al., 1984).
after the mixing of the upper 40 meter of the watermasses. The highest cod larval feeding ratio observed after mixing was 1.65 prey/larval gut, found in one sample from 25 m depth at 1000 h . The highest larval cod feeding ratio was found in samples from 20-30 meters depths.

The results of the gut content analyses of cod larvae from the 24 -hour station in the Vesteralsfjord are presented in Fig. 20 The larval feeding incidence varied between $35 \%$ and $61 \%$. The highest feeding incidence (59\% - 61\%) was found in samples from 20 m depth at 2300 h and 10 m depth at 1230 h . The larval feeding ratio varied between 0 prey/larval gut to 1.5 prey/larval gut. Larvae with empty guts were found in one sample from 20 m depth at 0130 h and the highest feeding ratio was found in larvae from 10 m depth at 1230 h .

## DISCUSSION

Gut content analyses of field sampled cod larvae and plankton enables conclusions to be drawn on the selection of prey species and size. This has been done for cod larvae in field studies by Wiborg (1948) who demonstrated a linear relationship between larval mouth size and prey width. Ellertsen et al. (1977) showed that the cod larvae, in the Lofoten area, were
more size selective than species selective, and that the sizes most frequently captured were within $140 \mu \mathrm{~m}-600 \mu \mathrm{~m}$. The main prey organism found from gut content analysis were nauplii of the copepod Calanus finmarchicus, the most dominant available prey in Lofoten (Wiborg, 1948; Ellertsen et al., 1981) during the main larval cod first feeding period (Ellertsen et al., 1977) .

Conclusions on the larval cod feeding conditions in sea must be based on the knowledge of larval feeding rate, gut passage rate and the digestability of different prey. These important ecological features were previously not well known. The larval feeding experiments presented in this study were performed under expected optimum levels both with regard to light conditions (Ellertsen et al., 1980) and prey density (Solberg and Tilseth, 1984). The results (Fig. 7) suggest that when the feeding conditions are optimal cod larvae are sporadic feeders pausing between feeding to digest food. Other fish larvae are known to be continuous feeders (largemouth bass, Micropterus salmoides, Laurence, 1971) and herring (Clupea harengus, Werner and Blaxter, 1981). This difference could be due to the relative small volume and rapid digestion rate in cod larvae varying from 30-90 minutes depending on the volume of digestable gut content (Fig. 6B). The larval feeding rate is obviously dependent on this strategy of feeding showing a linear increase in number of prey captured until gut maximum filling is reaching (Fig. 4 and Fig. 7). The maximum gut filling seem to be a function of volume or state of digestion of the gut content. This is demonstrated in Fig. 7B, showing that, when the larvae had continuous access to food, the number of prey in the gut increased in two steps from 0 prey/larval gut to 4.0 prey/larval gut interrupted by a digestion period then increasing again to 5.1 prey/larval gut. This was probably the maximum gut filling when over half of the completely digested contents consisted of undigestable bivalve veliger larvae.

Cod larvae do not seem to evacuate the gut at a constant rate, but at intervals (Fig. 7B) and only completely when maximum filling is reached. During periods of starvation the larvae
would not empty the gut completely but retained the gut content for several hours (Fig. 6B). These observations have been applied to define criteria for the analysis of larval cod gut content for evaluation of the feeding conditions in the sea by Tilseth and Ellertsen (1984b). They suggest that the larval cod feeding incidence (defined as the percentage of larvae with gut content) should be treated with care. A high feeding incidence does not necessarily indicate good feeding conditions, because cod larvae could keep parts of the gut content for several hours when the accessibility of food is reduced. In larval gut content analysis the feeding incidence should be estimated in concert with the larval feeding ratio. The magnitude of the feeding ratio indicate how close the larvae are to their maximum gut filling. Consequently a feeding ratio $\geqq 3$ nauplii/ larval gut and a feeding incidence $>90 \%$ indicate good feeding conditions at the time and place of capture. A feeding incidence $\geqq 50 \%$ and a feeding ratio $\geqq 1 \leqq 2$ nauplii/larval gut and if no newly eaten copepod nauplii are found in the gut content, then there is good reasons to believe that the larval population have been starving for several hours.

The results of the gut content analyses of cod larvae from four localities in the Lofoten area showed that the larval cod feeding incidence varied in proportion to the nauplii density. The highest feeding incidence was found in the sheltered localities, the Austnesfjord and the Vesteralsfjord, while the lowest larval feeding incidence was found in the most exposed areas with lowest food density (1-5 nauplii/1) west of the Lofoten islands. These differences in larval feeding incidence became even more clear when the youngest first feeding stages (stage 5 and 6) were compared. Except for one sample, these larvae had not been able to feed at all when the average nauplii density was 1 nauplii to 5 nauplii/l as observed west of the Lofoten islands. When comparing the larval feeding ratio it was evident that the Austnesfjord and the Vesteralsfjord provided the best feeding conditions. Only in samples from these localities were cod larvae found with gut content close to gut maximum filling (>3 nauplii/larval gut, Fig. 15B). In these areas the larval feeding incidence was $>80 \%$ in all
samples and the feeding ratio was $>3$ nauplii/larval gut in more than $50 \%$ of the samples. The cod larvae sampled west of the Lofoten islands must have been starving for several hours prior to sampling judging by the low feeding incidence, $<50 \%$, and low feeding ratio, <l nauplii/larval gut. Evidence presented in Fig. 16, shows a lower dry weight in larvae from this region than those from the Austnesfjord and the Vesteralsfjord, indicating that poor feeding conditions probably had existed for several days.

Patches of nauplii with densities exceeding larval cod density requirement to meet metabolic needs was found in the first feeding area (Fig. 12, 13), the size of these patches were small compared to the volume of water surveyed. They were, however, more frequently encountered in sheltered areas than exposed ones (Tilseth and Ellertsen, 1984a).

Detailed observations of the vertical distribution of cod larvae and nauplii with synoptic observation on wind force and the static stability of the water column are necessary for a better understanding between these biological and physical parameters. Such observations were made in the Austnesfjord, showing that increased vertical mixing with increasing wind force lead to a homogenous distribution of nauplii in the upper 40 m of the watercolumn (Fig. 17C) and no diurnal vertical migration could be observed neither in nauplii nor in cod larvae (Fig. 17D). The mixing of the surface layers and reduction in nauplii density caused a reduction in both feeding incidence and feeding ratio (Fig. 19). Prior to breakdown in water stability nauplii patches with densities between 40 nauplii/l and 60 nauplii/l were observed. This is close to the estimated average food density requirement for first feeding cod larvae (Fig. 9), and one should expect good feeding conditions. This was supported by the gut content analysis (Fig. 19), showing a larval feeding incidence between $90 \%$ $100 \%$ and a feeding ratio $\geqq 3$ nauplii/larval gut (close to maximum gut filling) in the majority of samples. During the first few hours after the break down in water stability, the larval feeding conditions became poorer judging by the gut
content analyses, showing a feeding incidence $<45 \%$ and feeding ratio <l nauplii/larval gut. The nauplii density varied between 10-20 nauplii/larval gut, which is close to the estimated critical prey density (about 20 nauplii/l, Fig. 9). This clearly indicates a diminished accessibility of food for the cod larvae.

When the upper surface layer of the water column remains stable for more than 24 hours, as observed during the diurnal station in the Vesterå sfjord, vertical migration was found both in cod larvae and copepod nauplii (Fig. 18). The nauplii density was not more than 1 nauplii/1 to 10 nauplii/l, and only small patches with more than 10 nauplii/l were observed, still below estimated critical density (Fig. 9). The results from the gut content analysis (Fig. 20) showed a feeding incidence between $10 \%$ to $50 \%$ and a feeding ratio $\geqq 1.0$ nauplii/larval gut in most of the samples. This indicate poor feeding conditions for the cod larvae in the Vesteralsfjord even if there was no or very little turbulence in the water column.

These observations supports Hjort's (1914) hypothesis and the hypothesis of Vlymen (1977) that fish larvae depend on small scale patchiness with high concentrations to meet their metabolic requirement. The rate of survival of the larval population and thereby the contribution to the yearclass strength could be dependent on the biological and physical factors affecting the distribution, frequency and stability of dense patches of larval cod food organisms.

## REFERENCES

Ellertsen, B., Moksness, E., Solemdal, P., Strømme, T., Tilseth, S., Westgård, T. and Øiestad, V., 1977. Vertical distribution and feeding of cod larvae in relation to occurrence and size of prey organisms. Coun. Meet. int. Coun. Explor. Sea, (F:34) 31 pp Mimeo.

Ellertsen, B., Moksness, E., Solemdal, P., Strømme, T., Tilseth, S., Westgård, T. and Øiestad, V., 1980. Some biological aspects of cod larvae (Gadus morhua L.). Fisk.Dir. Skr. Ser. HavUnders., 17: 29-47.

Ellertsen, B., Solemdal, P., Sundby, S., Tilseth, S., Westgård, T. and Øiestad, V., 1981. Feeding and vertical distribution of cod larvae in relation to availability of prey organisms. Rapp. P.-v. Cons. int Explor Mer, 178:

Ellertsen, B., Fossum, P., Solemdal, P., Sundby, S., and Tilseth, S. 1984. A case study on the distribution of cod larvae and availibility of prey organisms in relation to physical processes in Lofoten. In: E. Dahl, D.S. Danielssen, E. Moksness and P. Solemdal (Eds). The Propagation of Cod Gadus morhua $L$. Flфdevigen rapportser., 1, 1984.

Gjøsæter, J. and Tilseth, S., 1982. Primary growth increments in otoliths of cod larvae (Gadus morhua L.) of the Arctic-Norwegian stock. Fisk.Dir. Skr. Ser. HavUnders., 17: 278-295.

Hjort, J., 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P-v. Réun. Cons. Perm. int. Explor. Mer. 20: 1-228.

Houde, E.D., 1978. Critical food concentrations for larvat of three species of sub-tropical marine fishes. Bull. Mar. Sci. 28: 395-411.

Hunter, J. and Thomas, G.L., 1974. Effect of prey distribution and density on the searching and feeding behaviour of larval anchovy Engraulis mordax Girard. In: J.H.S. Blaxter (Editor), The Early Life History of Fish. Springer-Verlag, Berlin.

Ivlev, V.S., 1960. On the utilization of food by planktophage fish. Bull. Math. Biophysics. 22: 371-389.

Lasker, R., 1963. The physiology of Pacific sardine embryos and larvae. Cal. Coop. Oceanic Fish. Invest., X: 96-101.

Lasker, R., 1970. Utilization of zooplankton energy by Pacific sardine population in California current. In: J.H. Steele (Editor), Marine Food Chains. Oliver and Boyd publ. cop. Edinb.

Lasker, R. and Zweifel, J.R., 1978. Growth and survival of first-feeding northern anchovy (Engraulis mordax) in patches containing different proportions of large and small prey. In: J.H. Steele (Editor), Spatial Pattern in Plankton Communities. Plenum, New York, 470 pp.

Lasker, R., Feder, H.M., Theilacker, G.H. and May, R., 1970. Feeding, growth and survival of Engraulis mordax larvae reared in the laboratory. Mar. Biol. 5: 345-353.

Last, J.M., 1978. The food of three species of gadoid larvae in the eastern English channel and southern North Sea. Mar. Biol., 48: 377-386.

Laurence, G.C., 1971. Digestion rate of larval largemouth bass. N.Y. Fish Game J., 18: 52-56.
1974. Growth and survival of haddock (Melanogrammus aeglefinus) larvae in relation to planktonic prey
concentrations. J. Fish. Res. Bd. Canada 31: 14151419.

- 1977. A bioenergetic model for the analysis of feeding and survival potential of winter flounder, Pseudopleuronectes americanus, larvae during the period from hatching to metamorphosis. U.S. Fish. Bull. 75: 529-546.

Marak, R.R., 1960. Food habits of larval cod, haddock and coalfish in the Gulf of Manine and Georges Bark area. J. Cons. Perm. int. Explor. Mer. 25: 147-157.

May, R.C. 1974. Larval mortality in marine fishes and the critical period concept. In: J.H.S. Blaxter (Editor), The Early Life History of Fish. SpringerVerlag, New York.

Muiir, B.S. and Niimi, A.J., 1972. Oxygen consumption of the euryhaline fish aholehole (Kuhlia sandvicensis) with reference to salinity, swimming and food consumption. J. Fish. Res. Bd, Canada, 23: 1209-1248.

Phillips, O.M. 1977. Dynamics of the Upper Ocean. Cambridge University Press Cambridge. pp 207-209.

Rosenthal, H. and Hempel, G., 1970. Experimental studies in feeding and food requirements of herring larvae (Clupea harengus L.). In: J.H. Steele (Editor), Marine Food Chains. Univ. Calif. Press, Berkely.

Solemdal, P. and Ellertsen, B., 1984. Sampling fish larvae pumps; quantitative comparisons with traditional gear. In: E. Dahl, D.S. Danielssen, E. Moksness and P. Solemdal (Eds.). The Propagation of Cod Gadus morhua L. F1申devigen rapportser., 1, 1984.

Tande, K.S., 1979. Populationsdynamikk, reproduksjonsstrategi, karbon-nitrogeninnhold og vekst hos kopepoden calanus
finmarchicus (Gunnerus) i Balsfjorden, Nord-Norge. Hovedoppgave i marinbiologi. Inst. for biologi og geologi. Univ. i Tromsø. Mimeo.

Tilseth, S. and Ellertsen, B., 1984a. The detection and distribution of larval Arcto-Norwegian cod, Gadus morhua, food organisms by an in situ particle counter. U.S. Fishery Bulletin: 82(1) in press.

Tilseth, S. and Ellertsen, B., 1984b. First feeding cod larvae (Gadus morhua L.) food consumption rate and gut evacuation processes. In: E. Dah1, D.S. Danielssen, E. Moksness and P. Solemdal (Eds.). The Propagation of Cod Gadus morhua $L$. Flødevigen rapportser., 1 , 1984.

Solberg, T. and Tilseth, S., 1984. Growth, energy consumption and prey density requirements in first feeding larvae of cod (Gadus morhua L. In: E. Dahl, D.S. Danielssen, E. Moksness and P. Solemdal (Eds.). Flødevigen rapportser., 1, 1984.

Tilseth, S., Solberg, T. and Westrheim, K., 1984. Sublethal effects of the water-soluble fraction of Ekofisk crude oil on the early larval stages of cod (Gadus morhua L.) Marine Environmental Research, (In press).

Vlymen, W.J.III. 1977. A mathematical model of the relationship between larval anchovy (Engraulis mordax) growth, prey microdistribution, and larval behaviour. Environ. Biol. Fishes. 2: 211-233.

Werner, R.G. and Blaxter, J.H.S., 1981. The effect of prey density on mortality, growth and food consumption in larval herring (Clupea harengus L.) Rapp. P.-v. Réun. Cons. int. Explor. Mer, 178: 405-408.

Wiborg, K.F., 1948. Investigations on cod larvae in the coastal waters of northern Norway. Fisk.Dir. Skr. Ser. HavUnders. 9(3) 27 pp.

Winberg, G.G., 1956. Rate of metabolism and food requirements of fishes. Beloruss. State. Univ., Minsk. Fish. Res. Bd Can., Transl. Ser. No. 194 (1960).

Wyatt, T. 1972. Some effects of food density on growth and behaviour of plaice larvae. Mar. Biol. 14: 210-216.

# DISTRIBUTION AND ABUNDANCE OF POST LARVAL NORTHEAST ARCTIC COD AND HADDOCK 

by

Herman Bjørke and Svein Sundby<br>Institute of Marine Research

## ABSTRACT

From 1977 onwards an annual postlarvae survey has been carried out off northern Norway in June/July. The aim is to study the distribution of fish larvae, and to establish an index for the abundance of economically important fish species. A pelagic trawl is used for sampling, and depth for sampling is from 53m to surface.

In 1983 the station grid was designed to study mesoscale features of the larval distribution. It was found that cod larvae were mainly confined to coastal water masses and haddock larvae to the Atlantic water masses. The mesoscale circulation was found to influence the larval distribution. The same features were also found for the years 1980 and 1981. In 1979 the larval distribution was different, and the reason for this is discussed.

From 64 to $84 \%$ of the cod larvae were found in the upper 13 m . The vertical distribution indicates no diel migration, and no difference of the vertical distribution for the different length groups was found. The mean length of the cod larvae was highest in 1983, indicating good feeding conditions this year.

Indications of a high larval mortality from June to September in 1981 are discussed. The denser station grid introduced in 1983 gives probably a better quantitative index than the station grid used the previous years.

## INTRODUCTION

The Norwegian shelf constitutes important spawning grounds for fishes of great economical interest such as Northeast Arctic cod, saithe, capelin and Norwegian spring spawning herring (Anon, 1979). Eggs and larvae of these species are transported northwards and eastwards by the residual currents.

The Institute of Marine Research has since 1948 been sampling fish eggs and larvae at different localities along the Norwegian coast (e.g. Hognestad, 1969; Wiborg, 1960; Dragesund, 1970; Gjøsæter and Sætre, 1974; Ellertsen et al. 1981 and Bjørke, 1981, 1983). The sampling has taken place during the spring and summer seasons and has partly been aimed at the study of single species, such as, for example, herring and cod.

After 1966 a closer sampling grid was introduced from Stad to Vestfjorden in April and the sampling was aimed at the study of the herring larvae only.

Findings of oil along the Norwegian coast and the subsequent oil spill contingency plans introduced the need for increased and updated knowledge about the occurrance and distribution of fish eggs and larvae. These younger stages, with strongly reduced ability to choose their surroundings, are more vulnerable to the effects of oil and oil dispersants than the older ones.

Therefore, utilizing the sampling schemes already working, it was decided from 1976 onwards to identify and record all fish eggs and larvae caught with zooplankton gears.

Sampling of older larvae (postlarvae) offshore started in 1977. The aim was to study the distribution of larvae in June/July,
and if possible calculate an index for the abundance of the different species. In addition genetic investigations were made on cod and herring.

In June-July most of the larvae hatched on the Norwegian shelf are to be found north of Træna ( $66^{\circ} \mathrm{N}$ ) and most of the sampling was made in this area. In 1982 the sampling grid was extended southwards and started at Stad.

Ellertsen et al. (1981) showed that the cod eggs were confined to certain coastal water masses in Vestfjorden. Sundby (1983) showed that the distribution of cod eggs further north, off the coast of Troms, is confined to the coastal water masses, and that the distribution is influenced by the mesoscale circulation. This circulation in turn was shown to be strongly influenced by the bottom topography. On this background the question arose whether such mesoscale current features also may influenced the distribution of larvae later on, and further north. In 1983 the larva survey was designed to study possible mesoscale features of larval distributions due to bottom topography.

The aim of the present paper is to present some of the results of this work with emphasis on the distribution of cod in the area Lofoten - Bear Island.

USSR has since 1959 been conducting egg- and larvae-surveys partly overlapping the area presented in this work. The sampling periods have been April-May and June-July, e.g. Baranenkova and Khokhlina (1964); Baranenkova, Sorokina and Khokhlina (1973), and Muchina (1980).

MATERIALS AND METHODS

The geographical distribution of larvae was found by fishing with a small meshed midwater trawl. A trawl with an effective opening of $4 \times 10 \mathrm{~m}$ was used in 1977 , and the following years a trawl with an effective opening of $13 \times 13 \mathrm{~m}$. Both gears had varying mesh sizes and a cod end with 15 mm meshes.

Two kind of hauls were made in 1977, one with the headine at 40 , 20 and 10 m and a towing time of 20 minutes in each depthinterval. The other haul was made with five big floats on the headline and with a towing time of 60 minutes. The depth of the headline was checked with a depth measuring device.

From 1978 onwards a larger trawl was introduced. During the period 1978 - 1981 two hauls were made on each station, one with the headline in 40 and 20 m depth and a towing time of 15 minutes in each depth interval. The other haul was made at the surface with five big floats on the headline. Towing time was 30 minutes.

Only one kind of haul was made at each station in 1982 and 1983. Depths and towing time were the same as the previous year and five big floats were used on the headine during the haul.

Towing speed during all the years was 2-3 knots. The volume of filtrated water is not known. Therefore the computed index is based on the number of larvae caught per trawl haul. Oceanographic observations were made with a Neil Brown CTD-microprofiler down to 500 m depth.

Zooplankton hauls were made with a 180 micron Juday net, 36 cm in diameter, from 200 m to surface and from 20 m to surface.

All the fish larvae were identified, the length of 50 larva were measured when present, and the volume of the medusae recorded.

The results from the years 1979, 1980, 1981 and 1983 are plotted on horizontal maps, isolines drawn and the total number of larvae was estimated by using a planimeter on the isolines. Horizontal maps of the salinity distribution are also drawn to compare with the larval distribution. In 1978 and 1982 the station net was not dense enough to reveal meaningful mesoscale features, and therefore these data are not presented as isoline
distribution. They are only shown as numbers of larvae sampled at each station (Fig. 18 and Fig. 19).

The abundance index may be formalized:

$$
A=\int_{x, y} N(x, y) d x d y
$$

where $A$ is the abundance index
$N$ is the concentration of larvae expressed as number caught per trawl haul.
$x$ and $y$ are the geographical coordinates.

Fig. 1 shows local names used in the text.


Fig. 1. Local names used in the text.

## RESULTS AND DISCUSSION

## HYDROGRAPHY AND DISTRIBUTION OF COD AND HADDOCK LARVAE

Figs. 2-6 show results from the survey in June/July 1983. Fig. 2 shows the distribution of cod larvae, Fig. 3 the distribution of haddock larvae, Fig. 4 the salinity at 20 m depth, Fig. 5 the temperature at 20 m depth, and Fig. 6 shows delta-D at the surface with respect to the 150 dbar surface. In Fig. 6 the trajectory of a satelite tracked drifting buoy drogued at 30 m depth is plotted. The buoy drifted for 22 days from 22 June to 7 July a distance of about 80 nautical miles, i.e. an average residual current of $7,8 \mathrm{cms}^{-1}$.


Fig. 2. Distribution of cod larvae. 24 June to 17 July 1983.

Very high concentrations of cod larvae are found at Troms $\phi$ flaket and relatively high concentration are found at the north-western part of Nordkappbanken. More than $95 \%$ of the


Fig. 3. Distribution of haddock larvae, and station net. 24 June to 17 July 1983.


Fig. 4. Salinity at 20 m depth. 24 June to 17 July 1983.


Fig. 5. Temperature at 20 m depth. 24 June to 17 July 1983.
larvae were found at these two banks (Table 1). The highest concentrations are found in coastal water at salinities of $34,3-34,6 \%$ S. This salinity interval also covers the banks of Tromsøflaket and Nordkappbanken where anticyclonic gyres are found. These gyres are indicated in Fig. 6, which shows geostrophic stream lines in the area. At Ingфydjupet, where highly saline Atlantic water intrudes from the northwest, very small concentrations of cod larvae are found. Also off the shelf break to the west of Tromsøflaket small concentrations are found. However, cod larvae are found in a small area in Bjørnøyrenna, in the atlantic water mass.

While cod larvae occupy the coastal water on the banks, the haddock larvae are distributed in the highly saline Atlantic water masses, partly at Ingめydjupet, but mainly at Bjørnøydjupet.


Fig. 6. Delta-D at the surface relative to the 150 dbar surface. 24 June to 17 July 1983. Trajectory of satellite tracked drfiting buoy draugued at 30 m depth. 15 June to 7 July 1983.

Table 1. Frequency distribution (in percent) of cod larvae in the different geographical areas. 23 June - 14 July 1983.

|  | The continental <br> shelf Andøya- <br> Troms $\varnothing$ flaket | Troms $\phi$ - <br> flaket | Ingøy- <br> djupet | Coastal area Troms $\phi$ flaket Nordkapp | Northwestern Nordkappbanken and Hjelensøybanken | Porsanger fjord | Bjørnøy <br> Trench | SUM |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Frequency in percent | 1,2 | 87,7 | 1,2 | 1,1 | 7,7 | 0,6 | 0,5 | 100 |
| $\begin{aligned} & \text { Aręa in } \\ & \mathrm{km}^{2} \end{aligned}$ | 12.900 | 22.900 | 14.000 | 6.400 | 21.500 | 2.300 | 9.400 | 91.000 |



Fig. 7. Distribution of cod larvae. 20 June to 10 July 1979.

The features of watermasses and larval distribution in 1983 are rather detailed because the station grid was specially designed to reveal such mesoscale features. In the years 1979, 1980, and 1981 the station grid net was more dispersed. However, these data can still be used to show some rough mesoscale features. Figs. 7, 8 and 9 show the 1979 data of cod larvae, haddock larvae, and salinity at 20 m depth respectively, Figs. $10,11,12$ the 1980 data, Figs. $13,14,15$ the 1981 data. Fig. 9 reveals the same structures of the watermasses: coastal water extends above Tromsøflaket and Nordkappbanken, while Atlantic water intrudes into Ingøydjupet. These features were not that clear in 1980 (Fig. 12). However, these features of the water masses are reproduced in 1981 (Fig. 15).

In 1981 the larval distribution had the same general features as in 1983: the cod larvae are mainly found in the coastal water above the banks, and the haddock are found in Atlantic


Fig. 8. Distribution of haddock larvae, and station grid net. 20 June to 10 July 1979.
water at Biørnфyrenna. In 1981 the abundance of both haddock larvae and cod larvae was very poor (Table 3). However, also this year the haddock larvae are found in the Atlantic water masses.

In 1979 the larval distribution was somewhat different from the other years. Again, cod larvae were mainly found in the coastal water, but a larger part was also found in the Atlantic water to the west of the shelf break. The distribution of haddock larvae was even more anomalous with the main concentrations found close to the coast.

As shown above, the cod larvae seem mainly to be distributed in the coastal water masses and the haddock larvae in the Atlantic water masses. This is partly to be expected because the cod spawns in coastal water masses close to the coast and the


Fig. 9. Salinity at 20 m depth. 20 June to 10 July 1979.
haddock spawns in the Atlantic water masses at the shelf break (Anon, 1979). The cod eggs are then transported and spread northwards in the coastal water and the haddock eggs are transported and spread northwards in the Atlantic water as shown by Sundby (1983). Turbulent mixing is expected to gradually diminish these features, but the present data indicate that the features are still present in June/July. In 1979 the characteristic larval distributions were somewhat different. The haddock larvae were then distributed in the coastal water masses, and the cod larvae were partly distributed in the Atlantic water masses in the Norwegian Sea. This indicates that a large exchange of the Atlantic and coastal water masses had occurred after spawning. This is also indicated by the salinity distributions which show high values close to the coast.


Fig. 10. Distribution of cod larvae. 24 June to 10 July 1980.

The hydrographic data from all the years indicate that anticyclonic gyres exist above Tromsøflaket and the Northwestern part of Nordkappbanken, and that the Atlantic water flows cycIonically in Ingøydjupet. This will consequently influence the distribution of larvae whose residence time is most probable largest at the banks. This is confirmed at Troms申flaket by satellite tracked drifting buoy. Fig. 16 shows a drifting buoy that was trapped into anticyclonic whirls at Tromsøflaket for a period of approximately three weeks before it was released into Atlantic water.

Also the extremely high concentrations of cod larvae in 1983 indicate gyres at Tromsøflaket and Nordkappbanken. These two banks include about 49 percent of the total area where cod larvae were found, but contain more than $95 \%$ of the total number of cod larvae found.


Fig. 11. Distribution of haddock larvae, and station grid net. 24 June to 10 July 1980.

VERTICAL DISTRIBUTION OF COD LARVAE

Table 2 shows the number of cod larvae caught in the upper and lower hauls at stations where both hauls were made. Only offshore stations are included. From 61 to $84 \%$ of the larvae were found in the upper haul showing that the majority of the cod larvae are to be found in the upper 13 m . In 1977 , when a smaller trawl was used, $69 \%$ of the larvae were found in the upper 4 m .

There is no indication of a diel migration of the cod larvae in the present material. Ellertsen et al. (1980) found a light intensity of 0.1 - 0.4 lux as a treshold for feeding for young cod larvae. Gjøsæter and Tilseth (1982) measured light intensity at various depths in the middle of May in the Lofoten area. They found enough light for feeding throughout 24 hours


Fig. 12. Salinity at 20 m depth. 24 June to 10 July 1980.
a day at depths were the larvae was found, i.e. down to 30 m . It is thus conceivable that enough light for feeding are to be found in all sampling depths in the present material. Bogorov (1946) studied the vertical distribution of zooplankton organisms in the Barents and White Sea and found no diel vertical migration during summer. This could explain why no diel migration was observed in the present material.

Table 3 shows the mean length of the larvae from the upper and lower hauls. There are small differences in mean length of the larvae from the two kind of hauls, they are, however, significant at a $5 \%$ level. Fig. 17 shows the percentage distribution of cod larvae within length groups in the upper and lower hauls. No clear trend can be interpreted although the percentage of larvae in the deeper hauls seems to increase with length in 1979 and 1980.

Table 2. The percentage of cod larvae caught in the upper and lower hauls at stations where both kind of hauls were made.

| Depth <br> m | Year | 1977 | 1978 | 1979 | 1980 |
| :--- | :---: | :---: | :---: | :---: | :---: |
| $0-4$ | $69 \%$ |  | 1981 |  |  |
| $0-13$ | $31 \%$ | $81 \%$ | $84 \%$ | $71 \%$ | $61 \%$ |
| $40-10$ | 1153 | 3139 | 3659 | 118 | 5866 |
| 40-20 of <br> No. of <br> larvae |  |  |  |  |  |

Table 3. Mean length and standard deviation of cod larvae from the upper and lower trawl hauls.

| Year | 1977 |  | 1978 |  | 1979 |  | 1981 |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Upper h | Lower Is | Upper h | Lower ls | Upper h | Lower s | Upper <br> ha | Lower |
| No. of larvae measured | 362 | 393 | 737 | 380 | 981 | 362 | 673 | 865 |
| Mean length | 40.43 | 40.68 | 29.95 | 28.84 | 22.93 | 23.21 | 25.46 | 26.40 |
| Standard deviation | 10.39 | 11.43 | 6.17 | 5.14 | 4.21 | 4.17 | 6.11 | 6.01 |

It thus seems that the differences in the vertical distribution shown in Table 2 are due to other factors than time of day and length of the larvae.

LENGTH DISTRIBUTION OF COD LARVAE

Fig. 18 shows the length distribution of the cod larvae sampled in the period 1977-1983. The dates indicate the period when the larvae were sampled. The mean length of the cod larvae was highest in 1977, and, in decreasing order; 1983, 1978, 1982, 1ø81, 1979 and 1980. In 1977 the survey was made nearly one month later than the following years, and this year have to be


Fig. 13. Distribution of cod larvae. 5 June to 23 July 1981.
omitted when comparing the length distribution for the different years. Of the other years the majority of the larvae were caught before July 10 in 1979, 1980 and 1983, and later than July 10 in 19781981 and 1982. Kvenseth (1983) measured the growth rate of free-living cod larvae and found a growth-rate from 0.47 to $0.68 \mathrm{~mm} /$ day at an age of about 40 days. If a similar growth rate is to be found for the postlarvae, this results in a length increment of about 5 mm in 10 days. This is probably reflected in the high mean length for 1978, 1981 and 1982 when the majority of the larvae were sampled after July 10. Early sampling is probably reflected in the mean lengths for 1979 and 1980. However, in 1983, when nearly all the larvae were sampled before July 10 , the mean length was high and the length range of the larvae wide. Solemdal et al. (this meeting) found small differences in spawning period and peak of spawning for different years in Vestfjorden. Vest-


Fig. 14. Distribution of haddock larvae, and station grid net. 5 June to 23 July 1981.
fjorden is regarded as the main spawning area of the Northeast Arctic cod (Anon, 1979). This means that finding a high mean length early in July and a wide length range indicate good feeding conditions throughout the hatching period until the time of the postlarvae survey in 1983.

ABUNDANCE INDICES

Table 4 shows the abundance indices from the postlarvae survey. In addition the table shows the 0 -group indices from the international 0 -group survey in August-September (Randa, this meeting). From the present material three indices are omitted; the 1977 index due to sampling with different gear than the other years, and the indices for 1978 and 1982 due to inadequate coverage of the area. Figs. 19 and 20 show the distribution of cod larvae in 1978 and 1982.


Fig. 15. Salinity at 20 m depth. 5 June to 23 July 1981.

Table 4. Abundance indices from the postlarvae and 0 -group surveys.

| Year | 1979 | 1980 | 1981 | 1982 | 1983 |
| :--- | :--- | :--- | :--- | :--- | :--- |
| Postlarvae <br> index | 7,16 | 0,37 | 15,42 |  | 74,66 |
| 0-group <br> index <br> (logaritmic) | 0,40 | 0,13 | 0,10 | 0,59 | 1,69 |

The indices for the 0 -group investigations show that the index for 1983 was highest and that the indices for 1980 and 1981 were nearly at the same level and lowest. The postlarvae indices show a high index for 1983 followed by that of 1981 and a low for 1980.


Fig. 16. Trajectories of satelitte tracked drifting buoys drougued at 30 m depth, at Tromsøflaket. 14 April to 17 May 1982.

It is evident that the postlarvae index for 1981 is not in correspondance with the 0 -group index for this year. While the 0 -group indices for 1980 and 1981 are at the same level, the postlarvae indices are quite different.

Somehow this is not reflected in the 0 -group indices. Three explanations are suggested:

1) Incorrect 0-group indices.
2) Incorrect postlarvae indices.
3) Hign mortality among the cod larvae between the two investigations.

Randa (1981 and this meeting) studied the 0-group indices and the abundance of the same year class at age 3. He found a close relation between the two estimates.


Fig. 17. Percentage distribution of cod larvae in the upper and lower hauls at different lengths. Percentage in lower hauls is indicated by histogram.


Fig. 18. Length distribution of cod larvae sampled in the period 1977-1983. Dates indicate period when larvae were sampled.


Fig. 19. Number of cod larvae caught per hour in 1978.


Fig. 20. Number of cod larvae caught per hour in 1982.

Confidence limits are not calculated for the postlarvae indices. It is, however, clear that the abundance of cod larvae were higher in 1981 than in 1980 (Fig. 13 and 10).

The third possibility, high mortality of the cod larvae, could be an explanation of the discrepancies between the two sets of indices. This mortality could theoretically be due to lack of food for the 1981 year-class. Randa (this meeting) considered the 1982 year class as medium in size. Fig. 21 show the volume of the zooplankton biomass of this year. Compared to the biomass in 1981 (Fig. 22), it may be concluded that the biomass in 1981 were at least equal or even larger than in 1982. Therefore it may be concluded that at the time of the postlarvae sampling no indication of lack of food for the fish larvae could be shown. Another source of mortality could be predation of the cod larvae. Unfortunately, data to confirm this are not available.


Fig. 21. Zooplankton volume in ml per $\mathrm{m}^{2}$ surface in 1982. 200-0 m.


Fig. 22. Zooplankton volume in ml per $\mathrm{m}^{2}$ surface in 1981. 200-0 m.

The 1983 index for cod was highest both in the postlarvae and 0 -group surveys. This year the station grid was much closer during the postlarvae survey than the previous years and was planned to cover the distribution of the cod larvae only. This closer station grid revealed great differences from one station to another, and gave reasons to believe that a similar station grid is necessary to give a quantitative index for the abundance of postlarval cod in June-July.

## REFERENCES

Anon., 1979. The biology, distribution and state of exploitation of fish stocks in the ICES area. Part II. Int. Coun. Explor. Sea Coop. Res. Rep., 1977(86): 1-202.

Anon., 1983. Preliminary report of the international 0-group fish survey in the Barents Sea and adjacent waters in

August-September 1983. Coun. Meet. int. Coun. Explor. Sea, 1983 (G:35): 1-28.

Baranenkova, A.S. and Khokhlina, N.S., 1964. On the condition of formation of the Arcto-Norwegian cod stock in the 1956, 1960 and 1961 year classes during the first year of their life. Trudy PINRO, Vyp. 16: 195-214.

Baranenkova, A.S., Sorokina, G.B., Khokhlina, N.S., 1973. Distribution and abundance of eggs and larvae of main commercial fishes of the Barents Sea on drift routes from spawning areas in April-July 1969. Trudy PINRO, vyp. 33: 34-81. (in Russion, with English abstract).

Bjфrke, H., 1981. Distribution of fish eggs and larvae from Stad to Lofoten during April 1976-80. pp 583-603 in The Norwegian Coastal Current. Roald Sætre and Martin Mork (Eds). University of Bergen 1981.

Bjørke, H., 1983. Spawning of blue whiting (Micromesistius poutassou) in Norwegian waters. Coun. Meet. Int. Coun. Explor. Sea, 1983(H:35): 1-8.

Bogorov, B.G., 1946. Peculiarities of diurnal vertical migration of zooplankton in polar seas. J. Mar. Res. 6(1): 25-32.

Dragesund, 0., 1970. Factors influencing year-class strength of Norwegian spring spawning herring. FiskDir. Skr. Ser. HavUnders., 15: 381-450.

Ellertsen. B., Moksness, E., Solemdal, P., Strømme, T., Tilseth, S., Westgård, T. and Øiestad, V., 1980. Some biological aspects of cod larvae (Gadus morhua L.). FiskDir. Skr. Ser. HavUnders., 17: 29-47.

Ellertsen, B., Solemdal, P., Str申mme, T., Sundby, S., Tilseth, S., Westgård, T., and Øiestad, V., 1981. Spawning period, transport and dispersal of eggs from the
spawning area of Arcto-Norwegian cod (Gadus morhua L.). Rapp. P.-v. Réun. cons. int. Explor. Mer, 178: 260-267.

Gjøsæter, J. and Sætre, R., 1974. The use of data on eggs and larvae for estimating spawning stock of fish populations with demersal eggs. P. 139-149 in Blaxter, J.H.S. ed. The early life history of fish. SpringerVerlag, Berlin, Heidelberg, New York: 765 pp.

Gjøsæter, H. and Tilseth, S., 1982. Primary growth increments in otoliths of cod larvae (Gadus morhua L.) of the Arcto-Norwegian cod stock. FiskDir. Skr. Ser. HavUnders., 17: 287-295.

Hognestad, P.T., 1969. Forekomst av fiskelarver i nord-norsk kyst- og bank farvann våren 1969. Fiskets Gang 55: 58-61 (in Norwegian).

Kvenseth, P.G., 1983. Metode for produksjon av torskeyngel (Gadus morhua I.) i poll. Thesis. University of Bergen. (Unpublished).

Mukhina, N.V., 1980(1983). Distribution and abundance of early stages of cod, haddock and deepwater redfish in April-June 1980. Annls. Biol., Copenh., 37: 256-259.

Randa, K., 1981. Rekrutteringsindekser for Norsk-Arktisk torsk basert på materiale på dei internasjonale 0-gruppe unders $\phi$ kingane i Barentshavet. Thesis. University of Bergen. (Unpublished).

Sundby, S., 1983. Influence of bottom topography on the circulation at the continental shelf of northern Norway. Rapport fra Havforskningsinstituttet. FO 8303.

Wiborg, K.F., 1960. Forekomst av egg og yngel av fisk i vestnorske kyst- og bankfarvann og ved Skrova i Lofoten våren 1962. Fiskets Gang 48: 689-690 (in Norwegian).

SECTION II
Stock assessment

# ACOUSTIC ESTIMATES OF SPAWNING COD <br> IN THE LOFOTEN AREA IN 1982 AND 1983 

by

Odd Nakken
Institute of Marine Research

## ABSTRACT

The main spawning grounds for Arctic cod, the Lofoten area, were covered by acoustic surveys 7 times in 1982 and 12 times in 1983 during the prespawning and spawning season. The results indicated a spawning stock in the area of approximately 80 million specimens in 1982 and 50 million specimens in 1983. These figures were less than half the estimated total spawning stock of Arctic cod these years. The acoustic data were analyzed in order to estimate the migration rate in and out of the Lofoten area during the surveying period. The results indicate that in 1983 spent cod started to leave the grounds in the middle of March, and that the fish flux in and out of the area is an important factor to be considered when evaluating the acoustic survey results. In general acoustic surveys will tend to underestimate the number of spawners in the area under such circumstances.

## INTRODUCTION

The main spawning grounds of Arctic cod, the Lofoten area, have been more or less regularly echo surveyed during the spawning season for almost 50 years (Sund, 1938). The surveys have pro-
vided valuable information on the relative density distribution and migration patterns of spawning cod (Hylen et al., 1961; Monstad et al., 1969; Jakobsen, 1974), but few attempts have been made to estimate the number of fish actually present on the spawning grounds. From a series of surveys in 1975 of the inner Vestfjord, Blindheim and Nakken (1971) arrived at estimates of the number of spawners within that area. They concluded that even the highest of the obtained estimates, 14 million fish, amounted to only a fraction of the total spawning stock which that year was about 70 million specimens (Anon, 1982).

During the past 6-7 years the Institute of Marine Research has increased the survey activity on cod considerably in order to meet the need for fishery independant data for stock assessment (Hylen and Nakken, 1982). Since 1976 acoustic surveys have been carried out annually in February-March in the Barents Sea with the purpose of estimating the abundance of young cod and haddock (Dalen and Smedstad, 1979 and 1982). These surveys have contributed significantly to the knowledge of stock state and structure and the results have been used by the Working Group of Arctic Fisheries, ICES (Anon, 1982, Ulltang and Nakken, 1982), to calibrate the virtual population analysis. Because of the promising results obtained on young cod by using the acoustic technique, a series of acoustic surveys of the spawning grounds was undertaken both in 1982 and 1983. The aim of the surveys was to collect a data set which enabled us to estimate the number of spawners present at the Lofoten grounds throughout the main spawning season. The results have been reported by God $\phi$ et al. (1982 and 1983), and further used by Hylen and Nakken (1982 and 1983) in their assessments of both the total stock and the spawning stock of Arctic cod.

In the present paper the results from the acoustic surveys of spawning cod in the Lofoten area in 1982 and 1983 are summarized and discussed. In particular the reliability of the estimates are dealt with as to how well they represent the total spawning stock over the whole spawning season in the area.

The Lofoten region was covered 7 times in 1982 and 12 times in 1983 during the prespawning and spawning season. Details of the cruises such as survey grids and data sampling and processing schemes were reported by God $\phi$ et al. (1982 and 1983). The timing of the surveys and the research vessels used in the investigations appear from the text table below:

| Cruise no. | 1982 |  | 1983 |  |
| :---: | :---: | :---: | :---: | :---: |
|  | Date | Vessel | Date | Vessel |
| 1 | 29 Jan-1 Feb | Johan Hjort | 1-5 Feb | Michael Sars |
| 2 | 3-7 Feb | " " | 6-9 Feb | " " |
| 3 | 8-12 Feb | " " | 10-12 Feb | " " |
| 4 | 15-17 Feb | " " | 13-17 Feb | " " |
| 5 | 17-20 Feb | " " | 17-19 Feb | " " |
| 6 | 21-24 Feb | " " | 20-23 Feb | " " |
| 7 | 24-27 Feb | " " | 24-27 Feb | " " |
| 8 |  |  | 28 Feb-2 Mar | " " |
| 9 |  |  | 8-13 Mar | G.O. Sars |
| 10 |  |  | 15-18 Mar | Johan Ruud |
| 11 |  |  | 21-25 Mar | " " |
| 12 |  |  | 8-11 Apr | Michael Sars |

The cruises in February both years were a part of the scouting service under the Director of Fisheries, and the main objective of these cruises was to map the fish distribution in order to advice the fishermen about the migration of the mature cod. However, the survey grids applied within the Lofoten area were more or less the same for all cruises, and quite suitable for estimation of the abundance, and therefore approximately the same survey grid was adopted for the cruises in March-April 1983.

Reliable identification of the echo traces is one of the most important requirements to be met in acoustic abundance estimation. Usually such identification is undertaken by sampling the recorded fish layers by trawling. During the Lofoten cruises the research vessels were able to carry out trawling only to a limited extent due to the vast amount of gillnets and
longlines in the area. Yet, as a rule it was not difficult to discriminate between traces from cod and other scatterers, due to the echo strength (target strength) of the specimens. Most of the mature cod is more than 70 cm in length and has thus a significantly higher target strength than the other fish specimens in the area; saithe $40-50 \mathrm{~cm}$ in length and small redfish, Norway pout, blue whiting and herring all less than $35-40 \mathrm{~cm}$ in length and with considerably lower target strength than the mature cod. Thus, the separation of echo integration values for mature cod and other species and groups was a quite straight-forward process with a high degree of reliability.

The largest source of errors were the weather conditions, which caused two different types of errors to the estimates. In bad weather the upper layers of the sea are aerated. The airbubbles in the watermasses will significantly reduce the amount of acoustic energy which reaches the fish and the fish density will be underestimated unless some correction of the echo intensity is undertaken (Dalen and L申vik, 1982). If the transducer is towed at a depth below the aerated water no correction is needed. However, due to the large amount of fishing gears in the Lofoten area in February-March it is impossible to apply the towed transducer systems of the research vessels. The echo integration values were therefore corrected according to the method described by Løvik and Dalen (1982). The values for February 1983, cruise $1-6$ have not been used in the present analysis since all these cruises were carried out under extremely bad weather conditions. In February 1982 and in MarchApril 1983 weather conditions were favourable for acoustic density measurements and only minor corrections of the observed integration values were undertaken on some of the cruises.

On some cruises bad weather prevented a satisfactorily coverage of parts of the area (Godф et al., 1983). The estimates of abundance from these cruises are therefore too low and appear in brackets in the figures and tables.

## RESULTS AND DISCUSSION

## DISTRIBUTION OF PRESPAWNING AND SPAWNING COD

Godø et al. (1982 and 1983) presented detailed distribution maps from each survey. In Fig. 1 and Fig. 2 are presented two maps of the cod distribution, one from each year, and Fig. 3 shows how the Lofoten area was divided into subareas in order to study the movement of the fish.


Fig. 1. Distribution of mature cod in the Lofoten area 3-7

February 1982 (mm deflection per nautical mile of echo integrator).


Fig. 2. Distribution of mature cod in the Lofoten area 5-14 March 1983 (mm deflection per nautical mile of echo integrator).


Fig. 3. The Lofoten area. The subareas referred to in Tables 2 and 3 are framed.

Fig. 1 shows the distribution in the Lofoten-Vesteralen area in early February 1982. Dense patches, but very limited in extension, were observed on the main spawning grounds in the inner Vestfjord but the average fish density in the fjord was low; the bulk of the fish being found west of the Lofoten Islands and to the north of Vesteralen. Table 1 A shows how the number of fish in the inner Vestfjord increased during February 1982. Outside the Vestfjord at the western coast of the Lofoten Island the highest abundance was observed in the middle of February.

Fig. 2 shows the distribution at about 10 March 1983. The general trend is almost the same as in early February 1982; the fish being distributed in a narrow belt along the Lofoten Island and into the Vestfjord, but the quantities on the spawning grounds in the inner part of the fjord were much higher in March 1983 than in early February. Table 2B indicates the migration of fish within the Lofoten area in the period 25 February-9 April 1983. The total number of fish in the whole
area remains nearly constant, but significant changes takes place within each sub area. Outside the Vestfjord the number of fish was reduced during the first half of March reaching the lowest value around the middle of the month. In the inner Vestfjord the number of fish reached the highest value in mid-March.

The main impression we are left with from Figs 1 and 2 and Table 1 is as follows: On its spawning migration the bulk of the fish follows the edge of the continental shelf south to latitudes $68^{\circ} 40^{\prime}-68^{\circ} 50^{\prime}$, the south-westernmost part of the shallow Vesterålen banks. Then it migrates across the banks to the northwestern part of the Lofoten Islands and from there on it follows the 100 m contour line into the Vestfjord. Here the amount of fish increases rapidly during the month of February and reaches a maximum in the middle of March.

```
Table 1. Acoustic estimates of mature cod (numbers in millions)
    in the Lofoten area in February 1982 and in February-
    April 1983. Figures in brackets are underestimates
    due to insufficient area coverage.
```

| A | 1982 |  |  |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Date: | 1 | 5 | 10 | 16 | 19 | 22 | 26 |  |
|  | February |  |  |  |  |  |  |  |
| Outside Vestfjord | $(11)$ | 24 | 48 | $(22)$ | 43 | 40 | $(13)$ |  |
| Outer Vestfjord | $?$ | 6 | 10 | 15 | 13 | 10 | 10 |  |
| Inner Vestfjord | $?$ | 10 | 11 | 15 | 22 | 21 | 33 |  |
| Total | $(11)$ | 40 | 69 | $(52)$ | 78 | 71 | $(56)$ |  |


| B | 1983 |  |  |  |  |  |
| :--- | ---: | :---: | :---: | :---: | :---: | :---: |
|  | Feb | March |  |  |  | April |
|  | Date: | 25 | 1 | 12 | 17 | 23 |
| 9 |  |  |  |  |  |  |
| Outside Vestfjord | 20 | 8 | 7 | $(2)$ | 10 | $(8)$ |
| Outer Vestfjora | 5 | 10 | 4 | 7 | 12 | 5 |
| Inner Vestfjora | 22 | 30 | 35 | 33 | 24 | 26 |
| Total | 47 | 48 | 46 | $(42)$ | 46 | $(39)$ |

The three main factors influencing the abundance of cod in the total Lofoten area as well as the subareas are: The size of the spawning stock, the catch (fishery) and the migration in and out of the Lofoten area as a whole or between the subareas (Fig. 3).

The results from the 1982 and 1983 surveys were used by Hylen and Nakken (1982 and 1983) to assess the spawning stock sizes the two years. In Fig. 4 the total estimates from table 1 are plotted, and the estimates used by Hylen and Nakken are indicated by the horizontal lines called the best estimate.


Fig. 4. Acoustic estimates of mature cod in the Lofoten area (Table 1) in 1982 and 1983. The figures used by Hylen and Nakken, 1982 and 1983 are indicated.

Table 2 and Fig. 5 show the weekly catches in the Lofoten area the two years. Both years the catches reached a maximum in the middle and latter half of March and the 1982 catches were higher than the 1983 catches in terms of number of fish. The ratio between the total catches in 1982 and 1983 (1.4) is slightly less than the ratio between the best estimates of the
total number of fish the two years (1.6). This may partly have been caused by the "undercatching" by gillnets in 1982. That year a large portion of the spawning cod was too small sized to be effectively caught by the rather large meshed Lofoten gillnets. Thus, there appears to be good accordance between the estimated number of fish and the catches the two years from the rather rough comparison made here.

Table 2. Catches of spawning cod in the Lofoten area in 1982 and 1983.

| Week nо. | Date | Weight (tonnes) |  | Number | (millions) |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 1982 | 1983 | 1982 | 1983 |
| 5 | 31 Jan-5 Feb | 4806 | 6269 | 1.3 | 1.2 |
| 6 | 7 Feb-13 Feb | 4562 | 3408 | 1.2 | 0.7 |
| 7 | 14 Feb-20 Feb | 5802 | 4190 | 1.6 | 0.8 |
| 8 | 21 Feb-27 Feb | 7104 | 5122 | 1.9 | 1.0 |
| 9 | 28 Feb-6 Mar | 7787 | 9781 | 2.1 | 1.9 |
| 10 | 7 Mar-13 Mar | 8954 | 9553 | 2.4 | 1.8 |
| 11 | 14 Mar-20 Mar | 12518 | 12194 | 3.4 | 2.4 |
| 12 | 21 Mar-27 Mar | 12379 | 15309 | 3.4 | 3.0 |
| 13 | 28 Mar-3 Apr | 10331 | - | 2.8 | - |
| 14 | 4 Apr-10 Apr | - | 7682 | - | 1.5 |
| 15 | 11 Apr-17 Apr | 3541 | 6034 | 1.0 | 1.2 |
| 16 | 18 Apr-24 Apr | 3530 | 2152 | 1.0 | 0.4 |
| Total |  | 81314 | 81689 | $\approx 22$ | $\approx 16$ |

Sources: Lofotfisket 1982, Arsberetning Norges Fiskerier 1982, No. 5., Fiskets Gang 1983, No. 7-12.

Mean weights are taken from Hyien and Nakken (1982 and 1983).

In Table 3 is summarized the information on the spawning stock of Arcto-Norwegian cod in 1982 and 1983 as given by Hylen and Nakken (1982 and 1983). It is seen that the distribution of the total spawning stock is similar the two years. Somewhat less than half the stock was observed in the Lofoten area while an almost equal share was further to the north and less than 10 per cent to the south of Lofoten. The small differences between the two distributions are obviously not significant. Both years the 1975-yearclass made up the bulk of the total stock, in 1982 about one half and in 1983 about one third. It should, however, be noted that the 1982-spawning stock to the north of Lofoten was overestimated in Hylen and Nakken's 1982-assessment (Hylen
and Nakken, 1983). For the Lofoten area the corresponding numbers were 55 and 48 per cent, and the mature fish here were significantly older than in the areas further north (Table 3) both years.


Fig. 5. Landings of mature cod in the Lofoten area in 1982 and 1983.

Table 3. Number (in millions) by age of mature cod in various areas. Estimated from survey data (Hylen and Nakken 1982 and 1983).



Fig. 6 shows the number of fish on the main spawning grounds in the inner Vestfjord in per cent of the total number of fish in the Lofoten area. The bulk of spawners reached the inner part of the fjord during the last week of February, and the amount of fish in this area increased upto 75 per cent in the middle of March whereafter the percentage decreased. The number of observations in late March and early April were not sufficient to permit safe drawing of the curve for this period.


Fig. 6. The ratio (in per cent) between number of fish in the inner Vestfjord and the total number of fish in the Lofoten area as a function of time. Brackets indicate overestimation due to insufficient area coverage.

MIGRATION OF FISH IN AND OUT OF THE LOFOTEN AREA

Table 1 and Fig. 4 indicated that the total number of fish in the Lofoten area was approximately constant from 25 February to 23 March in 1983. During these four weeks about 8 million specimens (Table 2) were removed from the stock by the fishery. Thus there must have been a net influx of fish into the area of about 8 million specimens during this period.

At what time start the first specimens to leave the spawning grounds? As a rule spawning starts during the first week of March and reaches its maximum 1 month later (Ellertsen et al., 1983). Fig. 6 and Table 1 show that the abundance of fish in the inner Vestfjord was reduced by 9 million specimens from 17 to 23 March 1983. This reduction is 3 times greater than the amount removed by the fishery during the same period and it may thus be an indication that spent fish started to leave the spawning grounds in inner Lofoten in significant numbers about 15-20 March. If this is so, then the influx of fish, which compensated both the outflux and the catch, must have been larger than indicated above. As stated previously the observations in March and April are too scanty to throw light on this problem. But the data seem to indicate that the dynamics of the spawning population - the rate of migration to and fro the spawning grounds - is an important factor to be considered when evaluating the results from acoustic surveys. If the exchange of fish is large during the survey period, it simply means that the acoustic surveys grossly underestimate the total number of spawners in the Lofoten area. It also implies that a significant number of the fish observed to the north of Lofoten in early March (Table 3) will spawn in Lofoten. Hence, the percentages in Table 3 do not reflect the importance of the Lofoten area as spawning grounds for Arctic cod.

REFERENCES

Anon., 1982. Report of the Arctic Fisheries Working Group. Coun. Meet. Int. Coun. Explor. Sea, 1982/G 2: 1-53. (Mimeo.)

Blindheim, J. and Nakken, O., 1971. Abundance estimation of the spawning Lofoten cod 1971. Coun. Meet. Int. Coun. Explor. Sea, 1971/B 15: 1-5, 3 Tables, 2 Figs. (Mimeo.)

Dalen, J. and Smedstad, O.M., 1979. Acoustic method for estimating absolute abundance of young cod and haddock in
the Barents Sea. Coun. Meet. Int. Coun. Explor. Sea, 1979/G 51: 1-18, 2 Tables, 9 Figs. (Mimeo.)

Dalen, J. and Smedstad, O.M., 1982. Abundance estimation of demersal fish in the Barents Sea by an extended acoustic method. Symposium on Fisheries Acoustics, Bergen, June 21-24 1982. Contribution No. 36: 1-28. (Mimeo.)

Ellertsen, B., Fossum, P., Solemdal, P., Sundby, S. og Tilseth, S., 1983. Årsrapport 1982 fra prosjektet "Torskelarvens oppvekstvilkår i kyststrømmen". Report to Institute of Marine Research and the Norwegian Council for Fisheries Research (In Norwegian).

Godф, O.R., Nakken, O., Raknes, A. and Sunnanå, K., 1982. Acoustic estimates of spawning cod off Lofoten and Møre in 1982. Coun. Meet. Int. Coun. Explor. Sea, 1982/G 62: 1-16.

Godø, O.R., Nakken, O., Raknes, A. and Sunnanå, K., 1983. Acoustic estimates of spawning cod off Lofoten and Møre in 1983. Coun. Meet. Int. Coun. Explor. Sea, 1983/G 37: 1-24. (Mimeo.)

Hylen, A., Midttun, L. og Sætersdal, G., 1961. Torskeundersфkelsene i Lofoten og Barentshavet 1960. Fiskets Gang, (5): 101-114.

Hylen, A. and Nakken, 0., 1982. Stock size of North-East Arctic Cod estimated from acoustic survey data 1982. Coun. Meet. Int. Coun. Explor. Sea, 1982/G 61: 1-2. (Mimeo.)

Hylen, A. and Nakken, O., 1983. Stock size of northeast Arctic cod estimated from survey data 1982/1983. Coun. Meet. Int. Coun. Explor. Sea, 1983/G 57: 1-10.

Jakobsen, T., 1974. Skreiinnsiget $i$ Lofoten $i$ 1973. (The spawning migration of Arctic cod in Lofoten in 1973). Fiskets Gang, 60: 95-97.

Monstad, T., Nakken, O. og Nævdal, G., 1969. Skreiinnsiget 1969. Fiskets Gang, 34: 571-573.

Nakken, O. and Ulltang, Ø., 1982. A comparison of the reliability of acoustic estimates of fish stock abundances and estimates obtained by other assessment methods in the northeast Atlantic. Symposium on Fisheries Acoustics, Bergen, June 21-24, 1982. Contribution No. 38: 1-29. (Mimeo.)

Sund, O., 1983. Biological and oceanographic investigations. 8. Cod stocks in 1938. Fish movements and replacements. Årsberetning Norg. Fisk., 2: 87-102.

# THE EGG PRODUCTION OF ARCTO-NORWEGIAN COD (GADUS MORHUA L.) IN THE LOFOTEN AREA ESTIMATED BY EGG SURVEYS 

## By

SVEIN SUNDBY and PER SOLEMDAL Institute of Marine Research

## ABSTRACT

Spawning intensity measurements have been executed in Lofoten each year since 1976. They consist of egg net samples at selected spawning sites. In 1983, in addition, four quasi-synoptic egg surveys were conducted during the spawning season covering the total spawning area in Lofoten. These data are used to estimate the egg production during the spawning season 1983. The estimates are done by two methods. In the first method stage 1, 2 and 3 cod eggs are used in each survey to get $3 x 4=12$ estimates of the egg production per day at different times during the spawning season. The 12 values are used to construct an egg production curve for the spawning season. The curve is integrated to get an estimate of the total egg production. By the other method certain assumptions about the egg distribution field have to be done, and the total egg production is computed by combining the spawning intensity data with one quasi-synoptic survey. The first method is the most correct one. The second method is more rapid and needs less ships time and time for egg analysis. It is discussed how to get the second method more accurate.

## INTRODUCTION

Estimating the size of spawning stocks by computing the total egg production contains a number of problems which often is quite different for the different stocks. It is obvious that the methods and the field strategy should be quite different when estimating spawning stocks of demersal and pelagic spawners. But the problems may also be quite different for species of pelagic spawners with respect to the extent of the spawning area, spawning period, spawning behaviour, vertical distribution of the eggs, transport pattern of the eggs, characteristic concentrations and characteristic gradients of the eggs, mortality of the eggs, presence of other particles which may cause clogging of the sampling device, fecundity, and sex frequency of the stocks. All these variables should be considered when designing an eggsurvey.

The cod spawning in Vestfjorden is extremely concentrated. Within an area of less than $6,000 \mathrm{~km}^{2}$ more than 50 per cent of the Arcto-Norwegian cod spawns. The maximum concentration of cod eggs (found by traditional sampling device) may reach 15,000 per $\mathrm{m}^{2}$ surface (Sundby 1980). This is quite different from the North Sea mackerel which cover a spawning area of approximately $250,000 \mathrm{~km}^{2}$ and seldom reach concentrations of more than 1000 eggs per $\mathrm{m}^{2}$ surface (Iversen 1981). The cod eggs are found in a very narrow zone in the cold outflowing Vestfjord-water close to Lofotveggen. The distribution of the eggs is, to a certain extent, dependent on the wind conditions. Northeasterly wind, which causes downwelling at Lofotveggen, concentrates the older stages towards the shore, while southwesterly wind, causing upwelling spread the eggs out towards the central part of Vestfjorden (Furnes and Sundby 198I). The spawning which occurs near the bottom in the transition layer between the upper cold coastal water and the atlantic water beneath cause an opposite distribution of the newly spawned eggs. During upwelling the cod spawn at shallow depths close to the shore, while during downwelling the cod spawns at greater depths off shore (Ellertsen et al. 1981). The distributions described above are qualitatively illustrated in Fig. 1.


Fig.1. Two typical situations during spawning in Lofoten. Left: downwelling. Right: Upwelling. A: Newly spawned eggs. B: Old eggs.

The eggs ascend from the spawning depth ( $50-150 \mathrm{~m}$ depth) with velocities between 0.2 and $1.5 \mathrm{mmsec}^{-1}$. The highest concentration of the eggs are found in the surface layer, but due to the high degree of turbulence in the wind mixed layer eggs are found down to more than 50 m depth. At higher wind speeds ( $>10 \mathrm{~ms}^{-1}$ ) the eggs are almost homogeneous distributed in the upper layer (Solemdal and Sundby 1981, Sundby 1983).

Spawning intensity measurements have been made at three important spawning sites each year since 1975. These shows that the spawning starts during the first days of March and lasts until the last days of April. Maximum spawning intensity occurs during the first week of April (Solemdal, Sundby and Bratland 1983). These features seems to be very constant from year to year, and may lead to the conclusion that the cod spawning period is independent of physical and biological conditions of the sea water.

## MATERIALS AND METHODS

The material consists of four quasi-synoptic egg-surveys, and spawning intensity measurements taken approximately twice a week all through the spawning season at three important spawning sites.

## EGG SURVEYS

Fig. 2, 3, 4, 5 show the cruise tracks of the four egg surveys. At each station pelagic eggs were sampled with a traditional egg net ( 0.5 and $0.25 \mathrm{~m}^{2}$ opening and $375 \mu$ mesh size), and a C.T.D.station was taken. At the first survey the egg net was hauled from 50 m depth to the surface. At the other surveys it was hauled from 75 m depth. The effective filtration through the nets are not $100 \%$. Comparisons with integrated pump profiles during egg and larvae surveys during the years 1977, 1979, 1981, 1982 and 1983 in March-May, indicate a mean filtration efficiency of about 55\% (Solemdal and Ellertsen, in press). The larger part of the stations was identical with the standard stations used by the Cod Larvae Project since 1977. The distance between the stations in each section varies from 9 km to l km. Close to the shore the distance between the stations is small to map the large concentrations and the large lateral gradients. In addition to the standard section, selected stations were also taken between each section. The distance between stations long-shore is considerably larger than the distance between the stations cross-shore because characteristic gradients of the egg concentration are approximately 10 times larger cross-shore than longshore. The spawning area was divided in 6 sub areas shown in Fig. 6. Table 1 shows the number of stations taken at each cruise. The largest number of stations were taken in sub area II and III where the heaviest spawning occurs. Sub area VI was not covered during the first cruise due to the weather conditions. In the second survey sub area I was not covered, and in the third survey subarea $V$ and $V I$ were not covered.


Fig. 2. Cruise tracks 15-17 March 1983.


Fig. 3. Cruise tracks 21-25 March, 1983.


Fig. 4. Cruise tracks 25-27 March, 1983,


Fig. 5. Cruise tracks 8-11 April, 1983,


Fig. 6. Area of investigations divided in six sub areas. $x$ Positions of the spawning intensity stations.

Table I. Number of egg net- and C.T.D.-stations in the sub areas for the four quasi-synoptic surveys in 1983.

| Cruise | I | II | III | IV | V | VI | SUM |  |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
| 1. | $15-17$ March | 3 | 28 | 29 | 19 | 13 | 0 | 92 |
| 2. | $2 I-25$ March | 0 | 28 | 33 | 22 | 25 | 20 | 128 |
| 3. | $25-27$ March | 6 | 20 | 33 | 10 | 0 | 0 | 69 |
| 4. | $8-I I$ ApriI | 8 | 28 | 34 | 22 | 15 | 19 | 126 |

The cod egg concentrations (numbers per $\mathrm{m}^{2}$ ) of the stages 1,2 and 3 were plotted in horisontal maps, and the isolines of the concentrations drawn. The egg numbers were integrated for each sub area by using a planimeter on the isolines.

The cod eggs were classified in six developmental stages, according to the system of Westernhagen (1970), modified by Strømme (1977), using 3 temperatures during incubation, 2.5, 4.0 and $5.0^{\circ} \mathrm{C}$.

To check the duration of the three stages in situ experiments were carried out at the central spawning area at Hølla from the 26 March l983. Artificially fertilized eggs were transferred to three glass jars with plankton net at the top and lowered to depths of l-4, 55 and 120 meters. With intervals the jars were hauled and the development stage of the egg determined. Temperature profiles were recorded by Neill Brown CTD microprofiler.

The temperature in the upper 50 meters, where the majority of the eggs are distributed (Solemdal and Sundby 1981), is rather homogeneous with a mean of $3.0^{\circ} \mathrm{C}$.

Parallel series with the same eggs were also run at $3.0^{\circ} \mathrm{C}$ in the refrigerator-room of the research vessel.

At $3^{\circ} \mathrm{C}$ the duration of stage 1 was 48 hours from fertilization including stage I a $\beta$ (Westernhagen 1970). The egg stage 2 , from I a $\gamma$ including $I \mathrm{~b} \beta$, is from 2.0-4.38 days, and stage 3, from I br including II $B$, is from 4.38 to 7.0 days old. These values correspond fairly well with those cited from Strømme (1977). For the calculations the in situ values are used.

The identification of the eggs are routinously visual and performed onboard. The identifications are based on size, pigmentation etc. Early stages of cod and haddock eggs are impossible to separate, and difficulties also occur to separate cod eggs from eggs of saithe and Norway pout. To check the visual identifications special samples were frozen in liquid nitrogen and analyzed by a biochemical method, isoelectric focusing (Mork et al. 1983). The samples were taken in areas where mixing of different species usually occurs. Specially the relatively high egg densities on the south-eastern side of the Vestfjord, the inside of Lofotodden and the area off Lofoten have been sampled for biochemical identification. These areas are best shown in Fig. 16.

In Table 2 the results of eggs first visually identified as cod eggs and afterwards identified by isoelectric focusing are shown.

Table 2. Egg samples from three parts of the investigated area visually determined as cod eggs and checked by a biochemical method (Mork et al. 1983).

| Date | Area | Identification method |  |  |
| :---: | :---: | :---: | :---: | :---: |
|  |  | Visual | Biochemical |  |
|  |  | Nos. cod eggs | Nos. cod eggs | Nos. haddock eggs |
| 22 March | South East Vestfjord | 15 | 15 | 0 |
| 11 April | South East Vestfjord | 56 | 53 | 3 |
| 22 March | Inside Lofotodden | 6 | 6 | 0 |
| 11 April | Off Lofoten | 86 | 85 | 1 |
|  | Sum | 163 | 159 | 4 |

As shown in the table 98\% of the cod eggs are correctly identified by the visual method.

SPAWNING INTENSITY STATIONS

As mentioned above the spawning intensity investigation were made at three of the main spawning sites: Austnesfjorden and HøIla in subarea II, and Henningsværstraumen in subarea III. The sampling was made with an egg net of $0.25 \mathrm{~m}^{2}$ opening hauled from 100 m depth. Three stations were taken in Austnesfjorden, five stations at Hølla and four stations at Henningsværstraumen. Fig. 6 shows the position of the stations.

COMPUTING THE EGG PRODUCTION

The concentration of eggs per unit surface of stage $n$ on a spawning field may be expresses $C^{n}(x, y, t)$ where $x$ and $y$ represents the geographical coordinates and $t$ time. To compute the total production of eggs per time unit on a spawning field $f(t)$ the total area is integrated for each of the egg stages. This may be formalized mathematically:
(1) $f\left(t-\frac{\tau_{n}+\tau_{n+1}}{2}\right)=\int_{x} \int_{y} \frac{1}{\tau_{n+1}-\tau_{n}} c^{n}(x, y, t) d x d y$
where $\tau_{n}$ is the time of egg stage $n$ to start.

To get a numerical expression for eq. l the first approximation is to assumed that the quasisynoptic egg survey is conducted at a fixed point of time, $t_{1}$. This approximation should be valid if the time change of the egg production is small compared to the duration of the survey. The concentration field $C^{n}(x, y)$ obtain during one quasisynoptic survey is then integrated. In this work the three youngest egg stages are used. The egg production, $f(t)$, then may be computed at three points of time

$$
t_{1}-\frac{\tau_{1}+\tau_{2}}{2}, t_{1}-\frac{\tau_{2}+\tau_{3}}{2} \text {, and } t_{1}-\frac{\tau_{3}+\tau_{4}}{2} .
$$

The four quasisynoptic surveys conducted during the spawning season 1983 therefore give $(4 \times 3)=12$ egg production estimates at different times.

The total egg production during the spawning period, $T$, is obtained by time integrating eq. I.
(2) $F=\int_{T} f\left(t-\frac{\tau_{n}+\tau_{n+1}}{2}\right) d t=\int_{T} \int_{x} \int_{y} \frac{1}{\tau_{n+1}-\tau_{n}} C^{n}(x, y, t) d x d y d t$

The total number of eggs spawned during the spawning season is here computed in two ways:

1) In the first method the twelve egg production estimates from the synoptic surveys are used to construct a spawning period curve as shown in Fig. 10. The peak spawning and the end of the spawning is poorly covered by the synoptic surveys, and therefore the results from the spawning period stations are used to adjust the curve for those periods. At last the continuous curve is time integrated.
2) In the second method the spawning intensity curve is applied in a more direct way. Here the spawning intensity curve is time
integrated, and the level of this curve is determined by results from a synoptic survey. Thus one estimate is obtained by applying only one synoptic survey. From the present data twelve separate estimates of the total egg production may be obtained. The method is based on the assumption

$$
\begin{equation*}
\frac{C(t)}{f(t)} \approx \text { const. } \tag{3}
\end{equation*}
$$

where $C(t)$ is the mean concentration of eggs found at the spawning period stations. This means that the spawning intensity stations is supposed to be representative for the whole spawning area. It implies that the egg distribution field is constant with respect to time, only the concentration varies with the spawning intensity.

Thus the time dependent distribution field may be written

$$
\begin{equation*}
C(x, y, t)=C(t) \cdot c(x, y) \tag{4}
\end{equation*}
$$

where $C(t)$ is described by the spawning intensity curve and $c(x, y)$ is described by the quasi-synoptic egg surveys.

## RESULTS

THE FOUR QUASI-SYNOPTIC SURVEYS

Fig. 7, 8 and 9 show characteristic distributions of stage l, 2 and 3 cod eggs in Lofoten. The highest concentrations are found in sub areas II and III where the spawning period stations are located (Fig. 6). Besides in a small area in sub area VI also high concentrations are found.

The change of egg distribution from stage $I$ to stage 2 and stage 3 is typical: Older stages are found in a larger area indicating the influence of advection and diffusion. The distribution of eggs of higher stages than 3 are normally found in an area larger than that covered by the cruise. Therefore they are not included in these estimates.


Fig. 7. Distribution of stage 1 cod eggs, numbers per $\mathrm{m}^{2}$, 21-25 March 1983.


Fig. 8. Distribution of stage 2 cod eggs, numbers per $\mathrm{m}^{2}$, 21-25 March 1983.


In addition to the high concentrations of cod egg at the north-west side of Vestfjorden also some small concentrations of cod eggs are found in a narrow zone at the south-east side of Vestfjorden. These concentrations are not included in the estimates because it probably origins from coastal cod spawning. Investigations from earlier years show that these typical distributions partly extends into the fjords at the south-east side of Vestfjorden. However, the contribution to the total egg production in Lofoten is small, the order of less than $5 \%$.

Based on the four synoptic cruises, and the three youngest stages the mean egg production per day was computed for twelve point of time according to eq. l. These results are shown in Table 3. The table also includes results from a minor survey conducted during $23-25$ February, when spawning was at its very start. In those cruises, where some of the sub-areas were not covered (see Table I), the egg production was estimated by taking the fraction of egg production from the cruises where all sub-areas were covered.

Table 3. Estimated cod egg production per day $\times 10^{-9}$ in Lofoten based on four quasi-synoptic surveys and three egg stages. The data are also plotted in Fig. 10.

| 21 Feb. | 23 Feb. | 10 March | 13 March | 15 March | 18 March | 20 March |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 26.4 | 20.9 | 110.0 | 129.1 | 158.2 | 221.3 | 206.4 |
| 20 March | 22 March | 23 March | 25 March | 3 April | 6 April | 8 April |
| 276.5 | 407.3 | 496.5 | 672.7 | 747.5 | 737.3 | 530.7 |

In Fig. 10 the data from Table 3 are plotted versus time. The spawning intensity data indicate that the peak spawning occurred between 25 March and 3 April. As already mentioned the largest spawning occurs in sub-area II and III. In Fig. Il the egg production in sub-areas II and III is plotted versus time. The other curve in Fig. 10 represents the egg production in subareas I, IV, V and VI. About $70 \%$ of the egg production occurs in sub-areas II and III. Spawning outside this area is more evenly distributed over the spawning period. Fig. 12 indicates more detailed how spawning goes on in the four most important sub-areas. This shows that the peak spawning occurs at different time in each sub-area. The spawning seems to increase first in the outer regions. In sub-area IV a peak is seen 15 March. In the inner parts (sub-area II) the peak spawning occurs 25 March. Then the peak spawning towards the outer regions shows a time lag; sub-area III 3 April, sub-area IV after 8 April. In subarea VI very few data exists. However, the spawning here seems to be independent of the spawning in the inner sub-areas.

THE SPAWNING INTENSITY MEASUREMENTS

Fig. 13 shows the mean concentration of newly spawned cod eggs (0-2 days old) from the 12 spawning intensity stations shown in Fig. 6. The stations are located in the central spawning areas in sub-area II and III. Therefore, it more or less shows the same features as curve no. 1 in Fig. 11 , which represents the total spawning in sub-areas II and III. However, after the peak


Fig. 10. Estimates of egg production, numbers per day, based on the four quasi-synoptic surveys and stage 1,2 and 3 -eggs.


Fig. Il. Estimates of egg production, numbers per day, in sub areas II and III, and in sub areas $I$, IV and VI.


Fig. 12. Estimates of egg production, numbers per day, in sub area II, III, IV and VI.


Fig. 13. Mean concentration of stage 1 cod eggs from the 12 spawning intensity stations (shown in Fig. 6) during the spawning season 1983. Dotted line: Mean concentration of stage 1 cod eggs from the spawning intensity stations for the mean year 1976-1983.



Fig. 15. Distribution of stage 2 cod eggs, numbers per $\mathrm{m}^{2}$, 8-II April 1983.


Fig. 16. Distribution of stage 3 cod eggs, numbers per $m^{2}$, 8-11 April 1983.
spawning, 3 April, the spawning intensity stations show a very rapid drop while the synoptic survey no. 4 show that the spawning still is very high. This is explained by the special kind of egg distribution at that time. This is shown by Fig. l4, 15 and 16. The highest concentration is found off shore outside the spawning intensity stations.

COMPUTING THE TOTAL EGG PRODUCTION

The total egg production will here be computed in two ways as mentioned above.

Method I) is based on the data from the synoptic surveys. The peak spawning and the end of the spawning is adjusted by applying the spawning intensity curve. This is shown in Fig. 10. Integrating this curve gives the total estimate of the egg production during the spawning season, shown in Table 4. About $70 \%$ of the total egg production occurs in sub-area II and III.

Method 2) relies on that the spawning intensity data (Fig. 13) represents the spawning intensity of the entire spawning area. However, it was shown above that the 1983 spawning curve does not represent the spawning of the total area, because of the off shore displacement of the spawning during the first days of April. Therefore the mean spawning curve during the years 1976-1983 is used to describe the spawning intensity for the total area. (Dotted line in Fig. 13.) Eq. (4) is then used for each synoptic survey and each of the three stages to get separate estimates of the egg production during the spawning season. The results are shown in Table 4.

Table 4. Total cod egg production $\times 10^{-12}$ in Lofoten during the spawning in 1983.

| Method | Integrating the curve in Fig. $10 \quad 19.82$ |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Method | Applying eq. (4) |  |  |  |  |  |  |  |  |  |  |  |
|  | $\left\lvert\, \begin{aligned} & 10 \\ & \text { March } \end{aligned}\right.$ | $\begin{aligned} & 13 \\ & \text { March } \end{aligned}$ | $\begin{aligned} & \text { I5 } \\ & \text { March } \end{aligned}$ | $\begin{aligned} & 18 \\ & \text { March } \end{aligned}$ | $\begin{aligned} & 20 \\ & \text { March } \end{aligned}$ | $\begin{aligned} & 22 \\ & \text { March } \end{aligned}$ | $\begin{gathered} 23 \\ \text { March } \end{gathered}$ | $\begin{gathered} 25 \\ \text { March } \end{gathered}$ | $\begin{gathered} 3 \\ \text { April } \end{gathered}$ | $\begin{gathered} 6 \\ \text { April } \end{gathered}$ | $\begin{gathered} 8 \\ \text { ApriI } \end{gathered}$ | Mean |
|  | 34.60 | 14.62 | 12.04 | 12.29 | 15.67 | 12.35 | 17.84 | 22.02 | 19.20 | 23.69 | 20.45 | 18.62 |

## DISCUSSION

In the present work $0-7$ days old eggs divided in three stages has been used to compute the daily egg production. It has been assumed that the egg mortality is negligible in this period. Several authors have suggested that egg mortality may be considerable, e.g. mortality may be caused by the physical strain on the eggs by breaking waves. Pommeranz (1972) made thorough experiments on the effect of physical strain on plaice eggs, but he was not able to conclude that breaking waves would cause mass mortality of eggs. Besides only a small fraction of pelagic eggs are found in the top layer during stormy weather (Sundby 1983). Nevertheless mortality of eggs may also be caused by other reasons. However, the mortality of Arcto-Norwegian cod eggs is most probably on a rather low level. This is indicated by the results from the synoptic surveys, because the total production per day based on stage 3 eggs corresponds fairly well with
the production based on stage 1 eggs from the previous cruise (Fig. 10).

To compute the total egg production during the spawning season two methods have been used. The first method is simply based on integrating the data from quasi-synoptic egg surveys. This is obviously the most correct way of estimating the egg production because the total spawning area is covered for each survey. However, large effort has to be put into making synoptic surveys all through the spawning season. It is time consuming both with respect to ships time and analyzing time of the large number of egg samples. In the present investigation four synoptic surveys were made, but even this large effort was not enough to cover the total spawning period. The egg production more or less had to be guessed for the late interval of the spawning period (dotted lines in Figs 10 and ll).

In the second method it is assumed that the concentration of eggs from certain selected spawning period stations represents the spawning in the whole spawning area, i.e. it is assumed that the time variation of the spawning is equal at every spawning field. In this way the total egg production may be estimated in a cheap way based on one or two quasi-synoptic surveys combined with the spawning intensity curve (Fig. I3).

However, the assumptions made above that spawning intensity is equal at every point is not right, as shown by Fig. ll. Spawning outside the main spawning areas II and III is not that concentrated with respect to time. Besides special physical events, such as upwelling, may cause a different distribution of the eggs. This occurred during the fourth quasi-synoptic survey causing an anomalous drop of the egg concentration on the spawning period stations. Since the peak spawning, and the start and the end of the spawning in Lofoten is rather constant each year, the mean spawning intensity curve is supposed to give a better description of the spawning intensity than the data from 1983. The results in Table 4 are based on the mean spawning intensity curve for the years 1976-1983. The results seem to
correspond fairly well with those obtained by the first method when using the quasi-synoptic survey conducted during the peak spawning. The results from the first cruises does not correspond that well, probably because of the mismatch of time between the mean spawning period curve and the synoptic surveys. However, at the time of the peak spawning the spawning intensity flattens out for a short time. Therefore, the mean spawning period curve combined with two or three synoptic survey around the peak spawning time should be a reasonable alternative to the more elaborating and time consuming first method.

## REFERENCES

Ellertsen, B., Furnes, G.K., Solemdal, P. and Sundby, S., 1981. Influence of wind induced currents on the distribution of cod eggs and zooplankton in Vestfjorden. Proceedings from the Norwegian Coastal Current Symposium, Geilo, Norway, 9-12 Sep. I980, University of Bergen: 604-629.

Furnes, G.K. and Sundby, S., 1981. Upwelling and wind induced circulation in Vestfjorden. Proceedings from the Norwegian Coastal Current Symposium, Geilo, Norway 9-12 Sep. 1980, University of Bergen: 152-177.

Iversen, S.A., 1981. Spawning and trends in spawning stock size of the north sea mackerel during the period 1973-1980. Countal Meeting of the International Council for the Exploration of the Sea 1981/H:I6, 19 pp.

Mork, J., Solemdal, P. and Sundnes, G., 1983. Identification of marine fish eggs: a biochemical genetics approach. Canadian Journal of Fisheries Aquatic Sciences, 40(3): 361-369.

Pommeranz, T., 1972. Der Einfluss von Wellenschlag und Licht auf die Eier der Scholle (Pleuronectes platessa L.). Dissertation zur Erlangung des Doktorgrades der Mathematisch-Naturwissenschaftlichen Fakultät der Christian-Albrechts-Universität zu Kiel. 1972.

Solemdal, P. and Ellertsen, B. (in press). Sampling fish larvae with large pumps; Quantitative and Qualitative comparisons with traditional gear. Proceeding from symposium on the "Propagation of cod (Gadus morhua)" Arendal 14-17 June 1983.

Solemdal, P. and Sundby, S., 1981. Vertical distribution of pelagic fish eggs in relation to species, spawning behaviour and wind conditions. Countal Meeting of the International Council for the Exploration of the Sea, 1981/G:77: 27 pp. (Mimeo.)

Solemdal, P., Sundby, S. and Bratland, P., 1983. Spawning, distribution and drift of cod eggs in relation to hydrographic conditions off Lofoten and Vesterålen. Contribution to the PINRO/HI-symposium in Leningrad 26-30 Sept. 1983.

Strømme, T., 1977. Torskelarvens lengde ved klekking, og virkning av utsulting på larvens egenvekt og kondisjon. Eksperimentell unders $\varnothing$ kelse pa norsk-arktisk torsk (Gadus morhua). Cand. real-thesis. University of Bergen 1977.

Sundby, S., 1980. Utviklingen innen oseanografisk forskning i Vestfjorden [The development of the oceanographic research in Vestfjorden]. Fisken og Havet, 1980(1): 1I-25.

Sundby, S., 1983. A one-dimensional model for the vertical distribution of pelagic fish eggs in the mixed layer. Deep Sea Research, 30, (6A): 645-661.

Westernhagen, H., 1970. Erbrutung der Eier von Dorsch (Gadus morhua) Flunder (Pleuronectes flesus) und Schalle (Pleuronectes platessa) under kombinierten Temperatur und Salzgehaltsbedingungen. Helgoländ. wiss. Meeresunters. 21: 21-102.

# POPULATION FECUNDITY AND ABUNDANCE OF YEAR-CLASSES OF THE ARCTO-NORWEGIAN COD 

By

V.P. Serebryakov, V.M. Borisov, V.K. Aldonov All-Union Research Institute of Marine Fisheries and Oceanography (VNIRO), Moscow


#### Abstract

The population fecundity is one of the most important indicators of the reproductive ability of the population. The index, although not widely enough used, seems to be very useful in the study of aspects associated with the "stock-recruitment" problem.

The analysis of long term dynamics of the spawning stock of cod, their population dynamics and abundance of yearclasses is presented. Such an analysis, made on the basis of multivariate estimations, supports many workers' intuition that the commercial stock size is governed not only by conditions affecting the survival of eggs, larval and juveniles, but also by the abundance of spawners.


## INTRODUCTION

The population fecundity of cod in the period of 1946-1982 is assessed on the basis of data on the individual absolute fecundity, the numerical strength of age groups entering the spawning stock in each year of investigation, the sex ratio and portions of mature fish. (Here and further population fecundity means a sum of individual fecundities of all mature females or, in other words, the total number of eggs spawned in a given year). It has been ascertained that the maximum level of population fecundity is an order of magnitude greater than the minimum level. The comparison of the population fecundity and abundance, i.e. the numerical strength of three-year-olds spawned in a given year, has indicated that the survival rate of abundant yearclasses is approximately an order of magnitude greater than that of poor yearclasses regardless of the level of population fecundity and, consequently, the biomass of the spawning stock of cod. The data presented support the evidence that the commercial stock size depends not only on conditions under which eggs, larvae and juveniles have to survive, but also on the abundance of spawners.

In a previous paper (Aldonov, Borisov, Serebryakov, 1983) dealing with the assessment of the population fecundity of the Arcto-Norwegian cod, these data were suggested to be used to ascertain the size of the spawning stock needed to sustain its reproduction on an adequate scale. Such investigations have become of utmost importance because the size of the ArctoNorwegian population of cod as a commercial species is approaching a critical level. The present situation requires comprehensive knowledge of the spawning potential of the cod, its fluctuations and the admissible limit of decline. It should be admitted, however, that these aspects have not been given sufficient attention, though the history of the study of arctic cod is rather extensive.

## MATERIAL, METHODS AND SOME TERMS

Data are used on the individual absolute fecundity of 110 females of cod caught when they were approaching the spawning grounds on the Sorф, Fugløy, Malangen, Andøy, Vesterålen and Rost Banks in April-May 1971 and 1972. Their lengths ranged from 68 to 146 cm and weights from 3.2 to 31.8 kg , at ages from 6-18 years (Table 1). The weight of gonads at maturity stage Table 1. Individual absolute fecundity of the Arcto-Norwegian cod.

| Age, years | Number <br> of spe- <br> cimens | Length, cm |  |  | Weight, kg |  |  | Individual absolute fecundity.$\qquad$ |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | from | to | mean | from | to | mean |  |  |  |  |
|  |  |  |  |  |  |  |  | from | to | average | estimated |
| 3 |  |  |  |  |  |  |  |  |  |  | 0.06 |
| 4 |  |  |  |  |  |  |  |  |  |  | 0.26 |
| 5 |  |  |  |  |  |  |  |  |  |  | 0.63 |
| 6 | 1 |  |  | 71 |  |  | 3.00 |  |  | 1.23 | 1.15 |
| 7 | 11 | 68 | 92 | 78 | 3.20 | 6.70 | 4.33 | 1.24 | 4.25 | 1.89 | 1.81 |
| 8 | 47 | 73 | 98 | 88 | 3.25 | 10.20 | 6.42 | 1.06 | 6.44 | 3.00 | 2.65 |
| 9 | 28 | 82 | 105 | 94 | 4.10 | 10.30 | 7.62 | 1.35 | 6.97 | 3.77 | 3.66 |
| 10 | 8 | 91 | 108 | 101 | 6.90 | 14.35 | 10.43 | 3.78 | 9.41 | 5.60 | 4.88 |
| 11 | 5 | 98 | 110 | 103 | 9.20 | 11.10 | 10.04 | 4.72 | 9.03 | 6.20 | 6.20 |
| 12 | 2 | 113 | 115 | 114 | 15.70 | 15.90 | 15.80 | 10.97 | 11.33 | 11.15 | 7.74 |
| 13 | 3 | 113 | 122 | 119 | 15.40 | 19.60 | 16.98 | 9.57 | 10.87 | 10.27 | 9.46 |
| 14 | 2 | 118 | 124 | 121 | 16.85 | 19.30 | 18.08 | 9.14 | 9.21 | 9.18 | 11.35 |
| 15 |  |  |  |  |  |  |  |  |  |  | 13.43 |
| 16 | 2 | 137 | 146 | 142 | 30.25 | 31.80 | 31.02 | 19.14 | 19.30 | 19.22 | 15.69 |
| 17 |  |  |  |  |  |  |  |  |  |  | 18.14 |
| 18 | 1 |  |  | 134 |  |  | 24.00 |  |  | 18.16 | 20.77 |

IV (identified according to the scale suggeste by V.P. Sorokin, 1957) ranged from 105 to 3880 gm constituting $3.5-25.4 \%$ of the body weight. Eggs were counted in 0.3 gm of gonads and converted to their whole weight to obtain finally their individual absolute fecundity, i.e. the total number of eggs spawned by a female during a spawning period.

The sum of individual absolute fecundities of all specimens of a given age group of the spawning stock contributes to the population fecundity (Fi) of individual age groups. Fi was calculated by the formula:

$$
\text { Fi }=N i \operatorname{mi} f i \operatorname{IAFi}
$$

where $N i$ is the numerical strength at the age $i$ obtained by virtual population analysis, mi is the portion of mature fish

Table 2. Population fecundity of the Arcto-Norwegian cod in 1946-1982 (No. of eggs:10 ${ }^{12}$ ).

| Age, years | Indiv. absol $_{6}$ fecundity•10 | Year |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 1946 | 1947 | 1948 | 1949 | 1950 | 1951 | 1952 | 1953 | 1954 | 1955 |
| 4 | 0.26 | 2.5 | 2.1 | 0.3 | 1.3 | 0.5 | 3.9 | 3.9 | 5.5 | 5.1 | 1.1 |
| 5 | 0.63 | 7.9 | 10.2 | 5.8 | 6.7 | 3.2 | 7.9 | 8.4 | 12.2 | 10.6 | 12.2 |
| 6 | 1.15 | 13.7 | 12.1 | 17.1 | 21.6 | 10.0 | 11.3 | 9.2 | 9.9 | 12.0 | 15.6 |
| 7 | 1.81 | 16.5 | 13.9 | 38.9 | 25.2 | 24.4 | 15.2 | 10.3 | 6.7 | 8.1 | 13.4 |
| 8 | 2.65 | 28.6 | 8.2 | 17.8 | 17.0 | 26.2 | 20.4 | 6.9 | 8.0 | 5.6 | 8.0 |
| 9 | 3.66 | 141.6 | 31.8 | 19.2 | 14.8 | 22.3 | 23.6 | 13.5 | 7.7 | 5.9 | 4.6 |
| 10 | 4.88 | 101.5 | 120.0 | 20.9 | 11.9 | 14.9 | 17.4 | 13.2 | 11.6 | 6.6 | 6.1 |
| 11 | 6.20 | 40.0 | 77.4 | 78.9 | 14.9 | 12.0 | 11.7 | 9.4 | 8.4 | 6.9 | 3.3 |
| 12 | 7.74 | 24.5 | 46.0 | 29.0 | 41.9 | 12.5 | 3.9 | 6.0 | 4.3 | 3.6 | 2.9 |
| 13 | 9.46 | - | 57.0 | 18.4 | 15.2 | 28.9 | 3.6 | 1.5 | 1.2 | 1.8 | 1.4 |
| 14 | 11.35 | - | - | 28.7 | 10.7 | 8.7 | 12.5 | - | 0.2 | 0.8 | 0.8 |
| 15 | 13.43 | - | - | - | 15.2 | 10.6 | - | - | - | - | - |
| Total |  | 376.8 | 378.7 | 275.0 | 196.4 | 174.2 | 131.4 | 82.3 | 75.8 | 67.0 | 69.4 |

Table 2 (cont. I)

| Age, years | Indiv. absol, <br> fecundity•10 | Year |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 1956 | 1957 | 1958 | 1959 | 1960 | 1961 | 1962 | 1963 | 1964 | 1965 |
| 4 | 0.26 | 0.6 | 0.7 | 5.7 | 3.5 | 4.9 | 5.4 | 0.6 | 0.4 | 0.3 | 0.2 |
| 5 | 0.63 | 6.9 | 2.1 | 6.5 | 15.1 | 7.9 | 10.3 | 2.8 | 3.1 | 2.6 | 1.9 |
| 6 | 1.15 | 21.4 | 9.4 | 6.6 | 9.3 | 13.9 | 6.7 | 4.0 | 3.4 | 3.9 | 4.8 |
| 7 | 1.81 | 12.7 | 18.8 | 10.3 | 5.4 | 7.6 | 8.3 | 6.2 | 5.7 | 4.5 | 7.8 |
| 8 | 2.65 | 11.9 | 14.3 | 14.8 | 8.5 | 4.2 | 6.4 | 14.3 | 8.7 | 5.6 | 6.5 |
| 9 | 3.66 | 5.5 | 10.4 | 8.6 | 18.8 | 6.0 | 3.7 | 14.6 | 19.7 | 9.7 | 7.2 |
| 10 | 4.88 | 4.7 | 5.2 | 10.7 | 11.6 | 14.1 | 6.3 | 9.4 | 11.5 | 13.4 | 6.0 |
| 11 | 6.20 | 2.9 | 6.5 | 4.3 | 5.8 | 6.2 | 6.5 | 17.0 | 4.9 | 4.4 | 7.9 |
| 12 | 7.74 | 1.5 | 2.0 | 3.8 | 2.9 | 2.0 | 2.9 | 13.4 | 8.0 | 1.3 | 1.7 |
| 13 | 9.46 | 1.8 | 0.8 | 0.9 | 3.1 | 1.2 | 1.9 | 5.3 | 7.7 | 4.4 | 0.7 |
| 14 | 11.35 | 0.8 | - | - | - | 0.8 | - | 3.3 | 1.9 | 3.1 | 1.3 |
| 15 | 13.43 | - | - | - | - | - | - | 1.5 | 2.4 | 1.8 | 2.3 |
| Total |  | 70.7 | 70.2 | 72.2 | 84.0 | 68.8 | 58.4 | 92.4 | 77.4 | 55.0 | 48.3 |

Table 2 (cont. 2)

| Age, years | Indiv. $\mathrm{absol}_{6}$ <br> fecundity•10 | Year |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 1966 | 1967 | 1968 | 1969 | 1970 | 1971 | 1972 | 1973 | 1974 | 1975 |
| 4 | 0.26 | 0.5 | 1.0 | 0.8 | 0.1 | 0.1 | 0.1 | 0.3 | 0.6 | 1.3 | - |
| 5 | 0.63 | 1.4 | 3.3 | 6.4 | 5.0 | 0.6 | 0.5 | 0.1 | 1.6 | 1.5 | 0.8 |
| 6 | 1.15 | 3.4 | 3.1 | 7.3 | 11.0 | 8.0 | 1.2 | 1.0 | 1.6 | 1.3 | 2.6 |
| 7 | 1.81 | 9.9 | 7.5 | 8.1 | 14.7 | 20.7 | 14.6 | 3.0 | 2.2 | 2.6 | 3.7 |
| 8 | 2.65 | 13.4 | 16.0 | 12.6 | 14.0 | 17.6 | 28.7 | 22.5 | 5.7 | 3.2 | 3.5 |
| 9 | 3.66 | 10.2 | 20.2 | 21.6 | 19.8 | 14.8 | 20.2 | 32.9 | 30.6 | 7.5 | 4.2 |
| 10 | 4.88 | 6.2 | 8.9 | 15.2 | 17.3 | 11.0 | 10.0 | 13.9 | 18.3 | 10.0 | 10.0 |
| 11 | 6.20 | 3.9 | 4.2 | 5.3 | 10.1 | 8.8 | 5.5 | 6.6 | 5.8 | 13.0 | 11.1 |
| 12 | 7.74 | 3.9 | 2.6 | 1.8 | 3.1 | 3.4 | 4.6 | 2.9 | 2.4 | 3.4 | 6.1 |
| 13 | 9.46 | 1.4 | 2.7 | 1.5 | 1.5 | 1.6 | 2.9 | 3.4 | 1.7 | 1.2 | 2.2 |
| 14 | 11.35 | 0.2 | 0.6 | 0.8 | 0.5 | 0.5 | 0.6 | 1.4 | 0.9 | 1.0 | 0.2 |
| 15 | 13.43 | 1.2 | 0.2 | 0.6 | 0.6 | 0.5 | 0.4 | 0.5 | 1.0 | 1.2 | 0.6 |
| Total |  | 55.6 | 70.3 | 82.0 | 97.7 | 87.6 | 89.3 | 88.5 | 72.4 | 57.2 | 45.0 |

Table 2 (cont. 3)

| Age, years | Indiv. $\mathrm{absol}_{6}$ fecundity•10 |  |  |  | Year |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 1976 | 1977 | 1978 | 1979 | 1980 | 1981 | 1982 |
| 4 | 0.26 | - | 0.1 | - | 0.2 | - | - | 0.6 |
| 5 | 0.63 | 0.2 | 0.4 | 0.3 | 0.3 | 1.2 | 0.4 | 4.0 |
| 6 | 1.15 | 2.7 | 1.0 | 0.9 | 1.0 | 1.3 | 3.5 | 9.0 |
| 7 | 1.81 | 5.6 | 8.7 | 3.0 | 3.4 | 3.4 | 4.0 | 42.2 |
| 8 | 2.65 | 4.7 | 14.2 | 18.8 | 5.2 | 4.8 | 5.7 | 14.6 |
| 9 | 3.66 | 4.8 | 7.5 | 12.2 | 17.6 | 5.3 | 6.5 | 6.3 |
| 10 | 4.88 | 5.6 | 5.2 | 3.5 | 6.0 | 10.0 | 4.9 | 2.6 |
| 11 | 6.20 | 7.6 | 3.8 | 3.0 | 1.8 | 3.7 | 5.4 | 1.7 |
| 12 | 7.74 | 3.0 | 4.4 | 2.0 | 0.5 | 0.5 | 1.2 | 1.2 |
| 13 | 9.46 | 3.7 | 1.2 | 3.9 | 0.9 | 0.3 | 0.3 | 0.8 |
| 14 | 11.35 | 0.9 | 3.5 | 1.4 | 1.1 | 0.7 | 0.1 | - |
| 15 | 13.43 | 2.2 | 2.4 | 1.8 | 1.5 | 0.3 | - | 0.2 |
| Total |  | 41.0 | 52.4 | 50.8 | 39.5 | 31.5 | 32.0 | 83.2 |

at this age, fi is the portion of females among them and IAF is their mean individual fecundity.

The numerical strength in each age group by yearclass in the period from 1962 to 1982 is taken from the Reports of the Arctic Fisheries Working Group, ICES (Anon., 1981, 1982, 1983). The numerical strengths of age groups in the period of 19461961 are obtained on the basis of the catch statistics, age composition, mean weight of a specimen from each age group and spawning stock biomass (Anon., 1959; Garrod, 1967). In addition, data are also used on ogives of maturation of cod and their sex ratio available in literature (Rollefsen, 1953; Ponomarenko, 1982). The summation of all contributions gives the total population fecundity. Estimates are given in Table 2. Indices of abundance of pelagic (hydroacoustic surveys) and demersal juveniles (the number of specimens per hour of trawling), on the one hand, and the absolute abundance of cod at the age of 3 years, on the other hand, are used as criteria of the abundance of year classes. In the second case the following assumption is made: the yearclass is believed to be abundant if its estimated numerical strength at the age of 3 years is more than $1000 \cdot 10^{6}$; average, if it is estimated to be $500 \cdot 10^{6}$, and poor if the value is less than $500 \cdot 10^{6}$. The scale is used by workers of PINRO in the assessment of the abundance of year classes of cod.

## RESULTS

The comparison of the population fecundity of cod by year indicates that the maximum level (378.6.10 ${ }^{12}$ eggs) was in 1947 and the minimum level (31.5.10 ${ }^{12}$ ) in 1981, i.e. its fluctuations represent an order of magnitude in the period of 37 years. The mean long-term fecundity of the Arcto-Norwegian population of cod is $99.3 \cdot 10^{12}$ (Table 2) and since 1952 it has never exceeded the long-term mean. During 3 years (1979-1981) it was lower than $40 \cdot 10^{12}$ (such a value had never been registered previously), but in 1982 it increased to $83.2 \cdot 10^{12}$ and the maximum contribution, equal to $42.2 \cdot 10^{12}$ eggs, was made by 7 -year-old females of the 1975-yearclass. An almost similar value (38.9.10 ${ }^{12}$ ) in 7 -year-olds was observed only once, in 1948. In all the years under investigation the contribution to the population fecundity by various age groups is not constant. Most frequently (12 of 37 years) 9-year-olds make the greatest contribution to the population fecundity. High contributions were recorded in 5-year-olds in 1953 and 1961 and in 13-yearolds in 1950. The largest contribution to the population fecundity was made by the rich 1937-, 1948-, 1949-, 1950-, 1963-, 1964-, 1969-, 1970-yearclasses. The abundant 1937-yearclass between the ages of $9-13$ contributed from $141.6 \cdot 10^{12}$ to 28.9.10 ${ }^{12}$ eggs, which is more than any other yearclass. In 1956-1960 the maximum contribution (30.3-20.5\%) was from the abundant 1950 -yearclass though the value was a little lower than in the previous case (from 21.4 to $14.1 \cdot 10^{12}$ eggs).

The 1963-, 1964- and 1970-yearclasses made large contributions thrice during their lifespan in comparison with other yearclass es participating in spawning at that time. In 1982 the eggs of the 1975-yearclass constituted over $50 \%$ of the total.

During the period from $1946-1980$ rich yearclasses with over $1000 \cdot 10^{6}$ 3-year-olds, emerged only 7 times, whereas poor yearclasses (abundance less then $500 \cdot 10^{6}$ ) appeared in 15 cases between 1947-1979 and average yearclasses (500-1000.10 ${ }^{6}$ ) were registered 12 times.

Abundant yearclasses appeared in years characterized both by extremely high population fecundity, e.g. 1948, and by low fecundity, e.g. 1964, as well as when it was close to the mean

Table 3. Year classes of the Arcto-Norwegian cod ranked by the abundance of 3-year-olds.

| Abundant |  |  |  | Average |  |  |  | Poor |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Abundance <br> of 3- <br> year-olds <br> $\cdot 10$ | Fecundity <br> No. of <br> $\mathrm{eggs}_{12}$ <br> $\cdot 10^{1}$ | $\begin{aligned} & \text { Survival } \\ & \text { rate } \\ & \% \end{aligned}$ | Year | Abundance <br> of 3- <br> year-olds <br> -10 | Fecundity <br> No. of <br> eggs 12 <br> $\cdot 10^{1}$ | ```Survival rate %``` | Year | Abundance <br> of 3- <br> year-olds <br> -10 | Fecundity <br> No. of <br> eggs 12 <br> $\cdot 10$ | $\begin{aligned} & \text { Survival } \\ & \text { rate } \\ & \% \end{aligned}$ | Yea: |
| 1821 | 87.7 | 0.00208 | 1970 | 919 | 72.2 | 0.00127 | 1958 | 497 | 69.4 | 0.00072 | 195. |
| 1593 | 174.2 | 0.00091 | 1950 | 805 | 67.0 | 0.00120 | 1954 | 474 | 68.8 | 0.00069 | 1961 |
| 1584 | 77.4 | 0.00205 | 1963 | 794 | 45.0 | 0.00176 | 1975 | 468 | 376.8 | 0.00012 | 194 |
| 1293 | 55.0 | 0.00235 | 1964 | 791 | 70.2 | 0.00113 | 1957 | 440 | 75.8 | 0.00058 | 195. |
| 1192 | 196.4 | 0.00061 | 1949 | 778 | 92.4 | 0.00084 | 1962 | 405 | 82.0 | 0.00049 | 196: |
| 1090 | 275.0 | 0.00040 | 1948 | 731 | 84.0 | 0.00087 | 1959 | 362 | 57.2 | 0.00065 | 197. |
| 1016 | 97.7 | 0.00104 | 1969 | 710 | 378.7 | 0.00019 | 1947 | 339 | 58.4 | 0.00050 | 196 |
|  |  |  |  | 685 | 70.7 | 0.00097 | 1956 | 273 | 92.3 | 0.00033 | 195 |
|  |  |  |  | 644 | 131.4 | 0.00049 | 1951 | 243 | 41.0 | 0.00059 | 197 |
|  |  |  |  | 640 | 72.4 | 0.00088 | 1973 | 197 | 70.3 | 0.00028 | 196 |
|  |  |  |  | 633 | 88.5 | 0.00072 | 1972 | 170 | 48.3 | 0.00035 | 196. |
|  |  |  |  | 528 | 89.0 | 0.00059 | 1971 | 165 | 52.4 | 0.00037 | 197 |
|  |  |  |  |  |  |  |  | 117 | 50.8 | 0.00023 | 197. |
|  |  |  |  |  |  |  |  | 112 | 55.0 | 0.00020 | 196 |
|  |  |  |  |  |  |  |  | 89 | 39.5 | 0.00023 | 197 |

Table 4. Year classes of the Arcto-Norwegian cod ranked by survival conditions.

|  | Favourable |  |  | Average |  | Unfavourable |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Survival <br> rate <br> \% | Abundance Fecundity Year of 3- No. of year-olds eggs $\cdot 10^{6} \cdot 10^{12}$ |  |  | Survival Abundance Fecundity Year <br> rate of $3-$ No. of <br> $\%$ year-olds eggs <br>  $\cdot 10$ $\cdot 10$ |  |  |  | Survival Abundance Fecundity Yea   <br> rate of 3 - No. of <br> $\%$ year-olds eggs <br>  $\cdot 10$ $\cdot 10^{12}$ |  |  |  |
| 0.00235 | 1293 | 55.0 | 1964 | 0.00097 | 1593 | 174.2 | 1950 | 0.00049 | 405 | 82 | 196 |
| 0.00205 | 1584 | 77.4 | 1963 | 0.00091 | 685 | 70.7 | 1956 | 0.00049 | 644 | 131.4 | 195 |
| 0.00208 | 1821 | 87.7 | 1970 | 0.00088 | 640 | 72.4 | 1973 | 0.00040 | 1090 | 275.0 | 194 |
| 0.00176 | 794 | 45.0 | 1975 | 0.00087 | 731 | 84.0 | 1959 | 0.00037 | 166 | 52.4 | 197 |
| 0.00127 | 919 | 72.2 | 1958 | 0.00084 | 778 | 92.4 | 1962 | 0.00035 | 170 | 48.3 | 196 |
| 0.00120 | 805 | 67.0 | 1954 | 0.00072 | 633 | 88.5 | 1972 | 0.00033 | 273 | 82.3 | 195 |
| 0.00113 | 791 | 70.2 | 1957 | 0.00072 | 497 | 69.4 | 1955 | 0.00028 | 197 | 70.3 | 196 |
| 0.00104 | 1016 | 97.7 | 1969 | 0.00069 | 474 | 68.8 | 1960 | 0.00023 | 89 | 39.5 | 197 |
|  |  |  |  | 0.00065 | 362 | 57.2 | 1974 | 0.00023 | 117 | 50.8 | 197 |
|  |  |  |  | 0.00061 | 192 | 196.4 | 1949 | 0.00020 | 112 | 55.0 | 196 |
|  |  |  |  | 0.00059 | 528 | 89.0 | 1971 | 0.00019 | 710 | 378.7 | 194 |
|  |  |  |  | 0.00059 | 243 | 41.0 | 1976 | 0.00012 | 468 | 376.8 | 194 |
|  |  |  |  | 0.00058 | 440 | 75.8 | 1953 |  |  |  |  |
|  |  |  |  | 0.00050 | 339 | 58.4 | 1961 |  |  |  |  |

long-term value, e.g. 1969 (Table 3). The survival rates of these yearclasses (the ratio of the abundance of 3-year-olds to population density) were $0.00040 \%, 0.00235 \%$ and $0.00104 \%$, respectively (Table 4).

Poor yearclasses may originate not only in years with a low level of population fecundity, e.g. 1979, but in years with a high level, e.g. 1946, as well as in years with an average level, e.g. 1952. The survival rates of these yearclasses at the age of 3 years were $0.00023 \%, 0.00012 \%$ and $0.00033 \%$, respectively.

Average yearclasses originate in years with a very high level of population fecundity, e.g. 1947, and a very low level, e.g. 1975, as well as with an average level, e.g. 1962. The survival rates of these year classes were $0.00019 \%, 0.0017 \%$ and $0.00084 \%$, respectively.

When the data are grouped the mean survival rate of specimens at age 3 years will be as follows: $0.00135 \%$ in abundant year classes, $0.00096 \%$ in average yearclasses and $0.00042 \%$ in poor yearclasses.

The numerical strength of three-year-olds ranged from $89 \cdot 10^{6}$ to $1821 \cdot 10^{6}$ in the period investigated. The mean survival rate was $0.00078 \%$. Its fluctuations range by an order of magnitude, i.e. from $0.0023 \%$ when the population fecundity of the rich 1964 -yearclass was equal to $55 \cdot 10^{12}$ to $0.00012 \%$ when the population fecundity of the poor 1946-yearclass was equal to $376.8 \cdot 10^{12}$. The survival rate of the abundant yearclass differs from that of the poor yearclass almost by an order of magnitude though their levels of population fecundity are almost the same. On the other hand, at almost the same survival rate observed in 1949, 1971 and 1976 the abundance of the corresponding yearclasses was different: in the first case the yearclass was rich, in the second case it was average and in the third case it was poor. In addition, the population fecundity was 5 times greater in 1949 than in 1976, and in 1971 when the average yearclass appeared it was
twice as high as in 1976, but at the same time it was twice as low as in 1949 when the rich yearclass originated. Consequently, it may be assumed that if in 1.966 the survival rate had been the same as in 1964 and their levels of fecundity had been almost similar the 1966-yearclass would have been abundant. On the contrary, if in 1949 when the abundant yearclass originated the population fecundity had been, say, on the level of 1976, an abundant yearclass would have been unlikely to appear even if the survival rate was average.

The survival rate seems to be considered as an integrated indicator of conditions guaranteeing the favourable development of cod during the embryonal, larval and fry periods of their life.

Proceeding from the average survival rates which are characteristic for abundant ( $0.00135 \%$ ), average ( $0.00096 \%$ ) and poor ( $0.00045 \%$ ) yearclasses let's accept provisionally the following gradation for the survival rates of 3-year-old cod; The value of over $0.001 \%$ corresponds to survival conditions which are favourable for creating abundant yearclasses; the values from 0.00099 to $0.0005 \%$ correspond to conditions when average yearclasses appear and the value of $0.00049 \%$ or lower indicates that poor yearclasses are very likely to appear (Table 4).

The survival conditions favourable for creating abundant yearclasses were recorded in eight cases in the period investigated, but it was only in four of them (1963, 1964, 1969 and 1970) that abundant yearclasses emerged, the remaining four years are known as average yearclasses. Average survival conditions were registered in fourteen cases, but average yearclasses appeared actually only in 6 years. Under such conditions twice (in 1950 and 1949) abundant yearclasses appeared when the population fecundities were equal to $174 \cdot 10^{12}$ and $196.4 \cdot 10^{12}$, i.e. nearly twice the long-term mean. Poor year classes originated in 5 cases from the spawning stocks whose population fecundity was lower than $70 \cdot 10^{12}$ eggs (Table 4).

Conditions under which poor yearclasses might be expected were registered in 12 cases over the period of observation. Indeed, poor year classes were registered in nine cases, while one yearclass (1948) as three-year-olds was on the level of abundant generations, two yearclasses (1947 and 1951) were average. In both cases the population fecundities were fairly high, which seems to be responsible for the high abundance of three-year-olds.

It may thus be expected that at least eleven abundant yearclasses should have appeared in the period investigated. Actually only seven rich yearclasses are known to appear (four of them emerged owing to favourable survival conditions and three seemed to be due to a very high level of population fecundity). However, in 1954, 1957, 1958 and 1975 the levels of population fecundity were not high enough and in spite of favourable survival conditions only average yearclasses originated.

In 12 cases average yearclasses appeared, but judging from the survival conditions there should have been at least five additional average yearclasses, which infact turned out to be poor.

Unfavourable conditions were primarily responsible for Door yearclasses, yet in three cases the high population fecundity made its contribution. It might be expected that only 9 poor yearclasses should have appeared within the period of investigation, whereas, in fact, there were 15.

Inadequate levels of population fecundity were responsible for an additional six poor yearclasses. On the other hand, even under unfavourable ecological conditions when the survival rate dropped to $0.00019 \%$, e.g. 1947, the high level of population fecundity was responsible for the appearance of an average yearclass.

## DISCUSSION

The level of population fecundity at the beginning of the period investigated (1946-1948) was approximately tenfold that of population fecundity at the end (1979-1981) (Table 2). The consistent decline in the population fecundity started in 1977 and it was the entry of the 1975 -year class into the spawning stock that interrupted the trend. However, it may be assumed that the resulting yearclass could be poor because the spawning stock consists only of poor yearclasses. It is worth putting a question here if such a spawning stock could produce an abundant yearclass under favourable survival conditions. An example of such a spawning stock is given in Table 5. The population fecundity in this case was equal to $14.9 \cdot 10^{12}$ which is almost twice as low as the actual value in 1980. When the population fecundity is so low the abundance of three-year-olds will be also low despite optimal ecological conditions.

Table 5. Population fecundity of the spawning stock of the Arcto-Norwegian population of cod made up of poor yearclasses.

| Age, <br> years | Population <br> fecundity <br> $\cdot 10^{12}$ <br> eggs | Year | Yearclass | Characteristics <br> of abundance of <br> yearclasses <br> (3-year-olds) |
| :--- | :--- | :--- | :--- | :--- |
| 4 |  |  |  |  |
| 5 | 0.1 | 1972 | 1967 | poor |
| 6 | 0.9 | 1978 | 1972 | average |
| 7 | 2.2 | 1973 | 1966 | poor |
| 8 | 3.2 | 1974 | 1966 | poor |
| 9 | 3.7 | 1961 | 1952 | poor |
| 10 | 2.6 | 1982 | 1972 | average |
| 11 | 1.7 | 1982 | 1971 | average <br> 12 |
| 0.5 | 1979 | 1967 | poor |  |
| 13 |  | 1980 | 1968 | poor |
| 14 | - |  |  |  |
| 15 | - |  |  |  |
| Sum | 14.9 |  |  |  |

It is evident from this situation that when the spawning stock of the Arcto-Norwegian cod consists only of poor yearclasses there is no reason to believe that only an average yearclass could be produced.

Using as a "favourableness" criterium the ratio of the abundance of three-year-olds to the level of population fecundity (the survival rate) it is possible to ascertain a certain level of the population fecundity at which an abundant yearclass can appear even under unfavourable conditions. Using the estimated mean long-term age composition of the spawning stock it would be on the level of $833 \cdot 10^{12}$ which is twice as high as the highest recorded population fecundity ( $378.7 \cdot 10^{12}$ in 1947). It is difficult to say why the population fecundity has never reached such a level, but it is likely due to the fishery which inhibits the growth of the spawning stock to such a level. As another reason, it may be assumed that some factors associated with the density of the population also limit the formation of such a high abundance of spawners. Or perhaps the reason lies in the fact that the period of investigation has simply not covered such a potential situation.

It will be appropriate to ask at what value of population fecundity the potential of producing an average yearclass may occur under unfavourable survival conditions when, as rule, poor yearclasses originate. The estimate indicates that the population fecundity should be equal to $416.7 \cdot 10^{12}$. A corresponding situation was observed in 1947 when an average yearclass emerged under unfavourable conditions (the survival rate was $0.00019 \%$ ). In 1946 the population fecundity was almost the same $\left(376.8 \cdot 10^{12}\right)$, but the survival rate was very low ( $0.00012 \%$ ) and prevented the yearclass from getting into the average category though, proceeding from the abundance of three-yearolds, it seemed to be very near the average ( $468 \cdot 10^{6}$ instead of $500 \cdot 10^{6}$ ).

It is likely that the level of $400 \cdot 10^{12}$ eggs generally secures the production of abundant and average yearclasses,
even under very unfavourable conditions of survival for the eggs, larvae and juveniles.

Of greatest interest is the level of the population fecundity guaranteeing the appearance of abundant yearclasses under average conditions. The appearance of poor yearclasses is associated only with extremely unfavourable conditions (the survival rate is less than $0.00012 \%$ ). The population fecundity equal to $128.2 \cdot 10^{12}$ corresponds to this guaranteed level. A level of fecundity close to this was observed once, in 1951, when an average yearclass emerged under unfavourable surviving conditions. However, in all the subsequent years, despite population fecundity lower than the guaranteeing level, abundant yearclasses emerged in association with favourable survival conditions. In years when the fecundity level was higher than the guaranteed one, abundant yearclasses appeared also under average and unfavourable survival conditions.

The minimum tolerance level of the population fecundity of $64.1 \cdot 10^{12}$ seems to be where abundant yearclasses appear under favourable conditions, average year classes under average conditions and poor year classes under unfavourable conditions. This level secures a numerical strength of three-year-olds of not less than $500 \cdot 10^{6}$ at the average survival rate of $0.00078 \%$.

Levels of population fecundity close to the minimum tolerance level occur rather frequently. In $1946-1960$ it usually exceeded the minimum tolerance level and since 1973 it has been lower. In the period investigated the population fecundity was lower than the minimum tolerance level in 10 cases and produced eight poor yearclasses, one rich and one average. In the remaining 23 cases the population fecundity was higher than the minimum tolerance level and at that time six abundant yearclasses, ten average and only seven poor yearclasses (Table 3, 4) were spawned.

A special case should be reviewed when the level of population fecundity is so low that no abundant yearclass can be expected even under the most favourable survival conditions observed.

Critical fecundity, obtained with the use of the maximum survival rate registered ( 0.00235 ), is estimated to be $42.5 \cdot 10^{12}$. Population fecundities lower than the critical level occurred in four cases in 1976, 1979, 1980 and 1981. resulting in poor yearclasses 1976 when the survival conditions allowed the appearance of an average yearclass. The decline of the level of population fecundity to the critical value or below is dangerous because the probability of emergence of poor yearclasses increases even under average surviving conditions. If the conditions worsen the effect of both factors may aggravate the situation and may not improve despite one or two years of favourable survival conditions. Average yearclasses may emerge only in years when the survival rate is close to the maximum (over $0.0017 \%$ ). Since no one can expect that favourable conditions would last so long, the decline in the abundance of spawners should be arrested lest their level of population fecundity approach the critical level.

If the abundance of the spawning stock is maintained at the minimum tolerance level, average yearclasses will appear under average conditions. If the level of population fecundity gets lower than the minimum tolerance level, average conditions do not rescue us from poor yearclasses (as in 1974). A level of population fecundity lower than the minimum tolerance level is dangerous because poor yearclasses may appear not only under unfavourable surviving conditions, but under conditions usually responsible for average yearclasses. It is only extremely favourable conditions, e.g. in 1964 ( $0.00235 \%$ ), that may produce an abundant yearclass despite a level of population fecundity lower than the minimum tolerance level.

If the level of population fecundity does not drop lower than the required level the probability of producing abundant and especially average yearclasses increased. Maintenance of the guaranteed level by a greater number of spawners would have added eight abundant yearclasses to the four which occurred at a lower level of population fecundity under the same ecological conditions. As long ago as in 1952, however, the level of population fecundity was lower than the required level and
since then it has never exceeded this level. It means that since the 1950 s the commercial withdrawal of the mature portion of the stock has surpassed the admissible level.

Let's tackle the problem in detail with reference to Table 6 indicating published data on the spawning stock by years (Anon., 1982) and the required biomass of the spawning stock. The required biomass means that level of spawning stock biomass that secures the required level of population fecundity (128.2•10 ${ }^{12}$ eggs). Columns 5 and 10 show percentage estimated as follows:
spawning stock biomass • $100 \%$
required level of the spawning stock biomass

The percentage indicates how the actual level of the spawning stock biomass corresponds to the biomass level which would produce the necessary number of eggs to guarantee the appearance of abundant yearclasses under average conditions. Fluctuations in the required level of biomass of the spawning stock from 363000 t to 851000 t are very likely to be associated with differences in the age composition in each year.

As is seen, the actual level of the spawning stock had been higher than the requirement up to 1950; it corresponded almost completely to the required level of population fecundity in 1951. Since then a deficit has been consistently observed every year. In 1952-1963 the actual biomass of the spawning stock constituted $52-65 \%$ of the required biomass. In the 1960 s

Table 6. Actual and required levels of the spawning stock biomass (.000t).

| Year | Actual level of spawning stock biomass | Guaranteed level of spawning stock biomass | ```Surplus (+) or deficit (-) of spawning stock biomass``` | Spawning stock <br> biomass - 100\% <br> guaranteed level <br> of spawning stock <br> biomass |
| :---: | :---: | :---: | :---: | :---: |
| 1 | 2 | 3 | 4 | 5 |
| 1946 | 1244 | 423 | +821 | 294 |
| 1947 | 1073 | 363 | +710 | 296 |
| 1948 | 843 | 393 | +450 | 214 |
| 1949 | 621 | 402 | +219 | 155 |
| 1950 | 549 | 404 | +145 | 136 |
| 1951 | 463 | 471 | - 8 | 98 |
| 1952 | 327 | 509 | -182 | 64 |
| 1953 | 322 | 546 | -224 | 59 |
| 1954 | 293 | 564 | -271 | 52 |
| 1955 | 307 | 501 | -194 | 61 |
| 1956 | 312 | 571 | -259 | 55 |
| 1957 | 289 | 522 | -233 | 55 |
| 1958 | 307 | 543 | -236 | 56 |
| 1959 | 346 | 528 | -182 | 65 |
| 1960 | 259 | 550 | -255 | 54 |
| 1961 | 258 | 569 | -311 | 45 |
| 1962 | 204 | 405 | -201 | 50 |
| 1963 | 142 | 412 | -270 | 34 |
| 1964 | 98 | 423 | -325 | 21 |
| 1965 | 97 | 458 | -361 | 21 |
| 1966 | 139 | 472 | -333 | 29 |
| 1967 | 154 | 470 | -316 | 33 |
| 1968 | 178 | 482 | -304 | 37 |
| 1969 | 194 | 480 | -286 | 40 |
| 1970 | 251 | 426 | -175 | 59 |
| 1971 | 303 | 597 | -294 | 51 |
| 1972 | 276 | 526 | -250 | 52 |
| 1973 | 225 | 510 | -285 | 44 |
| 1974 | 157 | 468 | -311 | 33 |
| 1975 | 123 | 492 | -369 | 25 |
| 1976 | 150 | 528 | -378 | 28 |
| 1977 | 246 | 568 | -322 | 43 |
| 1978 | 238 | 569 | -327 | 42 |
| 1979 | 176 | 542 | -366 | 32 |
| 1980 | 127 | 492 | -365 | 26 |
| 1981 | 285 | 637 | -352 | 45 |
| 1982 | 391 | 851 | -460 | 46 |

the deficit became greater and has remained at this level, though subject to insignificant fluctuations.

Based on these data it is safe to say that if, in 1976-1982, the biomass of the spawning stock had been of the order of 490000-570000 $t$ instead of the actual 127000-285000 t, one or
two abundant and three or four average yearclasses could have appeared instead of a series of poor yearclasses.

As is seen, an opportunity for their appearance depended not only upon nature, but upon man who has not curbed the excessive catch of cod in due time. The maintaining of an adequate number of spawners needed for reproduction of the population, especially specimens in those age groups which support the spawning stock should be cared for by all organizations responsible for regulation of the fishery for cod. The situation observed nowadays makes us think of proclaiming a complete ban till the stock is recovered.

## REFERENCES

Aldonov, V.K., Borisov, V.M. and Serebryakov, V.P., 1983. Population fecundity of the Arcto-Norwegian cod. Rybnoe khosyajstvo, No. 1, p.33-34.

Anon., 1959. Report of the Arctic Fisheries Working Group, ICES, C.M. 1959.

Anon., 1980. Report of the Arctic Fisheries Working Group, ICES, C.M. 180/C-12, 50p.

Anon., 1981. Report of the Arctic Fisheries Working Group, ICES, C.M. 1981/G-2, p. 37.

Anon., 1982. Report of the Arctic Fisheries Working Group, ICES, C.M/G.

Anon., 1983. Report of the Arctic Fisheries Working Group, ICES, C.M./Assess:2, p. 62.

Garred, D.J., 1967. Population dynamics of the Arcto-Norwegian cod. J. Fish. Res. Bd. Canada, $24(\mathrm{I}), \mathrm{p} .145-190$.

Glebov, T.I., 1963. Cod off the Murmansk coast. Trudy PINRO, issue 15, p.69-130.

Ponomarenko, I.Ya., 1982. Portion of the mature cod specimens and sex ratio in different age and length groups within the 60's to 70's. ICES, C.M. 1982/G:18.

Rollefsen, G. 1953. Observations on the cod and cod fisheries off Lofoten. Rapp.-Proc.-Verb. Réun. Cons. Perm. Intern. Explor. Mer, 136, p.40-47.

Sorokin, V.P., 1957. Oogenesis and sexual cycle of cod (Gadus morhua morhua L.). Trudy PINRO, issue 10, p.125-144.

ESTIMATING THE MATURITY OGIVE FOR NORTHEAST. ARCTIC COD BY A MODIFIED MESH ASSESSMENT MODEL

## by

Arvid Hylen and Carl Jakob Rørvik Institute of Marine Research

## ABSTRACT

The exploitation (1967-77) of the Northeast Arctic cod is splitted in 12 different fisheries. The mesh assessment model is modified in order to estimate the maturity ogive on the basis of the length and the age distributions of the catches from these fisheries. The key fishery in the estimation is the gill net fishery in Division IIa which mainly takes part during the spawning season. The resulting ogives are similar to those derived by other methods for the same period. Although the estimated statistical variations of the results are underestimates due to unaccounted uncertainties in the fixed input parameters in the model, the present method may be an alternative or a check on other methods.

## INTRODUCTION

The working group on Arctic fisheries (Anon. 1983) estimated the spawning stock of Northeast Arctic cod for each of the years 1946-1982. In doing so the working group used different maturity ogives for different periods as derived from Rollefsen (1954), Garrod (1967), Hylen and Dragesund (1973), Ponomarenko, Ponomarenko and Yaragina (1980), Ponomarenko and Yaragina (1981), Ponomarenko (1982), and Hylen and Nakken (1982).

Garrod (1967) and Hylen and Dragesund (1973) based their ogives on the age compositions of the catches from the spawning fishery. The maturation curve given by Ponomarenko et al. (1980, 1981) and Ponomarenko (1982) are based on trawl sampling in the Barents Sea in period November-February. Hylen and Nakken (1982) based their maturation curve on acoustic surveys in February-March 1982 that covered the main areas of the distribution of the immature as well as the mature part of the stock. There are problems with all of these methods used for estimating the maturity ogives, and it is difficult to evaluate the size of the possible biases.

From the maturity curves summarized by Anon. (1983) there seems to be a gradual shift towards an earlier onset of maturity in the post-war years, which may correspond to an increasing growth rate (see Anon. 1983; Ponomarenko 1981). However, the different methods used to establish the different curves makes it difficult to assess accurately how much the maturation process actually has changed over the years.

The present paper do not address the problem of a change of the maturity ogive through time. We only intend to estimate the average maturity ogive for the period 1967-1977 using a method not applied before to this problem, i.e. a modification of the mesh-assessment method as described by Høydal, Rørvik and Sparre (1980, 1982).

## METHOD

The core of the method is a model that simulates biological characteristica of a fish stock and the individual fisheries on the same stock. The model takes into account the selective properties of the gears, the discard practice and the recruitment of the fish to the individual fisheries. This model has previously been used to estimate the effective mesh sizes in some fisheries (Hфydal 1977; Anon. 1979; Anon. 1980), and with slight modifications on a stock of lobster (Tveite and Rorvik 1982).

The basic model is STEP 1 as it is written out in mathematical details by H H ydal, R R rvik and Sparre (1980, 1982). Here we will only describe the modifications of this model as used in the present paper. In doing so we will use the same symbols as Høydal et al. (1982, p. 84-86). There are four modifications:

1. H申ydal et al. ( 1980 , 1982) simulate the relative age- or length-distributions of the catches. We use the absolute catch distributions and introduce the size of the initial stock $\mathbb{N}(T I)$ as an additional free parameter to be estimated.
2. Høydal et al. minimize the sum of squares of the difference between the observed and the estimated relative catch distributions. We prefer a modified chi-square function:

$$
\text { OBJECT FUNCTION }=\sum_{e} \sum_{i} \frac{(\operatorname{CL}(e, i)-\operatorname{OBSCL}(e, i))^{2}}{\operatorname{OBSCL}(e, i)}
$$

CL(e,i) and OBSCL (e,i) are the estimated and the observed number of fish (in thousands) respectively in length (or age)-group $i$ that are caught by fishery $e$. In the calculation of the object function, we have only included length- or age-groups containing 5 (thousands) or more fish.

Both the least square function as used by Hoydal et al. (1982), and the modified least chi-square function are strongly consistent estimators. However, contrary to the minimum least square the minimum chi-square estimator is asymptotically efficient. Therefore the latter estimator is to be preferred (Kirkwood 1982).

The chi-square estimator allows confidence intervals of the parameters to be calculated (Kirkwood 1982; James and Ross 1977; James 1978). However, these confidence intervals are only minimum intervals as they require that the fixed input parameters in the model are true and not subject to uncertainty. The only uncertainty is supposed
to be due to the variations in the observed length- (age-) distributions with a standard deviation $=\operatorname{OBSCL}(e, i)^{\frac{1}{2}}$. The true errors of the estimated parameters are likely to be considerably larger.

The parameters and their confidence intervals are estimated by a program called MINUIT-S that is developed at CERN in Geneva (James and Ross 1977; James 1978).
3. We have simplified the mesh assessment model as described by Hфydal et al. (1982) in that we only estimate (or use as input parameters) the $50 \%$ selection length of the individual gears. However, the ratio between the length at $75 \%$ selection and the $50 \%$ selection (FAC), as estimated in selection experiments, has to be given as fixed input parameters in the model.
4. For two fisheries, gill-net in Sub-area $I$ and gill-net in Division IIa, the selection curves are fixed on the basis of the work by Hylen and Jakobsen (1979). Instead the lengths at $50 \%$ recruitment (RL50\%) to the fisheries and the RL75\%/RL50\% ratio are estimated.

The recruitment curve that minimize the difference between the observed and the estimated catch at age (or length) distribution of gill-net in Division IIa is an estimate of the maturity ogive, since this fishery is mainly taking place in Lofoten during the spawning season.

## MATERIAL

## CATCH DISTRIBUTIONS

The working group on Arctic fisheries (Anon. 1983) utilized in their virtual population analysis (VPA) catch at age data splitted on 17 different fisheries for each of the years 1967-1982. These being:

| Number | Fishery |
| :---: | :---: |
| 1.-3. | USSR trawl, Sub-area I; Division IIa; Division IIb |
| 4.-6. | UK trawl, |
| 7. | Federal Republic of Germany, Sub-areas I-II |
| 8. | Other countries (except Norway), - " - |
| 9.-11. | Norway trawl, Sub-area I; Division IIa; Division IIb |
| 12.-13. | Danish seine, Sub-area I; Division IIa |
| 14.-15. | Gill net, - " |
| 16.-17. | Long- and Hand-line, - " |

In the present study, however, only the years 1967-1977 are considered as also done in a preliminary mesh assessment (Anon. 1979). The length distributions for these fisheries are available for this period as well.

In the simulations only the age-groups 1-14 are included, ignoring the insignificant $15+$ group. The simulations based on the length-distributions cover the range 15 to 130 cm .

In order to reduce the number of free parameters to be estimated several fisheries were pooled. The Norwegian trawl fishery in Division IIb was pooled with the UK fishery in the same area since data from the UK fishery is to a large extent used to calculate the catch distributions of the Norwegian trawlfishery in this Division.

The USSR fishery in Division IIa, which only took $0.35 \%$ of the total catch by number (1967-1977), were pooled with the Other countries' fishery.

A closer scrutiny of the basic data indicated large sampling variation of Danish seine. This gear only accounts for $1.3 \%$ of the total catch by numbers in the period 1967-1977. Therefore the two categories of Danish seine were pooled with Other countries' fishery.

The age compositions of the trawlers from the Federal Republic of Germany ( $2.2 \%$ of total catch by numbers, 1967-77) are not available for bottom trawl and midwater trawl seperately, both
gears being important in this fishery in the relevant period. Therefore the FRG data were pooled with the Other countries' fishery.

The Other countries' fishery thus become a kind of "rag-bag" category containing several less important fisheries that together make up $9.6 \%$ of the total catch by numbers (19671977).

By these poolings the catch compositions of the total fishery become divided in 12 categories. Thus for each simulation there are 15 parameters to be estimated, i.e. three more than in an ordinary mesh assessment with 12 fisheries (STEP 1) as described by H申ydal et al. (1982).

## INPUT PARAMETERS

The fixed input parameters that are used are summarized in Table 1. The same parameters are used both in the simulation of the age- and the length-distributions of the catches. The reason for choosing these parameters are summarized below:

## a) Von Bertalanffy_parameters

The parameters are based on a combined set of data from the USSR fishery in Sub-area $I$ and from the spawning fishery in Division IIa.
b) Selection factor (SEL(e)) and steepness of the selection curve (FAC(e))

As we are interested in the length at $50 \%$ selection and not the effective mesh sizes, SEL(e) is set equal to 1.00 for all fisheries (e). The ratio between the length at $75 \%$ and $50 \%$ selection (FAC(e)) is set equal to 1.09 for all of the eight trawl fisheries on the basis of the results from the joint USSR-Norwegian trawl experiments in. 1977 (Hylen and O1sen 1977; Ponomarenko, Nikeshin and Sakhno 1978).

Table l. Horth-east Arctic cod. Input parameters in model for the each of the 12 fisheries into which the total fishery is splitted. (S.-a. = Sub-area, Div. = Division)

Von Bertalanffy parameters: $T O=0.226, K=0.0677, L 8=200 \mathrm{~cm}$.
Natural mortality $(M)=0.20$

| Fishery | "steepness" of selection curve | Recruitment ${ }^{1)}$ |  | Derecruitment ${ }^{1)}$ | Discard |  | Maximum fishing mortality | Observed <br> catch <br> in numbers $\left(\times 10^{-3}\right)$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $\begin{aligned} & 50 \% \\ & (\mathrm{~cm}) \end{aligned}$ | $\begin{aligned} & 75 \% \\ & (\mathrm{~cm}) \end{aligned}$ | $50 \%$ $75 \%$ <br> $(\mathrm{~cm})$ $(\mathrm{cm})$ | $\begin{aligned} & \hline 50 \% \\ & (\mathrm{~cm}) \end{aligned}$ | $\begin{aligned} & 75 \% \\ & (\mathrm{~cm}) \end{aligned}$ |  |  |
| USSR trawl S.-a. I | 1.09 | 16.5(1.5) | 28.5(2.5) | 103.6(11) 96.8(10) | no di | ard | 0.179 | 206318 |
| UESR travil Div.IIb | 1.09 | 34.2(3) | 45.1(4) | 131.3(16) 118.6(13.5) | no di | ard | 0.084 | 60023 |
| UK trawl S.-a. I | 1.09 | $34.2(3)$ | 45.1 (4) | 89.6(9) $73.6(7)$ | 41.5 | 43.5 | 0.063 | 37215 |
| UK trawl Div.IIa | 1.09 | 64.7 (6) | 81.8(8) | no derecruitment | 41.5 | 43.5 | 0.039 | 8917 ■ّ |
| Ur+Norway trawl Div.IIb | 1.03 | 34.2(3) | 45.1 | 96.8(10) 89.6(9) | 41.5 | 43.5 | 0.015 | 12959 O |
| other countries trawl | 1.09 | 81.8(8) | 115.8(13) | no derecruitment | no di | ard | 0.069 | 44483 |
| Morway travil S.-a. I | 1.09 | 50.2(4.5) | $60.1(5.5)$ | 89.6(9) $73.6(7)$ | 41.5 | 43.5 | 0.087 | $3898:$ |
| :orvay trawl Div.IIa | 1.09 | 64.7(6) | 81.8(8) | 115.8(13) 103.6(11) | 41.5 | 43.5 | 0.047 | 9815 |
| Gillnet S.-a. I | 2) | $73^{3)}$ | $80^{3)}$ | 105 ${ }^{3)} 97^{3)}$ | 41.5 | 43.5 | 0.130 | 2352 |
| Gillnet Div.IIa | 2) | $73^{31}$ | $80^{3)}$ | $105^{31} 97^{31}$ | 41.5 | 43.5 | 1.523 | 1433 |
| Long- \& hand-line S.-a. I | 1.13 | $50.2(4.5)$ | $60.1(5.5)$ | 109.9(12) $96.8(10)$ | 41.5 | 43.5 | 0.037 | 17937 |
| Long- \& hand-line Div.IIa | 1.13 | E1.8(8) | 89.6(9) | no derecruitment | 41.5 | 43.5 | 0.509 | 9666 |

## Total

The corresponding age in years are given in brachets.
2) To be estimated by the model.
3) Not recruitment parameters, but parameters describing the ascendiag and decending selectivity of gillnet as determined by experiments (Hylen and Jakobsen 1979).

Hook selection curves seems to be less sharp than those for trawls. On the basis of the experiments reported by Sætersdal (1963) FAC(e) was taken to be 1.13 for the two long-line fisheries.

In the case of gill-net Hylen and Jakobsen (1979) give a selection curve for nylon material, which dominated in the actual period (1967-1977).

- 11


Fig. 1. Northeast Arctic Cod. Selection index for nylon gill nets. Redrawn from Hylen and Jakobsen (1979). Legend: l) Line fitted on the basis of points A (Hylen and Jakobsen 1979). 2) Refitted line based on both sets of points $A$ and $B$.

The solid line in Fig. 1 is the curve fitted by Hylen and Jakobsen (1973), and it should according to the authors approximate the selective properties of gill-net for fish caught with the head first in a single mesh, ignoring other ways of being caught.

The open circles in Fig. I represent points not included in the fitting of the solid line. Although these circles partly
represents observations with few observations, they as well as other data given by Hylen and Jakobsen (1979), indicate that less steep selection ogives should be applied for representing the total selectivity of gill-net.

We have applied the curve with the broken line (Fig. 1) which we fitted by eye. This curve has a $50 \%$ and $75 \%$ selection at 73 cm and 80 cm respectively, and a subsequent decreasing selection with the $75 \%$ and the $50 \%$ lengths at 97 cm and 105 cm respectively. These data stems from nets with a 190 mm mesh size (nylon) which was the most common mesh size used in the spawning fishery (Division IIa) and should also be fairly representative for the gill-net fishery in Sub-area I.
c) Recruitment

The recruitment curves should not be regarded in absolute terms as a fix proportion of an age- or length-group in the stock that is recruited to the area of fishing for a particular fishery. They express the proportion available to the fishery in relation to the maximum availability to the same fishery, which may only be a small percentage of the whole stock.

The parameters for the recruitment curves are difficult to assess. In general terms the younger age-groups tend to be in the eastern part of the Barents Sea (Sub-area I) or in Division IIb. The older age-groups tends to be farther west and south, in particular the mature part which have the main spawning grounds in Lofoten (Division IIa).

The later the fish recruit the lower the estimated selection ogive becomes and vice versa. None-recruited fish are not subject to fishing mortality. The model also assumes that all of the fish that escape through the trawl net survive. Therefore, possibly wrong recruitment parameters for the eight trawl fisheries, the two long- and hand-line fisheries, and gill-net in Sub-area I, are compensated for by the estimated selection curve of the gears. The fixed recruitment parameters therefore
have little effect on the estimated parameters for gill-net in Division IIa.

The recruitment parameters for gill-net are not input parameters (except for a first quess) as that is what is to be estimated by these simulations.

The figures for de-recruitment (Table 1) are of little importance in the present context. We do, however, believe that they are not biological unreasonable, and they generally give a better fit between the observed and estimated distributions, i.e. the catches by age 0 : length, or the fishing mortalities.
d) Discard_parameters

In the case of the two USSR trawl fisheries no discards are assumed to take place.

No discards were assumed to take place in the case of "Other countries" either, although this is hardly the case for all of the fisheries included in this "rag-bag" category. However, due to the relative small importance of this category this error is regarded as neglectable.

Observations on discard from Norwegian trawlers can be found in Hylen (1965, 1967 and 1969) and Hylen and Smedstad (1974). On the basis of the latter reference which reports on investigations in 1973, a discard curve with $50 \%$ and $25 \%$ discards at 41.5 cm and 43.5 cm respectively was established. This discard curve was applied to the three UK and the two Norwegian trawl fisheries as well as the four gill-net and line fisheries.

Considerable uncertainties are connected with the discard curves as it probably vary much between fisheries, areas, years and seasons, and it problably depends on the the catch rates. This add much uncertainty to some of the the estimated lengths at $50 \%$ selection of the different fisheries. There are, however, probably five exceptions to this reservation. The two first being the USSR trawl fisheries where discards are minimal
or none-existent. Furthermore the two gill-net fisheries and the long- and hand-line fishery in Division IIa land few fishes below 50 cm . This is not due to a seperate discard practice, but mostly due to minimal availability of the smaller fishes in Division IIa to these gears.
e) Fishing_mortalities_(EF(e))

The maximum fishing mortalities (EF(e)) for the individual fisheries (e) were adjusted so that the estimated number caught in proportion to the total number caught by all fisheries (Table 2) corresponded to the observed proportion in 1967-1977 (Table 1). The obtained values of $E F(e)$ which were based on simulating the age data, are given in Table 1 . These values of EF(e) were also applied to the length data.
f) Natural mortality_(M)

A constant $M$ of 0.20 for all age-groups was chosen. This is in line with the practice by the Arctic fisheries working group (Anon. 1983).

## RESULTS

The estimated lengths at $50 \%$ selection of the fisheries, the estimated yield and the contribution to the object function (chi-square) from the individual fisheries are given in Table 2.

The observed and the estimated age and length distributions are shown in Figs. 2-13 for the individual fisheries, and in Fig. 14 for the total fishery. Figs. 2-14 also show the estimated and the observed fishing mortalities. The observed fishing mortalities are the average for the years 1967-1977, and are derived from a VPA by splitting the total $\mathrm{F}^{\text {'s }}$ (Anon. 1983) between the individual fisheries on the basis of the catch at age data.

Table 2. North-east Arctic cod. Results from simulation based on the $1967-1977$ catch data.

| Fishery |  | AGE DATA |  |  | LENGTH-DATA |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | ```50% Selection \pm S.D. (cm)``` | Estimated catch in numbers $\left(x 10^{-3}\right)$ | CHI- <br> SQUARE | $\begin{aligned} & 50 \% \text { Selection } \\ & \pm \text { S.D. }(\mathrm{cm}) \end{aligned}$ | Estimated catch in numbers $\left(\times 10^{-3}\right)$ | CHI- <br> SQUARE |
| USSR trawl | s.-a. I | $42.10 \pm 0.02$ | 201265 | 4476.6 | $35.89 \pm 0.01$ | 213289 | 5747.6 |
| USSR trawl | Div.IIb | $49.67 \pm 0.03$ | 58773 | 1306.9 | $43.27 \pm 0.04$ | 62410 | 2052.9 |
| UK trami | S.-a. I | $49.72 \pm 0.04$ | 36186 | 2085.0 | $45.51 \pm 0.07$ | 34275 | 927.3 |
| UR trawl | Div.IIa | $51.61 \pm 0.15$ | 8471 | 519.0 | $43.35 \pm 0.07$ | 7983 | 437.8 |
| UK + Norway trawl | Div.IIb | $43.83 \pm 0.13$ | 12583 | 331.8 | $41.38 \pm 0.07$ | 10574 | 873.3 |
| Other countries' trawl |  | $35.37 \pm 0.09$ | 43207 | 1561.2 | $28.23 \pm 0.10$ | 36082 | 3410.8 |
| Norsay trasl | S.-a. I | $49.84 \pm 0.06$ | 37966 | 1107.0 | $47.14 \pm 0.03$ | 32513 | 1808.3 |
| Norway trawl | Div.IIa | $53.11 \pm 0.12$ | 9488 | 407.4 | $49.42 \pm 0.16$ | 8119 | 561.1 |
| Gillnet | S.-a. I | _1) | 2136 | 130.3 | 1) | 2194 | 103.3 |
| Gillnet | Div.IIa | -1) | 13224 | 326.7 | _1) | 12028 | 1399.7 |
| Long- \& Hand-line | S.-a. I | $50.72 \pm 0.09$ | 17667 | 405.1 | $45.93 \pm 0.17$ | 15917 | 461.1 |
| Lcng- \& Hand-line | Div.IIa | $92.63 \pm 0.08$ | 8825 | 545.4 | $86.07 \pm 0.25$ | 7747 | 2144.7 |
| TCTAL |  |  | 449791 | 13202.6 |  | 443131 | 19928.1 |
| Number of 1 year olds |  | $1175.9 \times 10^{6} \pm 0.8 \times 10^{6}$ |  | $1082.8 \times 10^{6} \pm 1.0 \times 10^{6}$ |  |  |  |

1) The length of $50 \%$ selection by the gear is not estimated. Instead the $50 \%$ and $75 \%$ recruitment is estimated (See Table 3).

## A: AEE-DISTRIBUTION



B: LENGTH-DISTRIBUTION


C: FISHING MORTALITIES


Fig. 2a-c. The USSR trawlfishery in Sub-area I. Numbers caught and fishing mortality. Legend:

1) Observed 2) Estimated from the age distribu-
tions 3) Estimated from the lenath distributions.

A: AEE-DISTRIBUTION


B: LENGTH-DISTRIBUTION


C: FISHING MORTALITIES


Fig. 3a-c. The USSR trawlfishery in Division IIb. Numbers caught and fishing mortality. Legend:

1) Observed 2) Estimated from the age distributions 3) Estimated from the length distributinnc

## A: AEE-DISTRIBUTION



B: LENGTH-DISTRIBUTION



C: FISHING MDRTALITIES


Fig. 4a-c. The UK trawlfishery in Sub-area I. Numbers caught and fishing mortality. Legend: Observed 2) Estimated from the age distributions 3) Estimated from the length distributions.

A: AEE-DISTRIBUTION

$\qquad$
b: LENGTH-DISTRIESTION

$\qquad$

C: FISHING MORTALITIES


Fig. 5a-c. The UK trawlfishery in Division IIa. Numbers caught and fishing mortality. Legend:

1) Observed 2) Estimated from the age distributions 3) Estimated from the length distributions.

A: AEE-DISTRIBUTION

$\qquad$

B: LENGTH-DISTRIEUTION


C: FISHING MORTALITIES


Fig 6a-c. The UK and the Norwegian trawlfishery in Division IIb. Numbers caught and fishing mortality. Legend: 1) Observed 2) Estimated from the age distributions 3) Estimated from the length distributions.

$\qquad$

B: LENETH-DISTRIEUTION


C: FISHING MORTALITIES


Fig. 7a-c. Other countries' trawlfisheries. Numbers caught and fishing mortality. Legend: 1) Observed
2) Estimated from the age distributions 3) Estimated from the length distributions.

A: AEEEDISTRIBUTION


B: LENGTH-DISTRIEUTION


C: FISHINS MORTALITIES


Fig. 8a-c. The Norwegian trawlfishery in Sub-area
I. Numbers caught and fishing mortality. Legend:

1) Observed 2) Estimated from the age distributions
2) Estimated from the length distributions.

A: AGE-DISTRIBITION

$\qquad$

B: LENGTH-DISTRIEUTION


## C: FISHING MORTALITIES



Fig. 9a-c. The Norwegian trawlfishery in Division IIa. Numbers caught and fishing mortality. Legend:

1) Observed 2) Estimated from the age distributions 3) Estimated from the length distributions.

A: AEE-DISTRIBUTION

$\qquad$ 1)
$\qquad$
b: Lexath-alstribution


C: FISHING MORTALITIES


Fig. loa-c. The gill-net fishery in Sub-area I. Numbers caught and fishing mortality. Legend:

1) Observed 2) Estimated from the age distributions 3) Estimated from the length distributions.

A: AEE-DISTRIEUTION

$\qquad$

B: LENGTH-DISTRIEUTION


C: FISHING MORTALITIES


Fig. Ila-c. The gill-net fishery in Division IIa. Numbers caught and fishing mortality. Legend:

1) Observed 2) Estimated from the age distributions 3) Estimated from the length distributions.

$\qquad$

B: LEESTH-DISTRIEUTION


## C: FISHING MORTALITIES



Fig. l2a-c. Long- and hand-line fishery in Subarea I. Numbers caught and fishing mortality. Legend: 1) Observed 2) Estimated from the aye distributions 3) Estimated from the length distributions.

A: AEE-DISTRIEUTION

$\qquad$ 1)

B: LENGTH-DISTRIEUTION


C: FISHING MCRTALITIES


Fig. 13a-c. Long- and hand-line fishery in Division Ila. Numbers caught and fishing mortality. Legend: 1) Observed 2) Estimated from the age distributions 3) Estimated from the lenath distri-

A: AEE-DISTRIBUTION


B: LENGTH-DISTRIBUTION


C: FIGHINE MORTALITIES

$\qquad$ 1)
*

Fig. l4a-c. Total fishery for Northeast Arctic cod. Numbers caught and fishing mortality. Leaend:

1) Observed 2) Estimated from the age distribu-
tions 3) Estimated from the length distributions.

In the case of the two gill-net fisheries the estimated recruitment parameters are given in Table 3.

Table 3. Estimated recruitment curves for the gillnet fisheries. Length $\pm$ S.D. at $50 \%$ recruitment, and the ratio between the length at $75 \%$ and $50 \%$ recruitment $\pm$ SD.

|  | Age data |  | Length-data |  |
| :---: | :---: | :---: | :---: | :---: |
|  | $\begin{gathered} 50 \% \\ (\mathrm{~cm}) \end{gathered}$ | 75\% / 50\% | $\begin{aligned} & 50 \% \\ & (\mathrm{~cm}) \end{aligned}$ | 75\% / 50\% |
| S.-a. I | $99.8 \pm 1.9$ | $1.1238 \pm 7 \times 10^{-4}$ | $92.8 \pm 0.6$ | $1.119 \pm 2 \times 10^{-3}$ |
| Div. IIa | $94.5 \pm 0.5$ | $1.0603 \pm 2 \times 10^{-4}$ | $93.3 \pm 0.1$ | $1.0681 \pm 3 \times 10^{-4}$ |

The maturation ogive (MAT(L)) as a function of length $L$ is given by the equation:
$\operatorname{MAT}(L)=1 /(1+\operatorname{EXP}(-(L-R L 50 \%) \log 3 /(R L 75 \%-R L 50 \%)))$

RL50\% and RL75\% are the lengths at $50 \%$ and $75 \%$ recruitment in Division IIa as derived from the gill-net fishery in this area (Table 3, Fig. 15).


Fig. 15. Northeast Arctic Cod. Maturity ogives. Legend: 1) From catch at age data. 2) From catch at length data. 3) From Hylen and Dragesund (1973). 4) From Ponomarenko et al. (1980). 5) From Ponomarenko (1982).

The estimated catch distributions follow the observed catch distributions relatively good, both in the case of the age data (Figs. 2a-14a) and the length data (Figs. 2b-14b).

The fit between the estimated and the observed fishing mortalities (Figs. 2c-14c), which are not part of the simulations, are more variable. In the case of the total fishery (Fig. 14c) the estimated fishing mortalities on 10 to 13 year olds are about 0.5 higher than the observed one. This is mainly due to the estimated fishing mortalities for long-line and gill-net in Division IIa (Fig. 11c and Fig. 13c). In order to get a simulated catch close to the observed one (Tables 2, 3) the fishing mortalities on these two spawning fisheries had to be increased considerably over the observed ones (Fig. 11c, 13c).

It is also seen (Table 2) that the estimated length at $50 \%$ selection generally tends to be lower for the simulations based on the length data than on the age data.

The initial stock estimates (1 year olds) are $1176 \times 10^{6}$ and $1083 \times 10^{6}$ in the case of the age- and the length-distributions respectively. It is the 1953-1976 year-classes that contribute to the age composition data (1-14 year olds, 19671977), the average of these being $678 \times 10^{6}$ at the beginning of age 3 (Anon. 1983, Table 18). Correcting for the assumed natural mortality at 0.2 this figure becomes $1011 \times 10^{6}$ at age 1. A minor addition ( $15 \times 10^{6}$ ) to this figure is due to discards (estimated from simulations) and catches of 1 and 2 year olds with some correction for natural mortality. The corrected total from VPA is thus roughly $1025 \times 10^{6}$, i.e. $5-13 \%$ below the initial stock figure as derived from these simulations. Considering the equilibrium assumption on which the mesh assessment model is constructed, we do not consider this to be an unacceptable difference.

The observed total number caught in the years 1967-1977 is $463,062 \times 10^{3}$ (Table 1), fairly close to the estimated total
catch of $449,791 \times 10^{3}$ and $443,131 \times 10^{3}$ for the two catch distributions respectively (Table 2).

There are two problems with the way the von Bertalanffy equation is used in the present study. The first being that the same equation is applied to all of the fisheries, while fishes of the same age that occur in different parts of the Barents Sea may have different growth rates. Our intention of using data from the eastern part of the Barents Sea in the case of the younger age-groups and combine them with data from the Lofoten for the older ones in order to estimate the parameters in the von Bertalanffy equation was to establish a kind of "average" curve for the fish that dominates the catches.

A second problem would be that the von Bertalanffy curve is applied in a deterministic way, while in reality there is a scatter around the "average" curve. This becomes a problem when there is a considerable overlap of the length distributions for the different age-groups. As Jones (1974) notes the relationship between the mean length and the age, versus the relationship between the length and mean age are not neccessarily the same, the latter one generally shows a greater growth rate. This factor problably being the main reason why the estimated parameters depends somewhat on whether the basis for the simulation is the observed age- or the length- distributions. However, the length distributions and the age distributons give similar recruitment curves for gill-net, in particular in Division IIa. This indicate to us that the von Bertalanffy parameters used are reasonable "averages".

There are a more general problem with the estimation of parameters that are pertinent to this study. That is the effect of correlations between the estimated parameters, which are always to increase the errors on the other parameters. If any of these two-by-two correlations get close to plus or minus one, that increase the difficulty to get an unique set of parameters from the model or the data available.

In the present case the great majority of the two-by-two correlations were close to zero ( $<0.20$ ). However, in the case of gill-net, in particular for the gill-net fishery in Division IIa, there were rather high correlations between the parameters, i.e. $\mathrm{r}(\mathrm{RL} 50 \%$, RL75\%/RL50\%) $=0.81$ and 0.82 on the basis of the age data and the length data respectively. This is also reflected in the global correlations (Eadie et al. 1971, p. 23) as given in Table 4.

Table 4. Global correlation coefficients of the estimated parameters as derived from the two sets of catch distributions.

| Parameter |  | Age-data | Length-data |
| :---: | :---: | :---: | :---: |
| USSR, trawl | S.-a. I ; L50\% | 0.12 | 0.01 |
| " " | Div.IIb ; L50\% | + | 0.03 |
| UK, trawl | G.-a. I ; L50\% | 0.01 | + |
| " " | Div.IIa ; L50\% | 0.01 | + |
| UK + Norway trawl | Div.IIb ; L50\% | 0.08 | 0.01 |
| Other countries' trawl | ; L50\% | 0.05 | + |
| Norway trawl | S.-a. I ; L50\% | 0.07 | + |
| " " | Div.IIa ; L50\% | 0.01 | + |
| Gill-net | S.-a. I ; RL50\% | 0.55 | 0.34 |
| " | Div.IIa ; RL50\% | 0.68 | 0.69 |
| Long- and hand-line | S.-a. I ; L50\% | + | + |
| " " " | Div.IIa ; L50\% | 0.17 | 0.03 |
| Gill-net | s.-a. I ; L75\%/L50\% | 0.52 | 0.32 |
| Gill-net | Div.IIa ; L75\%/L50\% | 0.69 | 0.69 |
| Stock estimate (I year | las; 15 cm$)$; $\mathrm{N}(\mathrm{TI})$ | 0.01 | + |

In the case the gill-net fishery in Division IIa, the high correlations indicate that an increase in the length at $50 \%$ recruitment ( $\mathrm{RL} 50 \%$ ) is to a large extent compensated by a less steep slope (RL75\%/RL50\%). These high correlations are also reflected by the elongated shape of the confidence regions for these two parameters (Fig. 16 ).


Fig. 16. 95\% confidence region of the length at $50 \%$ maturity versus the slope of the maturity curve at the inflection point. Legend: l) Best estimate.

The standard deviations of the lengths at $50 \%$ selections (Table 2) are in the range 0.1 to 2.5 mm . These standard deviations assume that all of the input data, except for the observed age- (or length-) distributions are correct and not subject to uncertainty. The estimates of the lengths at $50 \%$ selection are on the average about 5 cm larger when using the age data than the length data. This as well as our own experience from preliminary simulations with different fixed input parameters indicate that the true standard deviations of the length at $50 \%$ selection (or recruitment) may well be an order
higher than those given in Table 2. Although the estimated standard deviations indicate that the coefficient of variation of the estimated parameters varies considerably between the different fisheries (Table 2).

Contrary to some of the other fisheries the parameters for discards are not directly important in the case of gill-net, as also mentioned earlier. Since the selection parameters could be fixed from independent experiments for gill-net, the recruitment curve could be estimated rather than fixed on the basis of circumstantial evidence. This should give the estimated parameters for gill-net (Table 3) more trustworthiness than those for the other fisheries. However, the the considerations on the von Bertalanffy equation given above, the relatively high correlation coefficients for the four estimated parameters of the gill-net fishery (Table 4), and finally the relatively poor fit between the observed and estimated fishing mortalities (Fig. 11c) errode some of our confidence in the estimates.

As also mentioned earlier, the two recruitment curves which are derived from the age composition and the length-composition of the gill-net fishery in Division IIa, may be considered as maturity ogives.

In Fig. 15 the two maturity ogives as derived from the present investigations are drawn together with the maturity ogive given by Hylen and Dragesund (1973) which should represent the years 1967-1969, and data from Ponomarenko et al. (1980, 1982) which apply to the period 1967-1977. They are all similar except for the younger age-groups ( $\leqq 9$ years) where our model suggest about 1 year's later maturation. However, our estimates of the onset of maturation is to a large extent determined by the selection curve for gill-net. It should be evident from Fig. 1 that this curve is not very well defined for length-groups up to about 80 cm , i.e. fishes 8 years or younger.

We are unable to assess which of the maturity curves (Fig. 15) reflects the situation in the period 1967-1977 most accurately. However, depending on an independent assessment of input parameters this study does indicate that a modified mesh assessment model may be an useful approach to estimating maturity ogives in some cases.

## REFERENCES

Anon. 1979. Report of the Arctic fisheries working group. Coun. Meet. int. Explor. Sea, C.M. 1979 (G:20): 1-85 (Mimeo.).

Anon. 1980. Report of the Working group on redfish and and Greenland halibut in Region 1. Coun. Meet. int. Explor. Sea, C.M. 1980 (G:4): 1-107 (Mimeo.).

Anon. 1983. Report of the Arctic fisheries working group. Coun. Meet. int. Coun. Explor. Sea, C.M. 1982 (G:2): 1-53 (Mimeo.).

Eadie, W.T., Drijard, D., James, F.E., Roos, M., and Sadoulet, B. 1971. Statistical methods in experimental physics. North-Holland Publ. lo., Amsterdam.

Garrod, D.J. 1967. Population dynamics of the Arcto-Norwegian cod. J. Fish. Res. Bd. Can., 24: 145-190.

Hylen, A. 1965. Utkast av torsk fra trålfangster. Fiskets Gang, 1965(30): 433-435.

Hylen, A. 1967. On the estimation of cod and haddock discarded by trawlers using different chafers. Co-op. Res. Rep. int. Coun. Explor. Sea (B), 1966: 65-76.

Hylen, A. 1969. Discarding of fish in North-East Atlantic. Co-op. Res. Rep. int. Coun. Explor. Sea (B), 1966: 56-58.

Hylen, A. and Dragesund, 0. 1973. Recruitment of young ArctoNorwegian cod and haddock in relation to parent stock size. Rapp. P.-v. Cons. int. Explor. Mer, 164: 58-68.

Hylen, A. and Jakobsen, T. 1979. A fishery experiment with multifilament, monofilament, and monotwine gill nets in Lofoten during the spawning season of ArctoNorwegian cod in 1974. Fisk.Dir. Skr. Ser. HavUnders., 16: 531-550.

Hylen, A. and Nakken, 0. 1982. Stock size of North-East Arctic cod estimated from acoustic survey data 1982. Coun. Meet. int. Coun. Explor. Sea, C.M. 1982 (G:61): l-12 (Mimeo.).

Hylen, A. and Olsen, H.E. 1977. Seleksjon av torsk i bunntrål. Forelфpig rapport fra de norske forsøkene ved Bjørnфya i juni 1977. Fiskeridirektoratets Havforskningsinstitutt, 10 pp . (Mimeo.).

Hylen, A. and Smedstad, O.M. 1974. Observations from the Barents Sea in spring 1973 on the discarding of cod and haddock caught in bottom and midwater trawls fitted with double cod ends. Coun. Meet. int. Explor. Sea, C.M. 1974 (F:45): 1-8 (Mimeo.).

Høydal, K., Rørvik, C.J. and Sparre, P. 1980. A method for estimating the effective mesh sizes and the effects of changes in gear parameters. Coun. Meet. int. Explor. Sea, C.M. 1980 ( $\mathrm{G}: 28$ ): 1-33 (Mimeo.).

H申ydal, K., Rørvik, C.J. and Sparre, P. 1982. Estimation of effective mesh sizes and their utilization in assessment. Dana, 1982(2): 69-95.

James, F. 1978. Interpretation of the errors on parameters as given by MINUIT. CERN Computer Center Program Library, 16 pp. (Mimeo.).

James, F. and Roos, M. 1977. MINUIT. A system for function minimization and analysis of the parameter errors and correlations. CERN Computer Center Program Library, 46 pp. (Mimeo.).

Jones, R. 1974. Assessing the long term effects of changes in fishing effort and mesh size from length composition data. Coun. Meet. Explor. Sea, C.M. 1974 (F:33): 1-7 (Mimeo.).

Kirkwood, G.P. 1982. Some statistical aspects of the Beddington and Cooke estimation technique. Rep. int. Whal. Commn, 32: 471-473.

Ponomarenko, I.Ya. 1982. Portion of mature cod specimens and sex ratio in different age and length groups within the 60ies and 70ies. Coun. Meet. int. Explor. Sea, C.M. 1982 ( $\mathrm{G}: 18$ ): 1-20 (Mimeo.).

Ponomarenko, I.Ya. and Yaragina, N.A. 1981. Relation between mature and immature specimens among cod of different ages and sizes in 1978-80. Coun. Meet. int. Explor. Sea, C.M. 1981 (G:22): 1-11 (Mimeo.).

Ponomarenko, V.P., Ponomarenko, I.Ya. and Yaragina, N.A. 1980. Growth and maturation of the Lofoten-Barents Sea cod. Coun. Meet. int. Explor. Sea, C.M. 1980 (G:25): 1-28 (Mimeo.).

Ponomarenko, V.P., Nikeshin, K.N. and Sakhno, V.A. 1978. On selectivity of trawls with a mesh size of 120 and 135 mm in codends when fishing cod in the Barents Sea. Coun. Meet. int. Explor. Sea, C.M. 1978 (B:9): 1-12 (Mimeo.).

Rollefsen, G. 1954. Observations on the cod and cod fisheries of Lofoten. Rapp. P.-v. Réun. Cons. per. Int. Explor. Mer, 136: 40-47.

Sætersdal, G. 1963. Selectivity of long lines. Int. Commn Northw. Atlant. Fish., Spes. Pub.5: 189-192.

Tveite, S. and Rørvik, C.J. 1982. A stock assessment of lobster (Homarus gammarus) on the Norwegian Skagerrak coast. Coun. Meet. int. Coun. Explor. Sea, C.M. 1982 (K:7): l-20 (Mimeo.).

## ABUNDANCE AND DISTRIBUTION

OF O-GROUP ARCTO-NORWEGIAN COD AND HADDOCK 1965-1982
by

Kjell Randa
Institute of Marine Research


#### Abstract

The trawl data from the International 0 -group fish surveys in the Barents Sea are reanalysed for cod and haddock. Relative indices of yearclass abundance are estimated on a logarithmic scale. The most abundant yearclasses at the 0 -group stage, for cod, are the 1970, 1973 and 1975 yearclasses and the 1970, 1974 and 1975 yearclasses for haddock. The estimated indices of yearclass strength give a correlation of 0.92 for cod and 0.89 for haddock with VPA (Virtual Population Analysis) estimates for the corresponding yearclasses at age 3 for the yearclasses 1970-1976.

0 -group haddock show a more western distribution than cod which may be related to a more western spawning area for haddock. Both cod and haddock show similar trends in changes in the east-west distribution over time. This is probably related to hydrographical factors such as changes in the relative strength of the different currents in the area. A good correlation is found for both cod and haddock between the part of a yearclass found in the Barents Sea and the temperature anomalities in the Kola Meridian hydrographical section, but no correlation was found between the part of a yearclass in the Spitsbergen/


Bear Island area and temperature anomalies in the Bear Island West hydrographical section.

## INTRODUCTION

The knowledge of the size of the recruiting yearclasses is one of the basic needs for a successful stock assessment. The International 0 -group fish surveys in the Barents Sea have been conducted since 1965, and the results from these surveys have been used in the assessment of the Arcto-Norwegian cod and haddock stocks (Anon, 1983a).

Recruitment indices for several species have been computed based on the data from these surveys using a method described by Haug and Nakken (1977). The recruitment indices are calculated on basis of the number caught of a species and its area of distribution.

In this paper a new set of recruitment indices are calculated based on the number caught in different areas. The recorded data from each of the trawlhauls constitute the basic material for this analysis.

## MATERIAL

Each year since 1965 joint international (Norway, USSR and up until 1976 UK) 0 -group fish surveys have been carried out in the Barents Sea in August - September. The aim of these surveys is to measure the level of recruitment of the most important fish species in the area. This include species like cod, haddock, capelin, herring, redfish, polar cod, Greenland halibut and long rough dab.

The survey is a trawl survey carried out by three to five research vessels. Pelagic trawl hauls are taken at every 30 nautical mile or when echo recordings change, using a small meshed pelagic trawl. The trawl depth is decided fron the echograms, and the traw1 is towed in the depths of the recordings, mostly less than 50 m . If no recordings are present, the
trawl is towed at the surface using 6 big floats on the headrope. The trawl is towed for 1 nautical mile at about 3 knots.

In 1981 a new standard trawl procedure was chosen (Anon, 1981). After 1981 trawling has been done in a stepwise manner. The trawl is towed for 10 minutes with the headline in each of the following depths: $0 \mathrm{~m}, 20 \mathrm{~m}$ and 40 m . The towing speed is 3 knots.

## METHODS

RELATIVE FISHING POWER OF THE VESSELS

Altogether 11 different vessels have participated in the surveys in the period since 1965. Both the trawls and the vessels have increased in size and there has been a change from side to stern trawlers.

In order to assess the differences between vessels and trawls the relative fishing power of the different vessels and trawls have been estimated using the methods of Robson(1966). The calculations were done using a computer program described by Fox (1971), and also by Randa (1982).

## ESTIMATION OF RECRUITMENT INDEXES

As a basic index of yearclass abundance the stratified mean catch in numbers per 1.0 nautical mile towed on a logarithmic scale is used. A logarithmic scale is used to reduce the effect of a few large catches that are not representative for more than a very small area, and to normalize the catch data.

The total area was divided into 17 areas (Fig. 1) and area 1-1I make up the eastern area and area 12-17 the western area.

Trawl data are usually highly positively skewed and a transformation is necessary to normalize the data. Pennington and Grosslein (1978) indicate that the transformation $y=\ln (x)$,


Figure 1. The strata used in estimating abundace indices. The eastern area: Strata 1 - 11 .

The western area: Strata 12 - 17.
$x \neq 0$ is the most appropriate and Rand (1982) has shown that this transformation normalize catch data for 0 -group cod. For each area each year the following quantities are calculated:

The logarithmic mean

$$
\bar{X}_{j}=\frac{1}{N_{1 j}} \sum_{i=1}^{N_{1 j}} \ln \left(X_{i j}\right)
$$

The logarithmic variance

$$
s_{j}^{2}=\frac{1}{N_{1 j}-1} \sum_{i=1}^{N_{1 j}}\left(\ln \left(X_{i j}\right)-\bar{X}_{j}\right)^{2}
$$

The Proportion of nonzero hauls

$$
p_{j}=\frac{N_{1 j}}{N_{j}}
$$

The variance of this proportion

$$
S_{p j}^{2}=\frac{1}{N_{j}-1} p_{j}\left(1-p_{j}\right)
$$

$X_{i j}$ is the catch in number at station $i$ in area $j, N_{1 j}$ is the number of nonzero hauls in area $j$ and $N_{j}$ is the total number of hauls in area $j$.

An index of abundance in area $j$ is computed as $X_{j} \cdot P_{j}$. $A$ combined index for several areas is computed in the following way:

Calculate the stratified logarithmic mean catch and its standard error.

$$
\begin{aligned}
R & =\frac{1}{A} \sum_{j=1}^{k} a_{j} \cdot \bar{X}_{j} \\
S E R & =\sqrt{\frac{1}{A^{2}} \sum_{j=1}^{k} \frac{a_{j}^{2} S_{j}^{2}}{N_{1 j}}}
\end{aligned}
$$

where $a_{j}$ is the areal of area $j, A$ is the total areal and $k$ is the number of areas.

A areal weighted proportion for several areas and its standard error is calculated in the following manner:

$$
\begin{aligned}
Q & =\frac{1}{A} \sum_{j=1}^{k} a_{j} \cdot p_{j} \\
S E Q & =\sqrt{\frac{1}{A^{2}} \sum_{j=1}^{k} a_{j}^{2} \cdot S_{p j}^{2}}
\end{aligned}
$$

The final logarithmic index of yearclass abundance is then calculated as

$$
L=R \cdot Q
$$

CONFIDENCE LIMITS

Confidence limits of $L$ is obtained in the following manner (Harpelin and Mantel, 1963; Harpelin, 1964): First calculate $95 \%$ confidence limits on $R$ and $Q$ based on normal theory.

```
R - 2 . SER < R < R + 2 . SER or
    R'<R< R''
```

and

$$
\begin{aligned}
\mathrm{Q}-2 & \cdot \mathrm{SEQ}<\mathrm{Q}<\mathrm{Q}+2 \cdot \mathrm{SEQ} \\
\mathrm{Q}^{\prime} & <\mathrm{Q}<\mathrm{Q}^{\prime}
\end{aligned}
$$

Then the confidence limits for $L$ are given as

$$
\begin{aligned}
R^{\prime} \cdot Q^{\prime} & <R \cdot Q<R^{\prime \prime} \cdot Q^{\prime \prime} \text { or } \\
L^{\prime} & <L<L^{\prime}
\end{aligned}
$$

The size of these confidence limits are above $90 \%$ and probably near 95\% (Harpelin and Mantel; Harpelin, 1964). The calculated indices for cod and their confidence limits given in this paper differs from those given by Randa (1982) because of unweighted estimate of $Q$ was used in that paper.

RESULTS AND DISCUSSION

ANALYSIS OF FISHING POWER

The relative fishing powers of the different vessels for cod are taken from Randa (1982) and are given in table 1. Randa (1982) also gives a detailed description of how they are computed. The low values for the non-Norwegian vessels probably reflect the smaller trawls used by these vessels.

Since 0 -group cod and haddock are distributed in much the same area and depth and are of similar length during the survey period, it seems reasonable to assume that their catchability are much the same. Therefore the relative fishing powers estimated for cod are also used on the haddock catches.

Two vessels "Havdrøn" (Norway) and "Jastreb" (USSR) have only participated one year each in the survey and their relative fishing power for both cod and haddock is assumed to be 1.0 .

Table 1. Estimated fishing powers with confidence limits relative to G.O.Sars (1971-1979). Taken from Randa 1982.

| Vessel | Relative <br> Fishing Power | Confidence <br> Ifimits |
| :--- | :---: | :---: |
| G.O.Sars (1971-1979) | 1.000 |  |
| G.O.Sars (1970) | 0.221 | $0.060-1.706$ |
| G.O.Sars (1965-1969) | 0.493 | $0.148-2.931$ |
| J.Hjort (1965-1973) | 1.936 | $0.856-5.481$ |
| J.Hjort (1975-1979) | 1.536 | $0.697-4.172$ |
| E.Holt (Pelagic trawl) | 0.518 | $0.106-9.601$ |
| E.Holt (Boothbay trawl) | 0.574 | $0.175-3.291$ |
| Cirolana (Pelagic trawl) | 0.551 | $0.253-1.464$ |
| Cirolana (Boothbay trawl) | 0.040 | $0.012-0.220$ |
| A. Knipovich | 0.563 | $0.241-1.678$ |
| F.Nansen | 0.734 | $0.350-1.844$ |
| Poisk | 0.537 | $0.280-1.178$ |
| Odissey | 0.723 | $0.305-2.216$ |

The same assumption is made for the new vessels "Michael Sars" (Norway) and "Percey III" (USSR). This seems reasonable because both these vessels have used a trawl similar to that of the selected standard vessel "G.O. Sars".

INDICES OF YEARCLASS ABUNDANCE

Cod

The estimated indices of yearclass abundance for cod in the western, eastern and total area together with their confidence limits are given in Tables 2,3 and 4 , and are shown in Figs. 2,3 and 4 . Fig. 4 shows that there is a great variability in yearclass strength of about two orders of magnitudes. The strongest yearclasses are the 1970, 1973 and 1975 (Table 5). The distribution of the 1973 and 1975 yearclasses are very different from the 1970 yearclass. From Tables 2,3 and 4 it is seen that the 1973 and 1975 yearclasses had a very eastern distribution and were only found in small numbers in the Spitsbergen/Bear Island area. This is in contrast to the 1970 yearclass which also was numerous in the western area.

Table 2. Estimated indices with confidence limits of yearclass abundance for 0 -group cod and haddock in the western area.

| Yearclass | Cod |  |  | Haddock |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Logarithmic index | Confidence <br> limits (95\%) |  | Logarithmic index | Confidence limits (95\%) |  |
| 1965 | 0.00 |  |  | 0.01 | 0.00 | 0.01 |
| 1966 | $+$ |  |  | 0.01 | 0.00 | 0.02 |
| 1967 | $+$ |  |  | 0.04 | 0.00 | 0.08 |
| 1968 | + |  |  | + |  |  |
| 1969 | 0.18 | 0.07 | 0.33 | 0.47 | 0.19 | 0.89 |
| 1970 | 1.71 | 0.86 | 2.75 | 1.10 | 0.54 | 1.85 |
| 1971 | 0.32 | 0.13 | 0.60 | 0.38 | 0.18 | 0.63 |
| 1972 | 0.06 | 0.01 | 0.13 | 0.31 | 0.10 | 0.67 |
| 1973 | 0.11 | 0.03 | 0.25 | 0.22 | 0.05 | 0.49 |
| 1974 | 0.01 | 0.00 | 0.05 | 0.33 | 0.12 | 0.62 |
| 1975 | 0.07 | 0.01 | 0.19 | 0.23 | 0.09 | 0.45 |
| 1976 | 0.00 |  |  | 0.35 | 0.14 | 0.70 |
| 1977 | 0.22 | 0.08 | 0.43 | 0.34 | 0.09 | 0.69 |
| 1978 | 0.32 | 0.13 | 0.60 | 0.30 | 0.10 | 0.60 |
| 1979 | 0.63 | 0.31 | 1.06 | 0.30 | 0.11 | 0.60 |
| 1980 | 0.18 | 0.06 | 0.38 | 0.26 | 0.10 | 0.46 |
| 1981 | 0.13 | 0.04 | 0.30 | 0.07 | 0.00 | 0.27 |
| 1982 | 0.33 | 0.14 | 0.54 | 0.58 | 0.29 | 0.90 |

Table 3. Estimated indices with confidence limits of yearclass abundance for 0 -group cod and haddock in the eastern area.

| Year-class | cod |  |  | Haddock |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Logarithmic index | Confidence <br> limits (95\%) |  | Logarithmic index | Confid limits | $\begin{aligned} & \text { lence } \\ & (95 \%) \end{aligned}$ |
| 1965 | + |  |  | 0.02 | 0.00 | 0.04 |
| 1966 | 0.03 | 0.01 | 0.06 | 0.01 | 0.00 | 0.02 |
| 1967 | 0.09 | 0.04 | 0.15 | 0.09 | 0.04 | 0.19 |
| 1968 | 0.03 | 0.01 | 0.08 | 0.00 | 0.00 | 0.04 |
| 1969 | 0.27 | 0.18 | 0.39 | 0.21 | 0.12 | 0.32 |
| 1970 | 2.87 | 2.32 | 3.50 | 0.49 | 0.28 | 0.76 |
| 1971 | 1.00 | 0.73 | 1.32 | 0.21 | 0.13 | 0.31 |
| 1972 | 0.83 | 0.54 | 1.18 | 0.11 | 0.04 | 0.23 |
| 1973 | 2.49 | 1.98 | 3.05 | 0.25 | 0.13 | 0.44 |
| 1974 | 0.51 | 0.31 | 0.76 | 0.62 | 0.41 | 0.83 |
| 1975 | 1.50 | 1.10 | 1.37 | 0.80 | 0.52 | 1.19 |
| 1976 | 0.25 | 0.12 | 0.44 | 0.37 | 0.23 | 0.55 |
| 1977 | 0.63 | 0.45 | 0.85 | 0.33 | 0.20 | 0.48 |
| 1978 | 0.19 | 0.11 | 0.28 | 0.06 | 0.03 | 0.12 |
| 1979 | 0.32 | 0.16 | 0.54 | 0.15 | 0.08 | 0.24 |
| 1980 | 0.10 | 0.06 | 0.14 | 0.11 | 0.06 | 0.18 |
| 1981 | 0.11 | 0.04 | 0.16 | 0.01 | 0.00 | 0.02 |
| 1982 | 0.66 | 0.44 | 0.92 | 0.30 | 0.23 | 0.43 |

Table 4. Estimated indices with confidence limits of yearclass abundance for cod and haddock in the total area. Number of 3 years old is taken from Anon, $1983 a$ and Anon, l983b.

|  | Cod |  |  |  | Haddock |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Year- <br> class | No 3-years old (mill) | Logarithmic index | Confid 1imits | ence <br> (95\%) | No 3-years old (mill) | Logarithmic index | $\begin{aligned} & \text { Confid } \\ & \text { limits } \end{aligned}$ | ence (95\%) |
| 1965 | 170 | + |  |  | 20 | 0.01 | 0.00 | 0.04 |
| 1966 | 112 | 0.02 | 0.01 | 0.04 | 17 | 0.01 | 0.00 | 0.03 |
| 1967 | 197 | 0.04 | 0.02 | 0.08 | 164 | 0.08 | 0.03 | 0.13 |
| 1968 | 405 | 0.02 | 0.01 | 0.04 | 96 | 0.00 | 0.00 | 0.02 |
| 1969 | 1016 | 0.25 | 0.17 | 0.34 | 1032 | 0.29 | 0.20 | 0.41 |
| 1970 | 1818 | 2.51 | 2.02 | 3.05 | 291 | 0.64 | 0.42 | 0.91 |
| 1971 | 524 | 0.77 | 0.57 | 1.01 | 57 | 0.26 | 0.18 | 0.36 |
| 1972 | 620 | 0.52 | 0.35 | 0.72 | 50 | 0.16 | 0.09 | 0.27 |
| 1973 | 616 | 1.48 | 1.18 | 1.82 | 58 | 0.26 | 0.15 | 0.40 |
| 1974 | 371 | 0.29 | 0.18 | 0.42 | 131 | 0.51 | 0.39 | 0.68 |
| 1975 | 794 | 0.90 | 0.66 | 1.17 | 201 | 0.60 | 0.40 | 0.85 |
| 1976 | 241 | 0.13 | 0.06 | 0.22 | 188 | 0.38 | 0.24 | 0.51 |
| 1977 | (175) | 0.49 | 0.36 | 0.65 | (22) | 0.33 | 0.21 | 0.48 |
| 1978 | (257) | 0.22 | 0.14 | 0.32 | (15) | 0.12 | 0.07 | 0.19 |
| 1979 | (191) | 0.40 | 0.25 | 0.59 | (55) | 0.20 | 0.12 | 0.28 |
| 1980 |  | 0.13 | 0.08 | 0.18 |  | 0.15 | 0.10 | 0.20 |
| 1981 |  | 0.10 | 0.06 | 0.18 |  | 0.03 | 0.00 | 0.05 |
| 1982 |  | 0.59 | 0.43 | 0.77 |  | 0.38 | 0.30 | 0.52 |

( ) Preliminary

The yearclasses 1971, 1972, 1977 and 1982 may be considered. medium at the 0 -group stage, and the rest of the yearclasses in the period 1965 - 1982 are poor. From Fig. 5 it can be seen that it appears to have been two periods of poor recruitment to the Arcto-Norwegian cod. This is the period 1965-1969 and 1976 - 1981. Between these two periods of low recruitment there was a period of high recruitment.

The confidence limits for the recruitment indices (Table 4) show that the yearclasses 1965 - 1968 are very poorly estimated. The confidence limits are in the range of $100 \%$. This is due to several factors. In these years the survey was poorly standardized. The participating vesse1s used several different trawls and the trawl parameters are badly documented in the database. Number of hauls were fewer and the trawl depth was not easily determined due to lack of instrumentation. All these factors add variance components that are unknown and are not
caused by the variation in fish distribution. Therefore these four yearclasses are not used when the estimated indices of yearclass abundance are compared with other estimates of yearclass abundance. When the estimated indices (Table 4) are compared with the VPA (Virtual Population Analysis) estimates of number of 3 years old fish taken from Anon (1983a) it is obvious that the index for the 1969 yearclass is much too low and this estimate is considered as an outlier and is not used further in this comparative analysis.

It is assumed that the VPA gives reliable estimates for all yearclasses 1976 and oldtr. This gives a regression line for the relation between the estimated indices and the VPA estimates for the same yearclasses in the period 1970-1976 as follows: VPA $=582.7 \cdot L+162.6 \mathrm{r}=0.92$ which is a highly significant regression. This regression line is shown in Fig. 5.

The predicted number of 3 -years old cod from the regression line for the 1970-1982 yearclasses are given in Table 5. The greatest discrepancy is observed for the 1973 yearclass which is overestimated in the 0 -group survey by approximately $66 \%$ compared to the VPA estimate. Table 5 indicate that the yearclasses 1977 - 1981 are poor, but the estimates for the 1977 and 1979 yearclasses are well above the estimates given in Anon (1983a).

Several cautions should be taken when using this regression line for predicting yearclass abundance. Fig. 5 shows that this regression line is very dependent upon the 1970 point. Errors in either the VPA or the survey estimate for this yearclass would have a rather large effect on the regression line. Also there is a large intercept in the regression of 163 millions 3 year old fish. This mean that more than $50 \%$ of the estimate of a poor yearclass is made up of this intercept.

## Haddock

The estimated indices of yearclass abundance for haddock in the western, eastern and the total area together with their confi-


Fig. 2. Estimated yearclass strength at the 0-group stage in the western area. Cod shaded columns, haddock open.


Fig. 3. Estimated yearclass strength at the 0-group stage in the eastern area. Cod shaded columns, haddock open.


Fig. 4. Estimated yearclass strength at the 0-group stage in the total area. Cod shaded columns, haddock open.


Fig. 5. The regression line between 0-group estimates of yearclass strength on VPA estimates of th same yearclass at age 3 for cod.


Fig. 6. The regression line bewteen 0 -group estimates of yearclass strength on VPA estimates of the same yearclass at age 3 for haddock.
dence limits are given in Tables 2, 3 and 4 , and are shown in Figs. 2, 3 and 4. Fig. 4 shows that there is a great variability in yearclass strength, but not to the same degree as for cod. The strongest yearclasses are the 1970, 1974, 1975 yearclasses, medium yearclasses are the 1969, 1976, 1977 and 1982. The rest of the yearclasses in the period 1965-1982 appears to be of low abundance judged from the estimated indices.

Tables 2 and 3 indicate that the 0 -group haddock is more evenly distributed between the western and eastern area than cod. No yearclass is dominated totally by a western or eastern component.

For the same reasons as stated for cod only the 1970-1976 yearclasses are used in the regression between estimated indices and VPA estimates of three years old taken from Anon (1983a) with the modification stated in Anon (1983b). The

Table 5. Number of 3 years old cod and haddock predicted from the regression of 0 -group indices on VPA estimates.

| Year- <br> class | Cod | Haddock |
| :--- | ---: | :---: |
| 1970 | 1625 | 245 |
| 1971 | 611 | 77 |
| 1972 | 460 | 33 |
| 1973 | 1024 | 77 |
| 1974 | 332 | 187 |
| 1975 | 687 | 227 |
| 1976 | 238 | 130 |
| 1977 | 448 | 108 |
| 1978 | 291 | 15 |
| 1979 | 396 | 51 |
| 1980 | 238 | 29 |
| 1981 | 221 | - |
| 1982 | 506 | 130 |

resulting regression line is VPA $=440.8 \cdot L-37.5$ ( $r=0.89$ ) which is highly significant. This regression is shown in Fig. 6. Predicted VPA values from this regression is given in Table 5. Compared to the VPA estimates given in Table 4 there is a reasonable good agreement for yearclasses 1970-1975. The 1976 yearclass is underestimated by approximately $43 \%$ and the 1977 yearclass is very badly overestimated by the 0 -group index.

The yearclasses 1978 - 1981 seems to be very poor. The regression line gives estimates from 51 mill. 3 -years old and downwards, and this is well below the 1970 - 1976 average of approximately 140 mill .

The index for the 1982 yearclass gives an estimate of 130 mill . which is close to the 1970 - 1976 average.

The regression line for haddock has a negative intercept and will generate negative VPA estimates for all 0-group indices less than 0.085 . However, the regression is based on indices greater than 0.16 and should not be used to extrapolate values
outside the range of 0 -group indices used during the regression.

THE DISTRIBUTION OF 0-GROUP COD AND HADDOCK

Tables 6 and 7 show for each yearclass the percentage of the yearclass found in each of the 17 strata. Figs. 7 and 8 show the percentage of a yearclass found in the western and eastern area for both cod and haddock. This figures show that 0 -group haddock generally has a more western distribution than 0-group cod. This may have several explanations, but perhaps the most obvious would be to assume that haddock eggs start to drift from a point further to the west and south than the eggs of cod that start in the Lofoten area. Dragesund, Midttun and Olsen (1970) indicate that the spawning area for haddock is off the Norwegian coast between $63^{\circ} \mathrm{N}$ and the $\mathrm{R} \phi$ st Bank, which is in accordance with a more western distribution of the 0 -group haddock than observed for cod.

From Figs. 7 and 8 there seems to be a similar time trend in the percentage of a yearclass found in the western and eastern area for both cod and haddock. The percentage of a yearclass found in the eastern area increased to a maximum in the mid seventies and then fell off at the end of the seventies and early eighties.

These similarities in the changes in the distribution of both cod and haddock both probably reflect changes in the hydrographical condition in the Barents Sea. The 0 -group distribution of both cod and haddock are determined by the strength of the currents transporting them from the spawning area and into the Barents Sea and the Spitsbergen/Bear Island area. Such changes in the current condition may partly be read from temperature indices on standard hydrographical sections. In the eastern area the Kola Meridian section ( $\mathrm{N} 69^{\circ} 30^{\prime}$, $\mathrm{E} 33^{\circ} 30^{\prime}$ - $\mathrm{N} 70^{\circ} 00^{\prime}$, E33 ${ }^{\circ} 0^{\prime}$ ) is used and in the western area the Bear Island West section ( $\mathrm{N} 74^{\mathrm{O}} 30^{\prime}, \mathrm{E} 06^{\circ} 34^{\prime}-\mathrm{N} 74^{\circ} 30^{\prime}, \mathrm{E} 15^{\circ} 55^{\prime}$ ) is used. Temperature indices for $0-200 \mathrm{~m}$ for both these sections are given in Anon (1982a). Figs. 9 and 10 show the anomalies in these two

Table 6. Cod. The percentage of a yearclass found in the different strata during the survey.

| Yearclass | Strata number |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | East | West |
| 1965 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 100 | 0 | 0 | 0 | 0 | 0 | 0 | 100 | 0 |
| 1966 | 0 | 0 | 0 | 15 | 0 | 0 | 22 | 24 | 0 | 17 | 13 | 10 | 0 | 0 | 0 | 0 | 0 | 90 | 10 |
| 1967 | 0 | 0 | 0 | 27 | 10 | 9 | 18 | 22 | 8 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 100 | 0 |
| 1968 | 0 | 0 | 15 | 54 | 0 | 0 | 16 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 96 | 4 |
| 1969 | 0 | 0 | 3 | 20 | 0 | 2 | 8 | 20 | 19 | 0 | 10 | 6 | 0 | 7 | 0 | 5 | 1 | 81 | 19 |
| 1970 | 6 | 0 | 12 | 20 | 7 | 3 | 5 | 8 | 11 | 4 | 3 | 7 | 0 | 5 | 3 | 3 | 3 | 79 | 21 |
| 1971 | 0 | 0 | 4 | 16 | 9 | 3 | 6 | 17 | 16 | 3 | 13 | 7 | 0 | 3 | 0 | 1 | 3 | 86 | 14 |
| 1972 | 22 | 4 | 8 | 6 | 12 | 12 | 3 | 14 | 12 | 0 | 2 | 0 | 0 | 0 | 0 | 3 | 2 | 95 | 5 |
| 1973 | 20 | 6 | 21 | 11 | 11 | 8 | 3 | 8 | 7 | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 98 | 2 |
| 1974 | 0 | 6 | 17 | 31 | 18 | 5 | 2 | 10 | 4 | 3 | 3 | 0 | 0 | 0 | 0 | 1 | 0 | 99 | 1 |
| 1975 | 2 | 1 | 15 | 30 | 11 | 2 | 10 | 12 | 7 | 3 | 5 | 1. | 0 | 1 | 0 | 0 | 0 | 98 | 2 |
| 1976 | 0 | 0 | 6 | 29 | 24 | 3 | 6 | 13 | 8 | 4 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 100 | 0 |
| 1977. | 0 | 0 | 7 | 20 | 7 | 0 | 12 | 23 | 2 | 7 | 13 | 1 | 1 | 3 | 0 | 3 | 3 | 89 | 11 |
| 1978 | 0 | 0 | 0 | 8 | 3 | 0 | 9 | 13 | 7 | 8 | 12 | 4 | 0 | 9 | 0 | 19 | 10 | 58 | 42 |
| 1979 | 4 | 0 | 0 | 5 | 2 | 6 | 2 | 11 | 6 | 2 | 15 | 1 | 2 | 10 | 10 | 1.7 | 5 | 55 | 45 |
| 1980 | 0 | 0 | 0 | 2 | 4 | 0 | 0 | 15 | 6 | 7 | 28 | 6 | 0 | 4 | 0 | 21 | 8 | 61 | 39 |
| 1981 | 0 | 0 | 0 | 31 | 3 | 0 | 12 | 14 | 4 | 1 | 11 | 0 | 0 | 7 | 3 | 13 | 1 | 76 | 24 |
| 1982 | 2 | 0 | 2 | 20 | 13 | 0 | 8 | 21 | 7 | 2 | 13 | 1 | 0 | 4 | 2 | 5 | 3 | 85 | 15 |

Table 7. Haddock. The percentage of a yearclass found in the different strata during the survey.

| Yearclass | Strata number |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | East | West |
| 1965 | 0 | 0 | 0 | 0 | 0 | 0 | 22 | 42 | 0 | 0 | 15 | 0 | 0 | 21 | 0 | 0 | 0 | 79 | 21 |
| 1966 | 0 | 0 | 0 | 20 | 0 | 0 | 14 | 20 | 0 | 0 | 17 | 0 | 17 | 12 | 0 | 0 | 0 | 71 | 29 |
| 1967 | 0 | 0 | 0 | 14 | 0 | 0 | 8 | 30 | 7 | 5 | 23 | 3 | 0 | 0 | 0 | 0 | 10 | 87 | 13 |
| 1968 | 0 | 0 | 0 | 50 | 0 | 0 | 0 | 35 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 85 | 15 |
| 1969 | 0 | 0 | 0 | 5 | 2 | 0 | 1 | 19 | 13 | 5 | 21 | 6 | 4 | 12 | 0 | 11 | 2 | 65 | 35 |
| 1970 | 0 | 0 | 2 | 20 | 2 | 0 | 7 | 7 | 1 | 4 | 13 | 1 | 0 | 13 | 14 | 8 | 9 | 55 | 45 |
| 1971 | 0 | 0 | 0 | 0 | 2 | 2 | 5 | 25 | 13 | 0 | 20 | 2 | 0 | 14 | 0 | 10 | 8 | 66 | 34 |
| 1972 | 0 | 0 | 0 | 10 | 0 | 0 | 8 | 5 | 16 | 3 | 18 | 8 | 0 | 9 | 0 | 14 | 9 | 60 | 40 |
| 1973 | 0 | 0 | 10 | 13 | 1 | 0 | 5 | 18 | 5 | 6 | 18 | 5 | 0 | 10 | 0 | 3 | 6 | 76 | 24 |
| 1974 | 0 | 0 | 1 | 12 | 7 | 2 | 5 | 20 | 12 | 11 | 15 | 8 | 1 | 3 | 1 | 2 | 1 | 84 | 16 |
| 1975 | 0 | 1 | 8 | 29 | 4 | 1 | 10 | 21 | 8 | 2 | 5 | 4 | 0 | 3 | 1 | 2 | 0 | 90 | 10 |
| 1976 | 0 | 0 | 0 | 5 | 7 | 0 | 14 | 24 | 8 | 9 | 13 | 5 | 0 | 2 | 4 | 2 | 8 | 79 | 21 |
| 1977 | 0 | 0 | 0 | 8 | 4 | 0 | 15 | 32 | 1 | 4 | 18 | 2 | 3 | 3 | 0 | 5 | 5 | 82 | 18 |
| 1978 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | 12 | 1 | 12 | 23 | 10 | 0 | 12 | 0 | 19 | 6 | 53 | 47 |
| 1979 | 0 | 0 | 0 | 8 | 0 | 0 | 5 | 21 | 7 | 6 | 22 | 3 | 5 | 10 | 8 | 4 | 0 | 70 | 30 |
| 1980 | 7 | 0 | 0 | 0 | 2 | 0 | 0 | 17 | 5 | 7 | 27 | 3 | 5 | 8 | 0 | 12 | 7 | 65 | 35 |
| 1981 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 0 | 6 | 19 | 0 | 28 | 8 | 11 | 11 | 8 | 34 | 66 |
| 1982 | 0 | 0 | 0 | 4 | 2 | 0 | 7 | 27 | 8 | 2 | 21 | 1 | 3 | 7 | 4 | 8 | 5 | 72 | 28 |



Fig. 7. Cod. The percentage of a yearclass found in the western and the eastern areas, at the 0-group stage. Western area shaded columns, eastern open.


Fig. 8. Haddock. The percentage of a yearclass found in the western and the eastern areas at the 0 -group stage. Western area shaded columns, eastern open.
sections plotted for the period 1965-1982. Both sections show similar trends: A changing period 1965-1971 in the Kola section and 1965 - 1972 in the Bear Island West section, followed by a period of high temperature in the mid seventies. In both sections there is sudden drop in the temperature in 1977 and 1978 followed by an increasing trend up to 1982. The drop in 1977-78 is especially severe in the Kola Meridian where the following increase in temperature is slower than in the Bear Island West section.

The anomalities in the Kola Meridian have been correlated with the percentage of a yearclass in the eastern area for both cod and haddock for the period 1970-1982 and the anomalities in the Bear Island West section with the percentage of a yearclass in the western area for the period 1971 - 1982. (Anon, 1982a gives no temperature index for the Bear Island West section in 1970). The correlations are given in the following text-table:

|  | Kola <br> Meridian | Bear Island <br> West |
| :--- | :---: | :---: |
| Cod | 0.81 | 0.21 |
| Haddock | 0.60 | 0.34 |

There seems to be a good correlation between the temperature condition in the Kola Meridian and the percentage of a yearclass in the Barents Sea for both cod and haddock. This means that in years with a strong Atlantic influx in the Barents Sea there is a high probability that the major part of a yearclass will be transported into the Barents Sea.

On the other hand there seems to be no correlation between the percentage of a yearclass in the western area and the temperature anomalies in the Bear Island West section. This may have several explanations. The temperature condition in the Bear Island West section may be of only minor importance in determining the percentage of yearclass that will be transported into the western area. The division is probably dependant on the starting point of the eggs. A southern and western starting point favours transport into the western area. Cod spawn along

## KOLA SECTION



Fig. 9. The temperature anomalities in the Kola hydrographical section 1965-1982. Data taken from ANON 1982a.

## BEAR ISLAND WEST



Fig. 10. The temperature anomalities in the Bear Island West hydrographical section 1965-1982. Data taken from ANON 1982a.
the whole Norwegian Coast north of $62^{\circ} \mathrm{N}$ (Anon, 1982b) with the main spawning area in the Lofoten Islands. The part of the stock spawning south of Lofoten varies from year to year, and no data have been found that can be used to quantify this for the period 1965 - 1982. With such data present it would perhaps be possible to show some correlation between the percentage of a yearclass in the western area and the relative amount of cod spawning south of Lofoten.

## REFERENCES

Anon 1981. Preliminary report of the international 0 -group fish survey in the Barents Sea and adjacent waters in August - September 1981. Coun. Meet. int. Coun. Explor. Sea, 1981 (G:78): 1-26. Mimeo.

Anon 1982a. Preliminary report of the international 0-group fish survey in the Barents Sea and adjacent waters in August - September 1982. Coun. Meet. int. Coun. Explor. Sea, 1982 (G:44): 1-27. Mimeo.

Anon 1982b. Report on minisymposium on spawning, egg and larvae of cod: A comparison of the Icelandic and Arcto-Norwegian cod tribes. Minisymposium organized by the Working Group on Larval Fish Ecology, Biological Oceanography Committee, ICES. Reykjavik, 8-11 February, 1982.

Anon 1983a. Report of the arctic fisheries working group. Coun. Meet. int. Coun. Explor. Sea, 1983 (Assess:2): 1-62. Mimeo.

Anon 1983b. Reports of the ICES advisory committee on fishery management 1982. Int. Coun. Explor. Sea, Cooperative Res. Repr. 119 (1983).

Dragesund, O., Midttun, L. and O1sen, S. 1970. Methods for estimating distribution and abundance of 0 -group fish. In Dragesund, O. (Ed.) International 0-group
fish survey in the Barents Sea 1965 - 1968. Int. Coun. Explor. Sea, Cooperative Res. Rep., Ser. A, No. 18: 1-81.

Fox, W.W. 1971. User's guide to FPOW, a computer program for estimating relative fishing power and relative population density by the method of analysis of variance. Quantitative science paper No. 27. Center for quantitative science in forestry, fisheries and wildlife. University of Washington, Seattle. 1-6. Mimeo.

Harpelin, M. 1964. Interval estimation of nonlinear function. Parametric function II. J. Amer. Stat. Assoc. 59 (1964): 168-81.

Harpelin, M. and Mante1, W. 1963. Interval estimation of nonlinear parametric functions. J. Amer. Stat. Assoc. 58 (1963): 611-27.

Haug, A. and Nakken, 0. 1977. Echo abundance indices of 0 -group fish in the Barents Sea, 1965 - 1972. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 170: 259-64.

Pennington, M.R. and Grosslein, M.D. 1978. Accuracy of abundance indices based on stratified random trawl surveys. Coun. Meet. int. Coun. Explor. Sea, 1978 (D:31): 1- 35. Mimeo.

Randa, K. 1982. Recruitment indices for the Arcto-Norwegian Cod for the period 1965 - 1979 based on the international 0-group fish survey. Coun. Meet. int. Coun. Explor. Sea, 1982 (G:43): 1-22. Mimeo.

Robson, D.S. 1966. Estimation of the relative fishing power of individual ships. Res. Bull. int. Comm. NW. Atl. Fish, 3: 3-14.

# SURVIVAL OF BOTTOM-DWELLING YOUNG COD IN THE BARENTS SEA AND ITS DETERMINING FACTORS 

 byI.Y. Ponomarenko PINRO, Murmansk, USSR

## ABSTRACT

The factors determining different survival rates for young cod of various yearclasses from the bottom-dwelling 0-group to three-year-olds investigated. The most important of such factors are yearly fluctuations of:

- abundance of euphausiids - the primary food of 0-group cod;
- biological indices of fingerlings (length and weight of the body, fatness, condition factor, stomach fullness) at the onset of hydrological winter;
- temperature conditions in the Barents Sea during hydrological winter;
- abundance of cod fingerlings.

Through regression equations involving these factors, the survival rates of the subsequent yearclasses of cod may be prognosticated rather satisfactorily enabling advance verification of the strength of new recruitment to the commercial stock.

Prediction of survival rates $\left(R_{s}\right)$ for fingerlings to three-yearold fish is of practical value for all yearclasses regardless of abundance. However, under extremely low abundance of fingerlings prediction of $R_{s}$ is worthless, because the recruitment to commercial stock will in any case be very poor.

The frequent occurrence of extremely poor cod yearclasses in recent years stems notably from comparatively low abundance of eggs, i.e. from reduced total fecundity of the spawning stock due to lack of older cod.

## RESULTS AND DISCUSSION

In order to make an advance estimation of the strength of recruitment to commercial stock and long-term prognoses of catches and the efficiency of trawlers in the Barents Sea, quantitative assessment of young commercial fish has been carried out (Baranenkova 1957, 1957a, 1968). Based on the annual autumn/winter survey of bottom-dwelling young cod with length less than 36 cm , the abundance of each yearclass is estimated during three subsequent years, at an age of one, two and three incomplete years ( $0+$, $1+, 2+$ ).

Comparison of the survey results for separate yearclasses at a given age and of the values of the same yearclasses in landings throughout 6 years of fisheries (the summed catch of cod aged 3-8 per trawling hour) showed that the assessment of young fish at the age of 24 gives the most reliable estimate of recruitment. In the southern Barents Sea the correlation coefficients between the survey indices for separate yearclasses at ages of $2+, 1+, 0+$ and the strength of the same yearclasses in commercial catches are $0.86,0.75$ and 0.47 , respectively (Ponomarenko 1982). Thus, it follows that the young cod assessment at an age of $0+$ does not produce reliable abundance indices for the yearclasses entering the fisheries. This is caused, above all, by the rather high and variable mortality of fingerlings (0+).

The repeated assessments of each yearclass at age $0+1+$ and $2+$ enable quantitative estimation of survival for separate yearclasses assuming that the ratio of the average catch of 3-year olds ( $2+$ ) per trawling hour to the average catch of fingerlings ( $0+$ ) of the same yearclass per trawling hour is a relative index of survival (or the survival rate $R_{S}$ ). It should be emphasized that it is impossible to determine the absolute survival from the survey data currently available, because trawl selectivity is different for fingerlings and 3-year old fish (Baranenkova 1957a). Three-year-old fish, being larger, are caught by trawl in larger quantities than fingerlings, although being less abundant. That is why the ratio catch of $2+$ fish per trawling hr when used as the survival rate, is generally expressed in values above one, being higher with lower mortality of young cod from the fingerlings to 3-year-old fish stage. Only in cases of a very high mortality of young fish is $\mathrm{R}_{\mathrm{s}}$ below one.

Great variability of this index (Table I) was revealed when determining $R_{s}$ for 32 cod yearclasses (1948-1979). For the yearclasses with high, average and below average abundance, i.e. for all yearclasses excluding extremely poor ones*, the maximum values of $R_{s}$ may exceed minimum ones by a factor of 57-68. Owing to such fluctuations of $R_{s}$ the first estimate of a yearclass strength (at an age of $0+$ ) may change significantly by the third year: under high $R_{s}$ the yearclasses estimated as average may appear rich by their third year of life and under low $R_{S}$ - poor.

Hence, conditions during the early demersal period of young fish may change the strength of the subsequent recruitment. There were cases when cod yearclasses abundant at an age of $0+$ became average or even below average by $2+$ (e.g. the 1951, 1954, 1957 year classes with $R_{s}$ of $0.44,0.21,0.51$ respectively). And, conversely, other yearclasses, because of high survival from the 0 -group to the third-year stage, turned out to be strong regard-

[^0]Table 1. Abundance indices of cod yearclasses at age $0+$ and $2+$ and survival rates ( $R_{s}$ ) from fingeriings to 3-year-old fish.

| Year <br> class | Average catch per trawl hour, individuals |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Southern Barents Sea |  |  | Bear Island Spitsbergen area* |  |  | Total area |  |  |
|  | $0+$ | $2+$ | $\mathrm{R}_{\mathrm{s}} \frac{2+}{0+}$ | $0+$ | $2+$ | $\mathrm{R}_{\mathrm{S}} \frac{2+}{0+}$ | $0+$ | $2+$ | $\mathrm{R}_{\mathrm{s}} \frac{2+}{0+}$ |
| 1948 | 15.89 | 18.12 | 1.14 | - | 22.31 | - | 15.89 | 20.89 | 1.31 |
| 1949 | 6.13 | 28.62 | 4.67 | 0 | 10.07 | - | 4.51 | 25.85 | 5.73 |
| 1950 | 12.48 | 75.34 | 6.04 | 1.79 | 40.22 | - | 5.42 | 73.77 | 13.61 |
| 1951 | 13.50 | . 5.90 | 0.44 | 0.93 | 12.72 | - | 11.62 | 6.28 | 0.54 |
| 1952 | 1.24 | 2.84 | 2.29 | 3.11 | 5.90 | - | 1.33 | 3.17 | 2.38 |
| 1953 | 3.31 | 10.62 | 3.21 | 8.28 | 4.11 | - | 3.59 | 8.91 | 2.48 |
| 1954 | 25.95 | 5.39 | 0.21 | 60.90 | 11.90 | - | 29.31 | 6.05 | 0.21 |
| 1955 | 6.66 | 8.47 | 1.27 | 3.93 | 13.69 | - | 5.94 | 9.71 | 1.63 |
| 1956 | 11.55 | 10.32 | 0.89 | 5.03 | 17.55 | - | 10.89 | 12.92 | 1.19 |
| 1957 | 20.55 | 11.29 | 0.54 | 40.29 | 17.08 | - | 24.40 | 13.23 | 0.54 |
| 1958 | 10.04 | 15.70 | 1.56 | 16.99 | 21.00 | - | 12.54 | 17.87 | 1.43 |
| 1959 | 10.42 | 17.63 | 1.69 | 16.15 | 15.10 | 0.93 | 12.34 | 16.39 | 1.33 |
| 1960 | 7.08 | 9.27 | 1.31 | 25.06 | 18.37 | 0.73 | 14.46 | 13.09 | 0.91 |
| 1961 | 2.92 | 2.36 | 0.81 | 17.25 | 1.69 | 0.10 | 9.95 | 2.04 | 0.20 |
| 1962 | 14.42 | 6.96 | 0.48 | 6.03 | 3.17 | 0.53 | 10.90 | 5.23 | 0.48 |
| 1963 | 74.52 | 21.33 | 0.29 | 64.24 | 107.94 | 1.68 | 69.58 | 71.39 | 1.03 |
| 1964 | 39.60 | 48.95 | 1.24 | 21.05 | 43.01 | 2.04 | 31.18 | 46.28 | 1.48 |
| 1965 | 0.01 | 0.55 | 55.00 | 0.12 | 0.17 | 1.42 | 0.07 | 0.36 | 5.14 |
| 1966 | 0.03 | 1.46 | 48.67 | 0.01 | 0.02 | 2.00 | 0.02 | 0.98 | 49.00 |
| 1967 | 0.06 | 1.43 | 23.83 | 0.02 | 0.23 | 11.50 | 0.04 | 1.12 | 28.00 |
| 1968 | 0.21 | 6.80 | 32.38 | 0 | 0.97 | - | 0.13 | 4.28 | 32.92 |
| 1969 | 1.84 | 10.45 | 5.68 | 0.98 | 5.54 | 5.65 | 1.45 | 8.59 | 5.92 |
| 1970 | 20.14 | 74.37 | 3.69 | 62.56 | 78.81 | 1.26 | 38.45 | 76.26 | 1.98 |
| 1971 | 6.90 | 37.26 | 5.40 | 8.72 | 25.13 | 2.88 | 7.59 | 32.23 | 4.25 |
| 1972 | 4.48 | 53.34 | 11.91 | 4.64 | 22.27 | 4.80 | 4.55 | 40.10 | 8.81 |
| 1973 | 16.12 | 73.73 | 4.57 | 6.04 | 6.25 | 1.03 | 11.93 | 45.92 | 3.85 |
| 1974 | 0.87 | 5.92 | 7.05 | 0.14 | 0.87 | 6.21 | 0.54 | 4.02 | 7.44 |
| 1975 | 61.94 | 96.75 | 1.56 | 0.17 | 4.09 | 24.06 | 36.49 | 61.71 | 1.69 |
| 1976 | 0.62 | 4.07 | 6.56 | 1.26 | 0.32 | 0.25 | 0.86 | 2.71 | 3.15 |
| 1977 | 1.57 | 1.65 | 1.05 | 0.17 | 0.73 | 4.29 | 1.04 | 1.29 | 1.24 |
| 1978 | 0.25 | 1.45 | 5.80 | 2.01 | 2.45 | 1.22 | 0.89 | 1.84 | 2.07 |
| 1979 | 0.17 | 0.23 | 1.35 | 0.22 | 7.31 | 33.23 | 0.19 | 3.20 | 16.84 |
| 1980 | 0.05 |  |  | 0.06 |  |  | 0.06 |  |  |
| 1981 | 0.01 |  |  | 0.04 |  |  | 0.02 |  |  |
| 1982** |  |  |  |  |  |  | 3.40 |  |  |

* The centrai elevation included. For the $1948-1958$ yearclasses $R_{s}$ is not given due to a very small amount of adequate hauls.
** By preliminary data.
less of an abundance originally considered average or even below average, (e.g. the 1949, 1950, 1969 year-classes which had $R_{S}$ of $4.67,6.04,5.68$ respectively (Table ll). Therefore, in order to estimate the strength of recruitment to the commercial cod stock well in advance, it is essential to know if the average catch of 3-year-old fish per trawling hour increases or decreases as compared with that of fingerlings, i.e. to have available the data on $\mathrm{R}_{\mathrm{s}}$ of the various yearclasses.

Table 2. Food composition and some biological indices of 0-group cod in the Barents Sea.


As a result of long-term investigations on the nutrition and biological indices of cod fingerlings and the feeding and temperature conditions for their development (Ponomarenko 1968, 1978a, 19786, 1965, 1973, MS 1977, 1980, 1981, 1982), the factors determining different survival rates of young fish from separate year classes in the Barents Sea were demonstrated. The most important of such factors are:

1) yearly fluctuations of abundance of euphausiids (Thysanoessa inermi.s, Th. raschii, Meganyctiphanes norvegica) - the primary food object of bottom-dwelling 0-group of cod both by weight and by occurrence (Table 2). In years of high abundance of these crustaceans, when their average catch taken with a trawl-attached net exceeds 50 indivs. per trawling hour (geometric mean of separate one-hour catches), the survival rates for young cod are on the average 5 times as high as in years of low euphausiids abundance (Table 3). The increase in number of euphausiids in the late 60's early 70's (Drobysheva, MS 1980) had a positive effect on the survival of young cod of the 1969-1975 year classes;
2) quality, or condition, of fingerlings before the first wintering season (length, weight of the body, fatness, condition factor, stomach fullness). All the above indices are in a positive correlation with euphausiid abundance in corresponding years, on the one hand, and with the $R_{s}$ of the yearclasses on the other hand (Table 4). The length of fingerlings is also positively correlated with the heat content of the Barents Sea waters in the year of origin of the yearclass: as a rule 0-group cod are longer in warm years than in cold ones;
3) the temperature conditions during the temperature minimum period (wintering) of the two calendar years following the yearclass' appearance, the first wintering season being the most important. The average temperature $T_{a v}^{0}$ of the two coldest months (usually March and April) of the Kola (No. 6), Kharlov (No. 8, Stations l-4) and No. 10 sections in the 0200 m layer is taken as indicative of temperature conditions

Table 3. Survival rates for cod year classes under various food supply rates (Euphausiacea) during the first and second years of life (southern Barents Sea).


[^1]for the over-wintering young cod in the southern Barents Sea. As is seen from Table 4, the highest $R_{S}$ values (averaging 5.50) occurred in the yearclasses with the average index $T_{a v}^{\circ}$ above $2^{\circ}$ during the first and the second wintering seasons. With $T_{a v}^{\circ}$ from $1.56^{\circ}$ to $2.00^{\circ}$ they were somewhat lower (averaging 2.03) and with $\mathrm{T}_{\mathrm{av}}^{\mathrm{O}}$ below $1.56^{\circ}$ they were the lowest ( 0.84 on the average). For approximately equal values of $\mathbb{T}_{a v}^{0}$ the highest $R_{S}$ values were found for those yearclasses with the greatest length of fingerlings or those with high fatness and condition factor (see Table 4).
4) the abundance of fingerlings. The highest $R_{S}$ values (26.4 on average) are typical of extremely poor yearclasses, the lowest ones (1.15 on average) - for rich yearclasses, their abundance index as fingerlings being above 20 specimens per trawling hour. The average $R_{s}$ for yearclasses of average abundance is equal to 2.56 , and for those with below average abundance - 4.36 (Table 5). Fluctuations of $R_{S}$ are greatest for average yearclasses ( $\mathrm{R}_{\mathrm{S}} \max$ exceeds $\mathrm{R}_{\mathrm{S}} \mathrm{min}$ by a factor of 68) and have a narrower range in both the poorest and rich yearclasses for which $R_{S} \max$ exceeds $R_{S} \min$ only by a factor of 7-10.

Correlation coefficients for $R_{S}$ and each of the above factors are comparatively low ( $< \pm 0.65$ ). However, multiple correlation coefficients reach 0.88 - 0.96 , when the combined effect of several (2 - 4) factors is considered. Thus, it is possible to make up several prognostic regression equations to calculate $R_{S}$ for a given yearclass of cod from ages 0 to 3 years (except for extremely poor ones), and thus estimate the relative strength of recruitment to commercial stock $1.5-2$ years earlier than by the results of direct assessment of 3-year old fish.

The highest multiple correlation coefficients are obtained by combining the following factors:

- $x, z, 1, q$, where $x$ is the index of temperature conditions of the first wintering season, $z$ is the index of euphausiid abundance during the first year of life of the yearclass, 1 is the

Table 4. Survival rates of cod yearclasses under different winter temperature conditions with some biological indices of fingerlings (southern Barents Sea).

|  | Year <br> class | $\begin{aligned} & T_{\mathrm{av}}^{\mathrm{a}} \text { of } \\ & 1 \text { st and } \\ & \text { 2nd } \\ & \text { winter } \end{aligned}$ | $\mathrm{R}_{\mathrm{S}} \frac{2+}{0+}$ | Mean biological indices of fingerlings before their first winter |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | Length, cm | Fulton condition factor | Fatness, \% | Index of stomach fullness, $0 / 00$ |
|  | 1948 | 2.41 | 1.14 | 9.35 | 0.586* | 2.44* | 87* |
|  | 1949 | 2.62 | 4.67 | 10.52 |  |  |  |
| $\bigcirc$ | 1950 | 2.19 | 6.04 | 12.66 | $0.658 * *$ | $3.29 * *$ | 213** |
| $\stackrel{\sim}{\sim}$ | 1953 | 2.43 | 3.21 | 10.83 |  |  |  |
|  | 1971 | 2.08 | 5.40 | 10.59 | 0.601 | 3.09 | 81 |
| $\stackrel{8}{8}$ | 1972 | 2.07 | 11.91 | 11.72 | 0.633 | 3.37 | 93 |
| - | 1973 | 2.01 | 4.57 | 11.17 | 0.596 | 2.70 | 85 |
| 品 | 1974 | 2.15 | 7.05 | 11.65 | 0.602 | 2.32 | 68 |
| $\mathrm{O}_{\mathrm{E}}$ | Average | 2.24 | 5.50 |  |  |  |  |
| $\bigcirc$ | 1952 | 2.00 | 2.29 | 12.00 |  |  |  |
| $\sim$ | 1954 | 1.69 | 0.21 | 10.05 | 0.531 | 2.20 | 79 |
| + | 1958 | 1.85 | 1.56 | 10.28 | 0.632 | 2.72 | 94 |
|  | 1959 | 1.67 | 1.69 | 10.71 | 0.655 | 2.87 | 103 |
| $\stackrel{\square}{?}$ | 1960 | 1.88 | 1.31 | 10.81 | 0.612 | 1.96 | 60 |
| -1 | 1963 | 1. 67 | 0.29 | 10.75 | 0.590 | 2.21 | 49 |
| \% | 1969 | 1.82 | 5.68 | 11.05 | 0.686 | 3.48 | 137 |
| ${ }_{4}^{4}$ | 1970 | 1.69 | 3.69 | 10.50 | 0.650 | 3.15 | 77 |
|  | 1975 | 1.76 | 1.56 | 12.09 | 0.654 | 2.66 | 84 |
| $\mathrm{O}_{\mathrm{E}-1}$ | Average | 1.78 | 2.03 |  |  |  |  |
|  | 1951 | 1. 50 | 0.44 | 10.89 | 0.551* | 2.84* | 27* |
|  | 1955 | 1.46 | 1.27 | 9.69 | 0.631* | 2.30* | 62* |
| 낭 | 1956 | 1.37 | 0.89 | 9.67 | 0.621 | 2.78 | 104 |
| $\cdots$ | 1957 | 1.53 | 0.54 | 10.81 | 0.561 | 2.96 | 36 |
|  | 1961 | 1.55 | 0.81 | 9.96 | 0.605 | 2.51 | 107 |
| - | 1962 | 1.18 | 0.48 | 9.88 | 0.605 | 2.85 | 87 |
| - | 1964 | 1.34 | 1.24 | 11.24 | 0.643 | 3.10 | 67 |
| 号 | 1977 | 0.67 | 1.05 | 10.06 | 0.589 | 2.97 | 79 |
| $\mathrm{O}_{\mathrm{H}}$ | Average | 1.32 | 0.84 |  |  |  |  |

[^2]average length of fingerlings in autumn-winter, and $q$ is the index of fingerling abundance (average catch in specimens per trawl hour):
\[

$$
\begin{gathered}
R_{y}(x, z, 1, q)=0.96, \quad n=17 \\
y=1.29 x+0.056 z+2.151-0.0585 q-24.115
\end{gathered}
$$
\]

using three factors - $\mathrm{x}, \mathrm{z}, \mathrm{I}$ :

$$
\begin{gathered}
R_{y}(x, z, I)=0.94 ; \quad n=17 \\
y=1.36 x+0.064 z+1.9541-23.221 ;
\end{gathered}
$$

using two factors - $\mathrm{x}, \mathrm{z}$ :

$$
\begin{array}{cc}
R_{y}(x, z)=0.88 & n=17 \\
y=2.51 x+0.075 z-5.05 &
\end{array}
$$

Other combinations are applicable to predict $R_{s}$ : instead of 1 (or along with 1) the data on body weight, condition factor, fatness, stomach fullness of fingerlings may be used. However, the estimation of such indices is more complicated than determination of fish length.

Predicting $\mathrm{R}_{\mathrm{s}}$ for fish from 0 - to 3 -years-old in order to forecast the strength of the subsequent recruitment to the commercial cod stock is of practical value for yearclasses of average, above average and below average abundance. Such year classes have, as was stated above, the greatest fluctuations in survival rates and their final commercial abundance will depend on $R_{s}$. It is important to consider all this before developing the long-term prognosis of cod catches and of the efficiency of fishery.

Prediction of $\mathrm{R}_{\mathrm{s}}$ for extremely rich yearclasses (more than 60-70 0 -group fish per trawling hour) is less important, as fluctuations of $R_{s}$ for such yearclasses are comparatively small. These year classes will likely remain rich.

For extremely poor yearclasses prediction of $R_{s}$ is worthless. If abundance of fingerlings is extremely low as, for instance, for

Table 5．Survival rates of yearclasses with different abundances of fingerlings（southern Barents sea and Bear Island－Spitsbergen area）．

| Yearclags |  | Abundance index for 0－group （average number caught per trawl hour） | Survival rate $R_{s} \frac{2+}{0+}$ |
| :---: | :---: | :---: | :---: |
| $\bigcirc$ | 1954 | 29.31 | 0.21 |
| $0_{0} 0^{\circ}$ | 1957 | 24.40 | 0.54 |
| $\cdots$ | 1.963 | 69.58 | 1.03 |
| \％E ${ }^{\text {a }}$ | 1964 | 31.18 | 1.48 |
| 畐式和 | 1970 | 38.45 | 1.98 |
| $\begin{aligned} & 0 \\ & 0 \\ & 0 \\ & 0 \\ & 4 \\ & 0 \\ & 0 \\ & 0 \\ & \hline \end{aligned}$ | 1975 <br> Average | 36.49 | 1.69 |
|  | 1948 | 15.89 | 1.31 |
| ${ }^{\circ}$ | 1950 | 5.42 | 13.61 |
| ． | 1951 | 11.62 | 0.54 |
| $\stackrel{-}{+}$ | 1955 | 5.94 | 1.63 |
| $\stackrel{0}{0}$ | 1956 | 10.89 | 1.19 |
| ． | 1958 | 12.54 | 1.43 |
| 4 | 1959 | 12.34 | I． 33 |
| $\bigcirc$ | 1960 | 14.46 | 0.91 |
| ${ }_{\sim}^{\circ} \mathrm{H}$ | 1961 | 9.95 | 0.20 |
| $\bigcirc$ | 1962 | 10.90 | 0.48 |
| H | 1972 | 7.59 | 4.25 |
| $\begin{array}{ll} -1 \\ \text { in } \\ 0 \end{array}$ | 1973 | 11.93 | 3.85 |
|  | Average |  | 2.56 |
| $\stackrel{\square}{\square}$ | 1949 | 4.51 | 5.73 |
| $\stackrel{-1}{4}$ | 1952 | 1.33 | 2.38 |
| $\stackrel{0}{6}$ | 1953 | 3.59 | 2.48 |
| F | 1969 | 1.45 | 5.92 |
| 4 | 1972 | 4.55 | 8.81 |
| $\bigcirc$ | 1974 | 0.54 | 7.44 |
| ก 3 | 1976 | 0.86 | 3.15 |
| 9 | 1977 | 1.04 | 1.24 |
| ） 4 | 1978 | 0.89 | 2.07 |
| $\bigcirc$ | Average |  | 4.36 |
| 号 | 1965 | 0.07 | 5.14 |
| 4 | 1966 | 0.02 | 49.00 |
| $\stackrel{4}{9}$ | 1967 | 0.04 | 28.00 |
| $\bigcirc$ | 1968 | 0.13 | 32.92 |
| 荷 | 1979 | 0.19 | 16.84 |
| $\stackrel{\square}{4}$ | 1980 | 0.06 |  |
|  | 1981 | 0.02 | 26.38 |

the 1965-19.67 and 1980-1981 yearclasses (below 0.1 specimens per trawling hour, Table 1), even $100 \%$ survival, will not greatly affect the strength of the yearclass, and the recruitment to the commercial stock will be poor.

Hence in the periods when the yearclasses with polar abundance indices (rich or very poor) prevail, the relation between assessment indices for fingerlings and 3-year-old fish of the corresponding yearclass is well correlated, as observed in the last 17 years ( $r=0.87$ between bottom-dwelling fingerlings and 3-year old fish and 0.74 between pelagic 0 -group fry and 3-year fish for the 1963-1979 yearclasses). But when yearclasses of average and close to average abundance of fingerlings prevail, the correlation between number of $0+$ and $2+$ fish of the same yearclass decreases considerably, because in such cases the abundance of 3year old fish will depend on greatly fluctuating survival rates. For 32 yearclasses of the southern Barents sea cod (1948-1979) the correlation coefficient between the abundance indices of 3-year-old fish and fingerlings of the same yearclass was only +0.50 , but when multiplied by the calculated $R_{s}$ the correlation coefficient approaches 1 . This trend indicates the reliability of the calculated relative indices of yearclass survival.

The material for assessment of young cod over the last 20 years indicates a higher frequency of poor and very poor yearclasses (Table 1). In these years appeared nine of the ten poorest yearclasses of cod since 1946 (less than 300 million fish aged 3 by the VPA results, Anon. MS 1979, MS 1982). The reason for the increased appearance of poor year classes lie not only in unfavourable oceanographic conditions connected with the reduced temperature in the eastern part of the Norwegian and Barents Seas (Mukhin, Dvinina, 1982) but also, in our opinion, results from the low number of spawning cod and, in particular, from the small number of spawners aged 10 and older which have the highest individual fecundity. If, before the 60 's, the abundance of such spawners fluctuated by years from some tens to several hundreds of millions of specimens, then in 1065-1967 and 1976-1982 it declined to a level below 9 million (Fig. 1L. In these periods the poorest (1965-1967 and 1980-1981) yearclasses of cod appeared,


Fig. 1. Dynamics of spawning stock (biomass of fish aged 8 and older) and abundance of cod of the 1946-1981 yearclasses. Thick solid line - spawning stock biomass; broken line - abundance of cod aged 10 and older (calculated by V.L. Tretyak through the VPA); thin solid line - the same (the estimate of the ICES Working Group; chain-dotted line - abundance index of cod eggs of all stages (by the survey results); columns - abundance of yearclasses aged 3 (by the ICES Working Group estimate by the VPA).
the abundance indices of which were below 0.1 specimens per trawling hour at an age of $0+$ (Table l). When comparing these data to the results of the quantitative assessment of cod eggs and larvae carried out annually in spring-summer, it is evident that four out of five of the poorest yearclasses (1966-1967, 1980-1981) had low abundance already at the egg stage (Fig. 1) and, in particular, at the lst stage of egg development. The average 1959-1981 abundance index for cod eggs of stage 1 was 20.9 per haul according to the data of PINRO's laboratory of bottom fishes in the North European basin. In 1966-1967 and 1980-1981 this index ranged from 0.1 to 8.6 (mean 4.3) per haul, and so the low population fecundity of cod in these years was the primary reason for the extreme paucity of the 1966-1967 and 19801981 yearclasses. This is in turn connected primarily with low abundance of fish aged 10 and older (Fig. 1) where there is a greater proportion of females whereas males are prevalent among younger mature cod especially between 6-8 years old.

Comparatively low abundance of cod eggs in the mentioned years resulted also in low abundance of all subsequent stages: larvae, pelagic and bottom 0 -group fish. The abundance of the latter was so small (less than 0.1 specimens per trawling hour) that even under the highest known $\mathrm{R}_{\mathrm{s}}$ of fingerlings to 3-year old fish (49.00, Table 5) these yearclasses would be very poor.

For the 1959-1963 and 1965-1981 yearclasses for which PINRO quantitative assessment of cod eggs is available, the relationship between egg abundance indices (average number of eggs of all stages per one haul of egg net) and abundance indices of the same yearclasses estimated by the VPA has a correlation coefficient +0.69 at the confidence limit of 0.99 . This demonstrates the dependence of the abundance of cod yearclasses on the amount of spawned eggs and, consequently, on the amount and quality of spawners.

Certainly, with a large number of spawners, yearly fluctuations in their amount do not affect the strength of the yearclasses. However, with a decrease in the spawning stock the probability of
such effects appears and increases. Thus, in the last 20 years (1962-1981) when the abundance of older cod declined to below 20 million (Fig. 1), the relation between the yearly fluctuations in abundance of spawners aged 10 and older and fluctuations of yearclass abundance became apparent ( $\mathrm{r}=0.52$, at a 0.95 confidence limit). In the last 10 years (1972-1981) this correlation coefficient has been 0.64 . With the further decline in abundance and biomass of the spawning stock, which is inevitable under the existing comparatively high catch limits (F>Fmax) and poor recruitment, the connections between the parent stock and recruitment become closer. iro preserve and restore the cod stock it is necessary to considerably reduce the catch limits (no more than $F_{0.1}$ ) and to observe these limits and the national catch quotas strictly.

## REFERENCES

Anon., MS 1978, MS 1979, MS 1981, MS 1982. Report of the Arctic Fisheries Working Group. ICES CM 1978/G:64, 1979/G:20, 1981/G:2, 1982/G:2 (Mimeo).

Baranenkova, A.S. 1957. Comparative abundance of yearclasses of the cod and haddock in the Barents Sea according to the quantitative estimation of the young fish and the data on fisheries. "Trudy PINRO", 10:54-77.

Baranenkova, A.S. 1957a. The results of the young cod and haddock assessment in the Barents sea in winter 19561957. Nauchnotekhnich. bjull. PINRO, No. 4.

Baranenkova, A.S. 1968. The PINRO investigations into the estimation of the abundance of the Barents Sea fishes. "Trudy PINRO", 23:193-216.

Drobysheva, S.S. MS 1980. Long-term fluctuations of abundance indices of the Barents Sea euphausiids (Crustacea, Euphausiacea) according to the data from the autumnwinter survey. ICES CM 1980/L:9 (Mimeo).

Mukhin, A.I., E.A. Dvinina, 1982. Long-term fluctuations of water temperature and salinity in spring-summer in the border area of the Norwegian and Barents Seas. In: Ekologija i promysel donnykh ryb Severo-Jevropesskogo bassejna, Murmansk, PINRO, pp.98-112.

Ponomarenko, I.Ya. 1965. 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. ICNAF Spec. Publ., vol.6, B-7, pp. 349354.

Ponomarenko, I.Ya. 1968. Feeding, biological characteristics and survival of "bottom" young cod in the Barents Sea. "Trudy PINRO", 23:279-292.

Ponomarenko, I.Ya. 1973. The effects of food and temperature conditions on the survival of young bottom-dwelling cod in the Barents Sea. Rapports et proces-verbaux, vol. l64, pp. 199-207.

Ponomarenko, I.Ya. 1976. Food composition and quantitative indices of feeding of 0-group cod in the Barents Sea. Annls biol., 31:83-86.

Ponomarenko, I.Ya. MS 1977. Influence of wintering temperature conditions on the survival of young cod and haddock in the Barents Sea. ICES CM 1977/F:15.

Ponomarenko, I.Ya. 1978a. The effect of temperature conditions of hydrological winter on the survival of young cod and haddock. "Trudy PINRO", 40:125-132.

Ponomarenko, I.Ya. 1978b. Investigations on feeding and biological indices of 0-group cod in the Barents Sea. Annls biol., Copenh., 33:81-82.

Ponomarenko, I.Ya. 1979. Distribution, feeding, growth and survival of cod fingerlings of the abundant 1970 yearclass. "Trudy PINRO", 43:77-114.

Ponomarenko, I.Ya. 1980. Food, composition and feeding of 0group cod in the Barents Sea in 1978. Annls biol., Copenh., 35:127-129.

Ponomarenko, I.Ya. 1981. Food composition and feeding of 0group cod in the Barents Sea in 1978/1979. Annls biol., 36:109-110.

Ponomarenko, I.Ya. 1982. Fisheries estimation of the results of young cod and haddock assessment. In: Ekologija i promysel donnykh ryb Severo-Jevropejskogo bassejna, Murmansk, pp. 10-23.

THE USE OF FISHING EFFORT, JUVENILE ABUNDANCE AND PREVIOUS YEARS' CATCH DATA FOR THE FORECAST OF ARCTO-NORWEGIAN COD CATCH

## by

V.M. Borisov, V.v. Blinov<br>VNIRO, Moscow

## ABSTRACT

Assessment of cod yearclass by VPA provides population dynamics which fully correspond to the dynamics of their catches. This leads to the recognition of the fact that VPA results depend to a greater extent on the fishing intensity, and on the amount of effort fj exerted each year $j$, rather than on the initial abundance of yearclasses. This paper adjusts yearly catches Ci by the formula:

$$
\mathrm{Cj}^{\mathrm{cor}}=\mathrm{Cjfm} / \mathrm{fj}
$$

where fm is the mean annual effort for the period 1962-1982. Under this condition the catch of groups of the same age belonging to different yearclasses will depend primarily on their abundance at the outset of the year. The corrected cumulative catch of yearclasses for the entire period of their participation in the fishery from age 3 to age 15 (C $\left.\begin{array}{c}\text { cor } \\ 3-15\end{array}\right)$ correlates well with the juvenile count data at the age $2+$.

Examples of the use of such method for forecasting purpose are given.

## INTRODUCTION

Presently the most common methods of retrospective assessment of the fish stock are based on determination of the abundance of each year class through obtaining the sum of its catches for all the years of participation in the fishery. The longer (in terms of years), and the more intensively they were fished the more ample and accurate information on abundance will be. Ideal in this regard would evidently be the exemption that would leave no place for natural mortality. In this case the sum of yearly catches of a particular year class would equal its original abundance at the age of recruitment into the stock. But this possibility is only theoretical.

Nevertheless we can get a sufficiently accurate idea of the year classes whose age has not reached the limit yet, and of those fished for one or two years. This is possible by comparing the catches from the year class concerned with the catches of the same age groups from different year classes which have been fished in the same or similar conditions, primarily with an equal amount of fishing effort. If that is done, the yearly catch of the same age groups of different year classes will mainly depend on their abundance at the beginning of the year.

Comparison of catches from year classes exposed to the same effort can be used to assess the fished part of the stock, and to estimate TAC. Evidently this is more applicable to populations with long lifespans, for which the bulk of the annual yield is composed of year classes which have previously appeared in the fishery and for which recruitment is relatively a less significant.

However, forecast objectives also require data on the abundance of the new year classes recruiting into the fish stock. Their contribution to future catches can be estimated from the results of juvenile count survey.

This paper attempts to apply these provisions to Arcto-Norwegian cod.

## MATERIAL AND METHOD

The basic data for our assessments were taken from the materials of the Arctic Fishery Working Group for 1962-1982 (Anon,. 1980, 1981, 1982) which include the total volume of fishing effort in U.K. units, catch of cod by age groups, as well as year class abundance indices for cod aged $2+$ (individuals per one hour haul) obtained during juvenile groundfish count survey by PINRO vessels. Data from $1+$ and $2+$ age groups could extend the range of the forecasts but they are in fact less representative.

Judging by the analysis given by the Working Group Report for 1980, there exists a relationship between the catches of cod aged " $2+$ " per one hour haul $\left(J_{2}\right)$ and their absolute abundance by the beginning of the fourth year of life $\left(N_{3}\right)$ estimated by VPA. This relationship is described by the equation:

$$
\mathrm{N}_{3}=\sqrt{5616,58+32555,84 \mathrm{~J}_{2}}
$$

In Fig. 1 a great number of points deflect from the mean line of regression by $80-100 \%$. We are inclined to believe that one of the reasons for the great scattering of points is unrepresentative counts for some year classes at age $2+$. This is quite convincingly shown by the data on the contribution of individual year classes to the fishery, and the retrospective calculation of their abundance. Hence, the 1962 and 1969 year classes ( $J_{2}$ determined as 5,23 and 8,59 ) were probably underestimated. In catches, they showed themselves to be on the level of the rich year classes of 1971 and 1972 (their respective $J_{2}$ were 32,23 and 40,10 ).


Fig. 1. Deflection from the mean regression line $N_{3}=\sqrt{5616,58+32555,84 \mathrm{~J}_{2}}$.

Another important reason for the deflection of the points in a regression of $N_{3}$ on $J_{2}$ was a quite significant fluctuation of fishing effort over the years. A higher effort in some period results in a higher extraction of the year classes participating in the fishery. Therefore their cumulative catch $C_{3-15}$ turns out to be relatively higher as compared to the year classes which were fished less intensively.

It might appear that this should not influence the abundance of the year classes as measure by VPA with the use of differentiated rates of fishing mortality. However, the absolute correspondence of yearly variations $N_{3}$ (VPA) with the catches from the same year classes $C_{3-15}$ (see Fig.1) leads us to believe that the VPA results are more dependent on catch fluctuations than on the actual fluctuations of the stock. On the other hand it is known that catch is affected not only by stock size but also other factors, in particular volume of fishing effort.

To avoid the impact of yearly variations of effort (fj) on the catch from year classes, the actual annual catches ( $C j$ ) were corrected according to the value of the fishing effort for each year:

$$
\stackrel{\operatorname{cor}}{\mathrm{C}=\mathrm{Cjfm} / \mathrm{Fj}}
$$

where $f m$ is the mean value of fishing effort for 1962-1982 (equal to 1127 U.K. units). In other words, catch of the year $j$ decreased by as many times as the effort value of the same year $j$ exceeded the multiannual mean, and vice versa.

The values obtained $C_{j}^{\text {cor }}$ were further subdivided by ages (1) in accordance with the age composition of the catch specificed for the given year, which provided the correction of the catches by each age $\left(C_{j i}^{c o r}\right)$. The sum of all $C_{j i}^{c o r}$ belonging to one year class made up the value for its cumulative catch $C_{3-15}^{\text {cor }}$ for 13 years of the fishery (from age 3 to 15).

The procedure is of value because it provides a picture of what the catches from each year class would have been if the fishing effort throughout the period had been the same. The catches corrected in this way can now serve as indices of year class abundance since their values are not tied up to yearly fluctuations of effort but depend instead mostly upon the strength of year classes. What is more, these indices are more representative than $\mathrm{J}_{2}$ because of the much greater sampling basis.

## RESULTS

Catch forecast for different age groups of the same year class

Based on the correlated data on the cumulative catch of each year class Cor ${ }_{3-15}^{\text {cor }}$, and on the results of surveys of juvenile bottom cod age $2+\left(\mathrm{J}_{2}\right)$ a diagram was constructed (Fig. 2). An empirical regression equation was fitted which reflects the relationship between these two values:

$$
\begin{equation*}
C_{3-15}^{\operatorname{cor}}=\left(171,6+10,7 \mathrm{~J}_{2}\right) \quad\left(1-\mathrm{e}^{\left.-0,424 \mathrm{~J}_{2}\right)}\right. \tag{2}
\end{equation*}
$$

This equation enables us to use the juvenile count data for each year class in order to find the most probable level of yield of this year class (million fish), provided the average level of effort is maintained, rather than its assumed absolute abundance $\mathrm{N}_{3}$ as is usually done.


Fig. 2. Relation between index of abundance and correlated cumulative catch.

As an example, let us consider the 1959 year class. Its $\mathrm{J}_{2}$ is 16,4 based on the results of the survey and under formula (2) this gives about 350 million fish. Analysing the catch from year classes by ages (Table I.) we find that age group " 3 " usually makes up $4-9 \%$ (average $6,72 \%$ or 0,0672 ) of the total catch (excluding the atypical fishery of the 1970-1973 year classes). The most likely assumption therefore could be that of the 1959 year class considered, the catch of group "3" would be $350 \times 0,672=23,52$ million fish. We emphasize once again the reservation that this is true provided that the level of effort is the average, that is 1127 U.K. units in 1962. If the value of effort ( $f j$ ) is higher, $C_{3}^{c o r}$ has to be multiplied by $f j / f m$. Conversely, if it is lower than the average level (fm), $C_{3}^{\text {cor }}$ has to be decreased by fm/fj. Symbol^will mean the forecast values.

Likewise, we can forecast the catch from the yearclass at age " 4 " when we know the share of this age group in the total catch from the yearclass ( 0,212 in Table I). If we know from the experience of the previous years the most likely percentage of yield of the successive age groups, we can forecast their catch too. However, the reliability of forecasts based solely on these principles depends on the reliability of the $J_{2}$ estimates. If these estimates do not adequately reflect the strength of yearclasses, the forecasting error will increase with the increase of the proportion of successive age groups in the total catch.

Such a forecast has to be improved on an annual basis with the use of data on how this yearclass showed itself in the year's previous fishery. Hence, continuing to consider the 1959 year class we see that its actual catch for the first year of the fishery ( $\mathrm{C}_{3}^{\mathrm{cor}}$ ) in 1962 was $49,075 \mathrm{mln}$ fish. This gives $\hat{C}$ cor ${ }_{3-15}^{\text {cor }}$ $=49,075: 0,0672=730,3$ million fish. Then the catch of the group " 4 " forecast for 1963 comprising $21.1 \%$ of the total catch 0,212 will be on the level of $730,3 \times 0,212=154,8 \mathrm{million}$ fish. The actual $C_{4}^{\text {cor }}$ for 1963 was 128,915 million fish, which gives $\mathrm{c}_{3-14}^{\mathrm{cor}}=128,915: 0,202=608 \mathrm{million}$ fish. Now we have two estimates of $C_{3-15}^{c o r}$. One is 730 million fish for the catch of group " 3 ", the other is 608 mln fish for the catch of group " 4 ". Averaging these values we obtain $\hat{\mathrm{C}}_{3-15}^{\text {cor }}=669$ million fish which enables us to forecast the catch of group 5 for 1964 whose share is 0,2809 on the average. Then $\hat{C}_{5}^{\text {cor }}=669 \times 0,2809=188$ million fish. As we see, the forecast values correspond quite well with the actual ones. What is more, each successive year of fishery adds to the information on the exploited yearclass increasing the reliability of the forecast value $\hat{C} \hat{C}_{3-15}$, and hence of $\hat{C}_{j \mathrm{I}}^{\text {cor }}$.

Forecast of yearly catch with due regard to all the year classes participating in the fishery at one time

The forecast of the yearly catch includes elements of the above procedure. Its only distinctive feature is that we now have to
consider at the same time different age groups belonging to different yearclasses.

The year of 1972 can be taken as an example to describe the procedure of estimation. Fish from the 1957-1969 yearclasses participated in the fishery during that year. The only information about the 1969 yearclass in the year of the forecast (1971) comes from the results of juvenile survey. Its $\mathrm{J}_{2}=8,6$ means that the $\hat{C}$ cor $3-15$ of this yearclass by formula (2) will be 256,5 million fish, while the catch of group " 3 " will be $\hat{\mathrm{C}}_{3}^{\text {cor }}=$ $256,5 \times 0,0672=17,24$ with its middle share used in the total catch of the yearclass. $\lambda_{3}=0,0672$.

Regarding age group " 4 ", belonging to the 1968 yearclass, it is known that if the level of effort was average in 1971 it would have yielded a catch of 7,575 million fish at age "3", i.e. its $\hat{C}_{3-15}^{\text {cor }}=7,575 \times 0,0672=112,7$ million fish. We therefore can expect in $1972 \hat{\mathrm{C}}_{4}^{\text {cor }}=112,7 \times 0,212=24$ million fish.

As for age group "5", the data are more reliable. The year class to which it belongs (1967) was fished in 1970 and 1971 yielding $\hat{C}_{3-15}^{c o r}$ of 113,4 and 63,3 million fish respectively, the average being 88,3 million fish. This means that its $\hat{\mathrm{C}}_{5}^{\text {cor }}$ must be about $88,3 \times 0,2809=24,8$ million fish.

On the basis of three years' fishery the yearclass of 1966 can be assessed with still greater certainty. Three estimates are available for that year already: $\hat{C}_{3-15}^{\text {cor }}=36,25,54,16$ and 41,15. Using the average we obtain $\hat{\mathrm{C}}_{6}^{\mathrm{cor}^{-15}}=9$ million fish.

Other age groups belonging to older yearclasses are estimated in a similar way. A combined forecast estimate for 1972 is given in Table 2. The first column shows the yearclasses participating in the 1972 fishery. The second is their age, the third is the average shares which correspond to these ages in the total catch of the yearclass. Column 4 gives projected values of $\hat{C}_{3-15}^{\text {cor }}$. For the 1969 year class ( $k$ ) which is yet to participate in the fishery this value was obtained through $\mathrm{J}_{2}$
by formula (2): 256,5 million fish. For the following year class (k-1) using catch data at age 3 in 1971:

$$
\mathcal{C}_{(\mathrm{k}-1)}^{\mathrm{cor}}(3-1.5)=\underset{\mathrm{C}(\mathrm{kor}-1) 3: \lambda_{3}=7,575: 0,0672=112,723 \text { million fish } .}{\text { cor }}
$$

For the 1967 yearclass (age 5) data were used of its catch in 1970 and 1971:

$$
\begin{align*}
& \left.\underset{(k-2)}{\operatorname{cor}_{(k-15)}=\frac{1}{2}(C} \begin{array}{c}
\operatorname{cor} \\
(k-2) 3
\end{array}: \lambda_{3}+C_{(k-2) 4}^{\operatorname{cor}}: \lambda_{4}\right) \text { or }  \tag{3}\\
& \frac{1}{2}\left(\frac{7,621}{2,0672}+\frac{13,422}{0,212}\right)=88,35 \text { million fish }
\end{align*}
$$

The 1966 yearclass participating in the 1972 fishery at age 6 has the value of $\stackrel{\tilde{C}}{(\mathrm{cor}} \mathrm{c} 3)(3-15)=$

$$
\begin{align*}
& 1 / 3\left(C_{(k-3) 3}^{\operatorname{cor}}: \lambda_{3}+C(k-3) 4: \lambda_{4}+C\right.  \tag{4}\\
& 1 / 3\left(\frac{2,436}{0,0672}+\frac{11,483}{0,212}+\frac{11,559}{0,2809}\right)=43,855
\end{align*}
$$

Value $\hat{C} \underset{(k-10)(3-15)}{\operatorname{cor}}$ belonging to the 1959 yearclass (age 10) has 10 components which contain the entire information on the previous fishery from this year class.

For the sake of comparison of the predicted values column 5 shows the sum of catches by ages of the same year classes for their overall fishing period $\hat{\mathrm{C}}_{3-15}^{\mathrm{cor}}$. The next three columns show as follows: Column 6 - under the average multiannual level of effort; column 7 - under the actual effort of 1972 equal to 1097 U.K. units, column 8 - the actual catch of age groups by the Working Group data. Columns 9 and 10 show the relative deflection ( $\delta$ and $\gamma$ ) of the projected values $\hat{C}_{3-15}^{c o r}$ (column 4) and $\hat{C i}$ (column 7) from the actual $\hat{C}_{3-15}^{\operatorname{cor}}(\operatorname{column} 5)$ and $C_{R}$ (column 8) by expressions

$$
\delta=\left(\tilde{C}_{3-15}^{\operatorname{cor}}-\mathrm{C}_{3-15}^{\operatorname{cor}}\right) \text { and } \gamma=\frac{\left(\tilde{C}_{3} \mathrm{Cor}-\mathrm{CR}\right) 100 \%}{\mathrm{C}_{R}}
$$

The final stage of such a forecast must be the use of weights by each age group so that we could change over from numbers to the mass of expected catch. Values of column 7 should be
multiplied by weights corresponding to each age. The sum of the results will be the final figure for the catch forecast.

## DISCUSSION

A critical analysis of the described technique some possibilities for its improvement. Because of this the fact that the 1983 data for $J_{2}$ have not yet been received, we abandonned the estimation of the cod catch level for 1984, and then reduced our task to merely showing the principle of such forecasting.

As regards the stages which require improvement, the following may be pointed out.

1. For correction of yearly catches by effort it would be more justifiable to use non-linear dependence between these two values, rather than linear one. It is only for the first very rough consideration that directly proportional change of catch with effort can be assumed. The use of linear relationships is justified only at a particular interval.
2. With respect to those yearclasses which participated in the fishery for two years or more the appropriate value of $\hat{C} \begin{gathered}\text { cor } \\ 3-15\end{gathered}$ was found as the average of all the previous ones (see expressions 3 and 4 attributing equal weights to each of them). The results will probably be more accurate if the appropriate $\hat{\mathrm{C}}_{3-15}^{\text {cor }}$ is found as the weighted mean accounting for the share of each value which contributed to estimating $C_{i}^{\text {cor }}$.
3. The proportion of each age group in the total catch of the yearclass ( $\lambda i$ ), is assumed to be constant and independent of its abundance (column 3 in Table 2). The analysis of Table I shows that the contribution of equal age in different yearclasses has a great range of variation, and thus the share of the catch of younger ages is as a rule higher in strong yearclasses. This opens up three alternatives of specifying $\lambda i$. These are either finding an analogous year class (by $\mathrm{J}_{2}$ and by
$C_{i}^{\text {cor }}$ ); or fitting regression lines between $C_{i}^{c o r}$ and $\lambda i$; or introducing grades for $C_{i}^{\text {cor }}$ and corresponding grades for $\lambda i$.

The technique described enhances data requirements as regards the total international fishing effort of all countries which catch cod. It is implied by present catch statistics, that their age composition and juvenile counts are satisfactory. Essentially the $C_{i}^{\text {cor }}$ received are close to the generally accepted notion of "catch per unit effort" regardless of the fact that they are expressed by absolute rather than by relative values. The reliability of the results obtained depends therefore to a great extent on the reliability of results of international effort estimation. For such purposes it appears most reasonable to apply the fishing effort estimates obtained by A.I. Treschev's method (1978), for which we, unfortunately, do not yet possess sufficient multiannual data (unlike the ones that are available in U.K. units).

It can be seen that the technique presented fully allows for its various modifications, and does not claim to be anything complete. It appears, however, that even in the form explained here, the technique can be used for estimating TAC for cod for 1984 after the autumn juvenile survey data becomes available. In future, all the stages of estimation are intended to be formalized, and an appropriate computer program will be made.

## REFERENCES

Anon., 1980. Report of the Arctic Fisheries Working Group, ICES, C.M. 1980/G:12
Anon., 1981. Report of the Arctic Fisheries Working Group, ICES, C.M. $1981 / \mathrm{G}: 2$
Anon., 1982. Report of the Arctic Fisheries Working Group, ICES, C.M. 1982 /Assess :I
Treschev A.I. Application of the fished volume method for measuring fishing effort. Cooperative research Reports $N .79$, ICES, 1978.

# A METHOD OF ESTIMATING THE NATURAL MORTALITY RATES OF FISH AT DIFFERENT AGES <br> (EXEMPLIFIED BY THE ARCTO-NORWEGIAN COD STOCK) 

by
V.L. Tretyak PINRO, Murmansk, USSR


#### Abstract

The change in rates of fish natural mortality with age is presented by a convex downward one-minimum function tending to infinity when the age tends to the maximum possible of fish living under actual ecological conditions. A method of estimating this function's parameters which has been already applied to Arcto-Norwegian cod is suggested. Rates of natural mortality of cod at ages 3 to 16 are presented. The results are discussed, compared with those available and may be used in analysing the dynamics of Arcto-Norwegian cod abundance.


## INTRODUCTION

A quantitative estimate of the fish mortality indices has been possible since the beginning of the century when ichthyologists of various countries fishing intensively for flounder and other species in the North Sea obtained age samples, allowing the primary concept of the distribution of a commercial fish stock by age groups. The first investigator to formulate and apply a quantitative method of estimating the total indices of natural mortality and fishing mortality to the North Sea flounder was a Russian scientist Baranov (1918). He introduced a notion of
elementary diminution which theoretically considers a decrease in the year class abundance caused by any of the following: fishery, predation, parasites and disease, lack of food, change in abiotic conditions, natural metabolic disorders occurring, for instance, with age and other reasons. Baranov considered


Fig. 1. Catch curve for Arcto-Norwegi.an cod.
that the catch curve (Fig. I) in the interval [ $t_{c}^{\prime}, t_{\lambda}$ ] (where $t_{C}^{\prime}$ is the age at which all the fish are subjected to fishery, $t_{\lambda}$ is the maximum age of fish in the commercial stock diminishes and is close to a straight catch curve. He explained this tendency of the catch curve as due to stabilized intensive fishery with constant total fishing effort and exploitation coefficient and, also, a steady state of the commercial stock abundance.

The notion of elementary diminution and those important concepts presented an original achievement in applied ichthyology. The existence of a relationship between the fish stock and the catch and fishery intensity was demonstrated, and scientific bases for tacking the problem of fishery regulation have been elaborated. But those theses have inevitably brought Baranov to conclude that the rate of natural mortality (M) of fish in
each age group is constant, that it is constant over a large interval of fishery $\left[T_{0}, T_{I}\right]$ and that there is an inverse relationship between the fish maximum age and the fishery intensity.

Nevertheless, the experience of commercial fisheries in general and that of the Arcto-Norwegian cod in particular shows that it is impossible to choose such an interval of time in which the fishery may be considered to be stabilized. The shape of the catch curve described by Baranov may have another cause, as stabilization is not the only one possible. It was determined from simple mathematical models (Beverton, Holt, 1956; Ricker, 1958) that the linearity or near linearity of the catch curve in the interval $\left[t_{c}^{\prime}, t_{\lambda}\right.$ ] may be a result of the decreased accessibility to fishery with increasing age of fish. But when the rate of fishing mortality (F) increases with the age of fish, the catch curve in the interval considered is non-linear. If there exist considerable fluctuations in the fishery intensity or cyclic variations in recruitment abundance, the catch curve may have one or several points of inflexion (Thompson, Herrington, 1930; Bajkov, 1933; Jensen, 1939; Ricker, 1945, 1949, 1958; Fry, 1949; Kennedy, 1953, 1954; Rollefsen, 1954; Tester, l955; Gulland, 1968).

Modern ecology (Vilee, Dethier, 1974; Odum, 1975) recognizes five theoretically possible types of survival curves (Fig. 2). It is hypothesized that during the time from egg to mean age of mature fish ( $\bar{t}_{S}$ ) the survival curve is concave downward and there after it is convex upward in successive stages (Nikolsky, 1974; Sokolovsky, 1973). Accordingly, the survival curve of cod is close to the fourth type described in Fig. 2.

The results of age analysis of unexploited or nearly unexploited species give an idea of the survival curve behaviour only in the interval $\left[t_{c}^{\prime}, t_{\lambda}\right]$. The notion of the survival curve shape in the interval $\left[t_{r}, t_{C}^{\prime}\right]$ (where $t_{r}$ is the age of recruitment) may be obtained only when the abundance of age groups belonging to this interval is known.


Fig. 2. Types of survival curves (I - V)
$T_{p}$ - per cent of maximum possible lifetime;
lnn - abundance index.



Fig. 3. Catch curves for Newfoundland capelin (A), Barents Sea polar cod (B), blue whiting (C)
and beaked redfish of the Bear Island Spitsbergen population (D) in the first years of exploitation.

Catch curves for some fish species from the NW and NE Atlantic are available (Fig. 3) and present the age composition of each of these species taken during the first years of fishery. In order to exclude fluctuations of year class abundance the age samples from every commercial stock were combined for a series of years during which the fishery was not intensive, and also smoothed by a rumning average of three. These curves along with catch curves for a number of freshwater fish populations (Ricker, 1958) indicate that beginning from a certain age t $\geq_{C}^{\prime}$ the approximated survival curves are convex upward and diminish. This means that in the interval $\left[t_{C}^{\prime}, t_{\lambda}\right]$ there is an age beginning from which the rate of natural mortality of those fish populations increases.

In 1961 under the guidance of E.B. Burmakin a unique experiment was carried out (Rudenko, 1967). The eutrophic Somino Lake (Pskov Region) with an area of 21.4 hectares was poisoned with the pesticide polychlorpinene. Three years prior to this a traditional intensive fishery in the Lake had been closed. Straight-forward calculations produce data on the abundance of age groups of ll fish species dwelling in the lake beginning from age l+. The analysis of the age composition of those species indicates that survival curves in the interval [1+,3+] are convex downward and decrease, which means that the rate of natural mortality is reduced in this interval.

Thus, both Fig. 3 and data from the literature show us that in the interval $\left[t_{r}, t_{\lambda}\right.$ ] the approximated survival curves for some unexploited or nearly unexploited fish species may look like a monotonic decreasing function having, at least, one inflexion point. Therefore, the natural mortality rate may be expressed by an age function having one (positive) minimum and becoming infinite at $t$ tending to age $t_{e}$ which, in case of unexploitation, corresponds to the maximum possible lifetime of fish under actual ecological conditions. A similar conclusion can be found in papers by Gulimov et al. (1977) and Poluektov et al.(1980). Three such functions are given in Fig. 4 where the results of graphic approximation of $M$ obtained for two species


Fig. 4. Natural mortality rates of redfish from Chernyavskoe (1), Demenets Lakes (2) and rudd from Somino Lake (3).
of fish after the total lake chemical treatment are shown. The results of calculations and graphs were taken from Blinov's paper (1979). The $M$ for fish of each age was determined by Baranov's formula (1918):

$$
M_{t}=\ln N_{t}-\ln N_{t+1},
$$

where $N_{t}$ is fish abundance at age t. Fig. 4 shows that this function may have either a discrete or wide minimum range.

There have been repeated attempts to explain and describe changes in natural mortality with age.

Thus, developing Baranov's thesis (1981), Severtsov (1941) made some conclusions important to the theoretical bases of the population abundance dynamics:

- lifespan is species specific;
- a form of the population dynamics as well as its morphophysiological characteristics are representative of a species' lifetime;
- the index of natural mortality is higher for young fish than that for adults;
- natural mortality is lower for species with a long lifetime than for those with a short lifetime.

The penultimate statement may be further specified now: the index of natural mortality is higher for young and old fish than that for fish of mean age groups.

Nikolsky (1974) considers that survival curves and maximum possible lifespan of fish change under the action of ecological factors within insignificant limits and are always species specific.

Based on these postulates, Tyurin (1972) regards the index of natural mortality as "specific, historical, inheritable and, thus, rather conservative" and suggests assessing it at each point in the interval $\left[I, t_{\lambda}\right]$. The principles of the method consist in Baranov's formulated decrease in the number of fish in the commercial stock from one age group to another. It follows the law of decreasing geometrical progression with a denominator $e^{-Z}$ where $Z=M+F$ (the total mortality rate), and in inverse relationship between the maximum possible theoretical lifetime of fish and fishing intensity.

However, the concept of the constancy of $M, F$ and $Z$ in the interval $\left[t_{c}^{\prime}, t_{\lambda}\right]$ is just the first approximation to reality. The long-term intensive fishery not only reduces age $t_{\lambda}$, but also minimizes the action of density-dependent factors and limits the fish abundance. That's why, under conditions of intensive fishing, $t_{e}$ will increase rather than decrease and will tend to the maximum lifetime which is physiologically possible under ideal conditions when the action of ecological factors limiting the fish abundance is equal to zero.

Regardless of shortcomings, Tyurin's method is widely used by the Soviet ichthyologists. Borisov (1976, 1978) used it for estimating the rate of mortality $\psi_{M}$ for natural reasons in Arcto-Norwegian cod at ages 5 to 14 where

$$
\psi_{M}=\frac{M}{F+M}[I-\exp (-(F+M))]
$$

He concluded that the long-term intensive fishery leads to the increase of $\psi_{M}$ in cod of these ages.

Sokolovsky (1973) suggested approximating the variation in fish abundance during the interval from egg to the age at onset of maturity by the relationship:

$$
N_{t}=A t^{-n}
$$

The difficulty of using this equation for cod is in estimation of $A$ and $n$. They may only be obtained after estimating the year class abundance in at least two different moments over a given period of time.

The method of fish mortality index estimation in inland waters suggested by Gulin (1967, 1971) is based on the determination of differences between the age composition of a commercial stock and that of a catch. Under conditions of marine fishery it is inapplicable as yet.

The possibility of estimating the natural mortality rate in Arcto-Norwegian cod at different ages was first discussed by Borisov and Shatunovsky (1973). The authors suggested a physiological method of $\psi_{M}$ estimation in cod at ages 7 to l5. The fish with a higher moisture content index were supposed to be exhausted and suceptible to higher natural mortality due to the action of biotic and abiotic factors. The exhaustion was characterized by an energetic index value inversely proportional to the ratio of dry residue/water. $\psi_{M}$ was assumed to be directly proportional to the number of exhausted fish in each age group. The authors of the physiological method emphasized that, since
it excludes age composition of the commercial stock, $\psi_{M}$ is overestimated and the curve approximating its value indicates only a tendency towards changing of $\psi_{M}$ with cod age. It was also noticed that cod energetic index started to decrease in 9-year-olds meaning that the fish had the minimum $\psi_{M}$ at age 9.

A theoretically "true" description of changing $\psi_{M}$ with fish age was suggested by Blinov (1977). Using the formalism of automatic regulation theory he analysed the functioning of the model of "elimination - potential survival" and presented a general view of the function

$$
\psi_{M}(t)=1-A[\exp (-B t)-\exp (C t)]
$$

It contains three factors, the determination of which is possible given reliable estimates of $\psi_{M}$ for fish in at least three age groups. Unfortunately, this equation cannot be adapted to numerous ichthyological data due to lack of the above estimates in most species. Using $\psi_{M}$ values obtained for Arcto-Norwegian cod at ages 8,12 and 16 by physiological method, Blinov estimated the factors of $\Psi_{M}(t)$ function and was able to calculate its values for cod of all age groups. Since overestimated $\psi_{M}$ values were used to determine the factors, it may be assumed that the calculated $\psi_{M}(t)$ values are also not free of error.

To obtain the empirical relationships suggested by Gulin and Rudenko (1973) and Bulgakova and Efimov (1982), reliable estimates of the natural mortality index of 2 to 3-year-old fish are also needed. Another shortcoming of these relationships is that they describe changes in the natural mortality rate beginning from age $t \geq t_{c}^{\prime}$. This shortcoming is particularly undesirable for the Arcto-Norwegian commercial cod stock since the fish of some age groups in the interval [ $t_{r}, t_{C}^{\prime}$ ] account for a considerable portion of the catch taken in the southern Barents Sea (Fig. 1).

While determining the Arcto-Norwegian cod stock abundance the Working Group used a mean natural mortality for ages 3 to 16
$(\bar{M})$ equal to 0.20 . The $\psi_{M}$ estimate corresponding to this $\bar{M}$ value differs from that of Borisov (1976) and Blinov (1977) more than by 100\%. Estimates of $\psi_{M}$ also differed markedly in the data of these investigators.

Let us discuss one possible formal description of change in natural mortality with fish age.

## METHOD

Let us assume that for unexploited populations the change in the natural mortality rate of fish in each yearclass may be presented in the interval $\left[t_{r}, t_{e}\right]$ by the function

$$
\begin{equation*}
M(t)=a\left[-t-\left(t_{e}-\bar{t}_{s}\right) \ln \left(t_{e}-t\right)\right]+b \tag{1}
\end{equation*}
$$

This function is defintte, continuous and has a single stationary point $\bar{E}_{S}$ in the considered interval; $\lim M(t)=\infty$, with $a \geq 0 \mathrm{~min} M(t)=M\left(\bar{t}_{S}\right)$. Assuming that the function minimum $M(t)$ conforms with the mean age of mature fish (Nikolsky, 1974; Sokolovsky, 1973), $\bar{t}_{s}$ and $t_{e}$ have a concrete biological meaning. $a$ and $b$ have no biological meaning.

The instantaneous rate of yearclass abundance variation is expressed by equation

$$
\frac{d N}{d t}=-M(t) \cdot N
$$

Having calculated it we shall obtain the relative abundance of the yearclass at any given age $t_{r} \leq t<t_{e}$ :

$$
\begin{aligned}
& \frac{N(t)}{N\left(t_{r}\right)}=\exp \left\{\frac{1}{2} a\left(t^{2}-t_{r}^{2}\right)-b\left(t-t_{r}\right)-\right. \\
& \left.a\left(t_{e}-\bar{t}_{S}\right)\left[\left(t_{e}-t\right) \ln \left(t_{e}-t\right)-\left(t_{e}-t_{r}\right) \ln \left(t_{e}-t_{r}\right)+\left(t-t_{r}\right)\right]\right\}
\end{aligned}
$$

For unexploited yearclasses we shall write the relative abundance
of the year class at age $t$ in the form

$$
\begin{equation*}
\frac{P(t)}{N\left(t_{r}\right)}=N(t) \cdot w(t) \tag{2}
\end{equation*}
$$

where $w(t)=a_{1}{ }^{L_{\infty}}{ }^{b_{1}}\left\{1-\exp \left[-K\left(t-t_{0}\right)\right]\right\}^{b_{1}}$ which is the von Bertalanffy equation characterizing the weight increase of fish; $\mathrm{L}_{\infty}$, K and $t_{0}$-parameters of equation; $a_{1}$ and $b_{1}$ - parameters of the allometric growth equation.

From the first two conclusions of Severtsov and Nikolsky and Tyurin's theory of the conservatism of natural mortality index, we can assume that the form of the $M(t)$ function also will not change for heavily fished stocks. Merely its parameters will change, probably according to the intensity and pattern of fishery and other ecological conditions. The action of different factors which depend on density and limit the fish abundance will grow weaker, so the natural mortality of fish will decrease (Bukhanevich, 1973; Odum, 1975, Sergeev, 1979; Pianka, 1981). This will lead to the increase in $t_{e}$ which will tend in this case to age $t_{p}$ equal to the maximum possible physiological lifetime. For the first approximation $t_{e}$ may be assumed to be constant and it is usually known. $\bar{t}_{\text {s }}$ will decrease. It may be easily determined by the results of fishery and biological statistics.

To estimate $a$ and $b$ two different values with known $M(t)$ should be available in the interval [ $t_{r}, t_{e}$ ]. This requirement is fulfilled in exceptionally rare cases. Therefore, let us assume that, under conditions of exploitation so intensive that the area contains few fish older than $t_{\lambda}^{\prime \prime}$ (where $t_{\lambda}<t_{\lambda}<t_{e}$ ), there is an age $t_{m}$ or an interval $\left[t_{1}, t_{2}\right]$ for which the natural mortality presumed to be constant may be estimated by known methods (Bukhanevich, 1973; Rikhter and Efanov, 1977; Gulin and Rudenko, 1975; Dorovskikh, 1981; Silliman, 1943; Beverton and Holt, 1957; Paloheimo, 1958; Watt, 1959; Pauly, 1978, 1980; Fridgeirsson, l979; Carscadden and Miller, 1980). Usually the ratio $t_{C}^{\prime} \leq t_{1} \leq t_{m} \leq t_{2} \leq t_{\lambda}$ and the equation $N\left(t_{\lambda}^{\prime \prime}+l\right)=0$ are possible.

Let us assume further that fish removed during the fishery will die only for natural reasons in accordance with $M(t)$ function. In this case equation $N\left(t_{\lambda}^{\prime \prime}+1\right)=0$ is impossible since some fish from this category will live to age $t_{e}$. We shall assume that the abundance of this cohort at ages $t_{e}-1$, $t_{e}$ and $t_{e}+1$ meets inequalities

$$
\begin{align*}
& N\left(t_{e}-1\right)>1 ;  \tag{3}\\
& N\left(t_{e}\right) \geq 1 ;  \tag{4}\\
& N\left(t_{e}+1\right)<1 ; \tag{5}
\end{align*}
$$

At age $t_{e}^{-1}$ the abundance of these fish will be equal to

$$
\begin{equation*}
\sum_{\tau=t_{r}}^{t_{\tau}^{\prime \prime}} c_{\tau} \exp \left\{-\int_{\tau}^{t} e^{-1} M(t) d t\right\} \tag{6}
\end{equation*}
$$

where $c_{\tau}$ is number of specimens caught at age $\tau$ ( $\tau$ is equal to sum of $t$ and coincides with the beginning of a given calendar year). The fish which, under exploited conditions, have died for natural reasons will live now only to age $t_{\lambda}^{\prime}<t_{\lambda}^{\prime \prime}$.

Equation (6) contains two unknown parameters $a$ and $b$ which should meet the requirements that $a>0$ and $m i n ~ M(t)>0$, inequalities (3-5) occur and function (2) has one minimum or maximum.

If the natural mortality rate is known at point $t_{m}$ (let us denote it as $M_{t m}$ ), taking into account (1) we shall find that

$$
\begin{equation*}
b=M_{t m}+a\left[t_{m}+\left(t_{e}-\bar{t}_{S}\right) \ln \left(t_{e}-t_{m}\right)\right] \tag{7}
\end{equation*}
$$

If it is known only in the interval $\left[t_{1}, t_{2}\right]$ (in this case we shall denote it as $\bar{M}$ ), then having determined parameter $b$ from equality

$$
\begin{equation*}
\bar{M}=\frac{1}{t_{2}-t_{1}} \int_{t_{1}}^{t_{2}} M(t) d t \tag{8}
\end{equation*}
$$

we shall have

$$
\begin{align*}
& b=\bar{M}+\frac{a}{2}\left(t_{2}+t_{1}\right)-a \frac{t_{e}-\bar{t}}{t_{2}}\left[\left(t_{e}-t_{2}\right) \ln \left(t_{e}-t_{2}\right)-\right. \\
& \left.\left(t_{e}-t_{1}\right) \ln \left(t_{e}-t_{1}\right)+\left(t_{2}-t_{1}\right)\right] \tag{9}
\end{align*}
$$

Estimates $\mathrm{M}_{\text {tm }}$ and $\overline{\mathrm{M}}$ are supposed to be unbiased.

In the formula

$$
\mu=\frac{1}{t_{e}^{-t_{r}}-1} \int_{t_{r}}^{t} e-l_{M(t)} d t
$$

where $\mu$ is mean value of the natural mortality rate in the interval $t_{r}$ to $t_{e-1}$, we shall substitute $b$ for right parts of equations (7) and (9) and have: in the first case;

$$
a=\frac{\mu-M_{t m}}{t_{m}+\left(t_{e}-\bar{t}_{s}\right) \ln \left(t_{e}-t_{n}\right)-0,5\left(t_{e}+t_{r}-1\right)-\frac{\left(t_{e}-\bar{t}_{s}\right)\left(t_{e}-t_{r}\right) \ln \left(t_{e}-t_{r}\right)}{t_{e}-t_{r}-1}}, \quad \text { (10) }
$$

and in the second;

$$
a=\frac{u-\bar{M}}{\frac{t_{2}+t_{1}}{2}-\frac{t_{e}-\bar{t}_{s}}{t_{2}-t_{1}}\left[\left(t_{e}-t_{2}\right) \ln \left(t_{e}-t_{2}\right)-\left(t_{e^{-t_{1}}}\right) \ln \left(t_{e}-t_{1}\right)+\left(t_{2}-t_{1}\right)\right]}
$$

1
$\frac{t^{+t_{r}}-1}{2}-\frac{t_{e} e^{-\bar{t}}}{t_{e} t_{r}}\left[\left(t_{e}-t_{r}\right) \ln \left(t_{e}-t_{r}\right)-\left(t_{e}-t_{r}-1\right)\right]$
Believing that $M(t)=$ const= $\mu$ we shall find that the year class biomass will be maximum at age $t_{3}$ if

$$
b_{1} K \exp \left[-K\left(t_{3}-t_{0}\right)\right]-\mu\left\{1-\exp \left[-K\left(t_{3}-t_{0}\right)\right]\right\}=0
$$

whence it follows that

$$
\mu=\frac{b_{1} k}{\exp \left[k\left(t_{3}-t_{0}\right)\right]-1}
$$

In formulae (10) and (11) we shall substitute $\mu$ for the right part of the last equality and having applied the scanning method (Rastrigin, 1974) with $t_{3}$ specified we shall easily determine parameters $a$ and $b$ meeting all the necessary requirements. If it happens that there are some pairs of $a$ and $b$ meeting requirements (3-5) we shall choose a pair where $N\left(t_{e}-1\right)$ is maximum. From the above, and the assumption that for both non-exploitation and intensive exploitation the maximum possible lifetime of fish is the same, we shall obtain a reliable upper estimate of parameters $a$ and $b$.

In the first years of exploitation when the number of fish caught may be negligible, there are two intervals $\left[t_{1}, t_{2}\right]$ and [ $\left.t_{1}^{\prime}, t_{2}^{\prime}\right]$ on the catch curve lasting a year or more for which the natural mortality rate may be estimated by Baranov's method (1918). If in the first interval the natural mortality rate is equal to $\bar{M}$ and in the second to $\bar{M}^{\prime}$, then solving the two equations:

$$
\begin{aligned}
& \bar{M}=\frac{1}{t_{2}-t_{1}} \int_{t_{1}}^{t_{1}} M(t) d t \\
& \bar{M}^{\prime}=\frac{1}{t_{2}^{\prime-t_{1}^{\prime}}} \int_{t_{1}^{\prime}}^{t_{2}^{\prime}} M(t) d t
\end{aligned}
$$

we shall find that
$a=\frac{\bar{M}-\bar{M} \cdot}{\frac{t_{2}^{\prime}-t_{2}-t_{1}+t_{1}}{2}+\frac{t_{e}-\bar{t}}{t_{2}-t_{1}}\left[\left(t_{e}-t_{2}\right) \ln \left(t_{e}-t_{2}\right)-\left(t_{e}-t_{1}\right) \ln \left(t_{e}-t_{1}\right)+\left(t_{e}-t_{1}\right)\right]}$ 1
$\overline{t_{e}-\bar{t}_{s}}\left[\left(t_{e}-t_{2}^{\prime}\right) \ln \left(t_{e}-t_{2}^{\prime}\right)-\left(t_{e}-t_{1}^{\prime}\right) \ln \left(t_{e}-t_{1}^{\prime}\right)+\left(t_{2}^{\prime}-t_{1}^{\prime}\right)\right]$

In this case parameter $b$ is calculated from equation (9).

Thus, if it is known a priori that the fishing mortality rate may be ignored the parameters $a$ and $b$ can be estimated for the
function $M(t)$ without data on the number of fish caught at each age. In this case all the necessary requirements mentioned above should be fulfilled.

Theoretically the method allows estimation of the natural mortality of each yearclass of fish. Unfortunately, we cannot determine the mean age of mature cod for each separate year class, hence parameter $\bar{t}_{s}$ is assumed to be the same for all considered yearclasses. According to data of numerous Soviet and other researchers (Marti, 196I; Garrod, 1967; Mankevich, 1965, 1966, 1967, 1970, 1972, 1973; Rollefsen, 1954; Sætersdal, Hylen, 1959; Beverton, 1960; Hylen, $1965 \mathrm{a}, \mathrm{b}$ ) the mean value of $\bar{t}_{s}$ for 1946 to 1978 is equal to 9 years. This parameter tends to decrease with time (Fig. 5).


> Fig. 5. Arithmetic mean of $\bar{t}_{S}$ by 5 -year-periods: $x=1$ pertains to $1946-1950 ; x=2$ pertains to $1951-1955$ and so on.

According to Nikolsky (1974) $t_{e}$ is assumed to be equal to 30 years. It seems to be the most probable value of $t_{e}$ since the largest cod specimen of all known at present (Suvorov, 1948; Svetovidov, 1948; Babayan, 1978) is 169 cm long. According to
the von Bertalanffy equation

$$
I(t)=L_{\infty}\left[1-e^{K\left(t-t_{0}\right)}\right]
$$

(parameters of which are obtained by Table 1 data using the method of Tomlinson and Abramson (1961) and have values: $L_{\infty}$ $217 \mathrm{~cm}, \mathrm{~K}-0.048, t_{0}-(-1.005)$ ) cod attain this length at $t=30.4$ years.

A fairly reliable estimate of natural mortality rate is obtainable for 10 to ll-year-old cod. It is achieved by the method of Beverton and Holt in Watt's modification (Watt, l959) according to data of the ICES Working Group on the number of cod of the 1936 to 1958 yearclasses caught in the Barents and Norwegian Seas at ages 10 and older, and also from data on total annual fishing effort for 1946 to 1968 (Tretyak, 1976). This estimate pertains to the middle of a two-year interval, therefore $t_{m}$ is assumed to be equal to 11 years. The number of specimens caught at age $\tau$ are in the interval [ $t_{r}, t_{\lambda}^{\prime \prime}$ ] where $t_{\lambda}^{\prime \prime}=20$ and is assumed to be the mean for the same period (Table l). According to the calculations $M\left(t_{m}\right)=0.09$. Parameters of the allometric growth equation are determined from Table 1 data by the least squares method and have the values: $\mathrm{a}_{1}-0.688 \cdot 10^{-5}, \mathrm{~b}_{1}-$
3.069. Parameters $a$ and $b$ are calculated according to the routine compiled for computer "Minsk-32" in "FORTRAN" and are equal to 0.105414 and 7.76761 respectively. From the assumption of constancy of $M\left(t_{m}\right)$ and constancy of age composition of fish caught $C_{\tau}$ and parameters $\bar{t}_{S}, L \infty, K, t_{0}, a_{1}$ and $b_{1}$, we shall believe that under conditions of modern intensive exploitation the function (1) for all considered cod yearclasses can be written in the form

$$
M(t)=0.105414[-t-21 \ln (30-t)]+7.76761 .
$$

Its graph is presented in Fig. 6.

Table 1. Mean length ( $\overline{1}$ ), mean weight $(\bar{W})$ and mean number ( $\overline{\mathrm{C}}$ ) of cod caught at different age in 1946 to 1968.

| $\tau, y r s$ | $\bar{I}, \mathrm{~cm}$ | $\overline{\mathrm{w}}, \mathrm{kg}$ | $\overline{\mathrm{c}},\left(\times 10^{-3}\right)$ |
| :---: | :---: | :---: | :---: |
| 1 | 20.8 | 0.07 |  |
| 2 | 30.6 | 0.27 |  |
| 3 | 38.0 | 0.52 | 20.621 |
| 4 | 44.7 | 0.83 | 77574 |
| 5 | 52.2 | 1.28 | 99152 |
| 6 | 60.6 | 1.99 | 75054 |
| 7 | 69.0 | 2.87 | 43849 |
| 8 | 77.3 | 4.03 | 22845 |
| 9 | 84.4 | 5.41 | 15272 |
| 10 | 90.3 | 6.63 | 9606 |
| 11 | 96.6 | 8.43 | 6383 |
| 12 | 101.8 | 9.49 | 2895 |
| 13 | 107.8 | 13.76 | 1685 |
| 14 |  |  | 909 |
| 15 |  |  | 711 |
| 16 |  |  | 255 |
| 17 |  |  | 169 |
| 18 |  |  | 72 |
| 19 |  |  | 35 |
| 20 |  |  |  |

The mean value of the natural mortality rate ( $\mu_{1}$ ) in any interval of the fish life from $t_{r}$ to $t_{e-1}$ may be derived from the formula

$$
\mu_{1}=\frac{1}{t_{5}-t_{4}} \int_{t_{4}}^{t_{M}} M(t) d t
$$

where $t_{4}$ and $t_{5}$ are limits of the interval. For instance, in the interval from 3 to 16 years $\mu_{1}=0.120$.


Fig. 6. Change in natural mortality rate of Arcto-Norwegian cod with age.

## DISCUSSION

The calculated $\mu_{1}=0.120$ is 1.7 times less than the corresponding estimate adopted by the ICES Working Group. The $\psi_{M}$ index, obtained from our data excluding the fishing mortality rate and hence slightly overestimated (Table 2), was equal to $11 \%$ in the interval from 3 to 16 years. This was determined earlier for cod of middle age groups (Ponomarenko, 1969) and was almost 4 times less than that we obtained from Blinov's data (1977). Values of $\psi_{M}$ obtained from our data and from those of Borisov (1976) and Blinov (1977) differed notably especially for fish of older age groups (Table 2).

It follows from Blinov's paper (1977) that Arcto-Norwegian cod have $\psi_{M}$ minimum at age 5. At age 8 and older the index of their natural mortality sometimes exceeds that obtained from our data. Assuming that cod natural mortality agrees with the $\psi_{M}(t)$ function it appears that the maximum possible ecological age of cod will be slightly higher than 35 years and abundance

Table 2. Indices of cod natural mortality according to our data and to the results obtained by Borisov (1976) and Blinov (1977).

| Age, years | Indices of cod natural mortality by our data for 1946-1979 |  |  | $\psi_{\mathrm{M}}$ parameters obtained by Borisov (1976) in different periods of fishery |  |  |  |  | $\psi_{M}$ parameter obtained by Blinov (1977) for 1971 and 1972 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | M ( t ) | $\mu_{1}$ | $\psi_{M}$ | 1946-195 | 1-19 | 6-19 | 1-196 | 6-197 |  |
| 3 | 0.155 | 0.144 | 0.14 |  |  |  |  |  | 0.21 |
| 4 | 0.134 | 0.124 | 0.13 |  |  |  |  |  | 0.08 |
| 5 | 0.115 | 0.107 | 0.11 |  |  | 0.16 | 0.14 | 0.13 | 0.04 |
| 6 | 0.100 | 0.094 | 0.10 | 0.10 | 0.13 | 0.13 | 0.12 | 0.12 | 0.07 |
| 7 | 0.089 | 0.085 | 0.09 | 0.08 | 0.11 | 0.12 | 0.12 | 0.12 | 0.13 |
| 8 | 0.082 | 0.080 | 0.08 | 0.09 | 0.11 | 0.12 | 0.11 | 0.10 | 0.20 |
| 9 | 0.079 | 0.080 | 0.08 | 0.08 | 0.12 | 0.13 | 0.12 | 0.10 | 0.29 |
| 10 | 0.082 | 0.085 | 0.08 | 0.10 | 0.12 | 0.13 | 0.13 | 0.11 | 0.37 |
| 11 | 0.090 | 0.097 | 0.09 | 0.10 | 0.12 | 0.15 | 0.16 | 0.16 | 0.45 |
| 12 | 0.104 | 0.114 | 0.10 | 0.13 | 0.14 | 0.19 | 0.24 | 0.22 | 0.53 |
| 13 | 0.125 | 0.134 | 0.12 | 0.19 | 0.20 | 0.26 | 0.26 | 0.30 | 0.59 |
| 14 | 0.154 | 0.172 | 0.14 | 0.26 | 0.24 | 0.35 |  |  | 0.65 |
| 15 | 0.192 | 0.214 | 0.17 |  |  |  |  |  | 0.71 |
| 16 | 0.238 |  |  |  |  |  |  |  |  |

at age 3 will be greater than $0.7 \cdot 10^{27}$, while function (2) will have one maximum at age 6 . These data show that the natural mortality of cod at age 8 and older, obtained by the index of moisture content and used by Blinov for estimating the $\psi_{M}(t)$ function factors, is much overestimated. Values of $\psi_{M}$ index calculated by Blinov for most age groups are also much overestimated. As for the $\psi_{M}(t)$ minimum it is difficult to believe that it occurs at age 5 since "the tendency towards a decrease of energetic index becomes apparent in 9-year-old fish" (Borisov, Shatunovsky, 1973).

According to Borisov's data (1976) the age at which cod $\psi_{M}$ reaches minimum is just $1-2$ years younger than the mean age of mature fish mentioned above (Table 2). For cod at ages 5 to 10 the $\psi_{\mathrm{M}}$ estimates are similar to those obtained from our data while at age 11 and older they exceed ours considerably and the rate of their increase is also higher (Fig. 7).


Fig. 7. Change in $\psi_{M}$ parameter with cod age according to data by Blinov (curve 1), our data (curve 2), and data by Borisov for 1966-1972 (curve 3).

The results obtained by Borisov do not agree with Ricker's data (1970) concerning the variation of the natural mortality rate for fish aged 15 to 20 (within 0.2-0.5) . Borisov (1978) explains such a variation of natural mortality rate by the presence in each yearclass of cod (as well as for most other species) of groups of early, middle and late maturing fish. According to this hypothesis each group consists of specimens with a certain specific genotype. Under conditions of intensive exploitation late maturing specimens have little chance of reaching the first or successive spawning periods. The abundance of this fish group decreases so that their reproductive contribution approaches zero while that of early and middle maturing fish with a shorter lifetime and, consequently with a higher rate of natural mortality, increases. These fish have an advantage in the formation of successive yearclasses and in the creation of the spawning stock gene pool.

If it is assumed that there are three groups of spawners which become mature at an early, middle and late age, then one should expect that an intensive exploitation with its selective effects would have caused an increase in the portion of mature fish, not only when analysed by age, but first of all by size. However, it does not occur in practice. The investigations carried out by V.P. Ponomarenko, I.Ya. Ponomarenko and Yaragina (Ponomarenko, Ponomarenko and Yaragina, 1980; Ponomarenko and Yaragina, 1981) showed that in the southern Barents Sea the portion of mature specimens among cod of the same length did not differ notably in the $30-40^{\prime}$ s from the portion of mature fish in the corresponding length groups in the 60-70's and in late 70's (using Kolmogorov-Smirnov's $\lambda$-criterion (Smirnov, Dunin-Barkovsky, 1969) at the significance level of 0.05). Thus, a sharp increase of the $\psi_{M}$ parameter in Arcto-Norwegian cod at age 11 and older and the conclusion that the increase of this parameter in fish of all age groups is due to the longterm intensive exploitation cannot be regarded as convincing.

Table 3. Values of $M(t)$ function at ages 3,4...16 at different age composition of catch and various values of parameters $\bar{t}_{s}$, $t_{e}$ and $M_{t m}$.

| Period of fishery | Parameter |  |  | Age, yrs |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\bar{t}_{s}$ | $M_{t m}$ | $t_{e}$ | a | b | 3 | 4 | 5 | 6 | 7 |
| 1946-1950 | 9 | 0.09 | 30 | 0.1044 | 7.6934 | 0.155 | 0.133 | 0.115 | 0.100 | 0.089 |
|  | 10,5 | 0.09 | 30 | 0.1218 | 8.4204 | 0.230 | 0.198 | 0.169 | 0.144 | 0.123 |
|  | 10.5 | 0.12 | 30 | 0.1172 | 8.1362 | 0.255 | 0.244 | 0.196 | 0.172 | 0.152 |
| 1951-1955 | 9 | 0.09 | 30 | 0.1065 | 7.8438 | 0.156 | 0.134 | 0.115 | 0.100 | 0.089 |
|  | 10.1 | 0.09 | 30 | 0.1186 | 8.3429 | 0.209 | 0.180 | 0.154 | 0.132 | 0.114 |
|  | 10.1 | 0.11 | 30 | 0.1153 | 8.1316 | 0.226 | 0.197 | 0.172 | 0.151 | 0.133 |
|  | 10.1 | 0.11 | 30.5 | 0.1089 | 7.9051 | 0.218 | 0.191 | 0.167 | 0.147 | 0.131 |
| 1956-1960 | 9 | 0.09 | 30 | 0.1058 | 7.7932 | 0.156 | 0.134 | 0.115 | 0.100 | 0.089 |
|  | 9.7 | 0.09 | 30 | 0.1130 | 8.0901 | 0.188 | 0.162 | 0.139 | 0.119 | 0.104 |
|  | 9.7 | 0.10 | 30 | 0.1116 | 7.9999 | 0.197 | 0.171 | 0.148 | 0.129 | 0.114 |
|  | 9.7 | 0.10 | 31 | 0.0996 | 7.5528 | 0.183 | 0.161 | 0.141 | 0.125 | 0.112 |
| 1961-1965 | 9 | 0.09 | 30 | 0.1051 | 7.7431 | 0.155 | 0.133 | 0.115 | 0.100 | 0.089 |
|  | 9.2 | 0.09 | 30 | 0.1073 | 7.8417 | 0.164 | 0.141 | 0.121 | 0.105 | 0.093 |
|  | 9.2 | 0.09 | 31.5 | 0.0911 | 7.2303 | 0.150 | 0.131 | 0.115 | 0.102 | 0.092 |
| 1966-1970 | 9 | 0.09 | 30 | 0.1058 | 7.7932 | 0.156 | 0.134 | 0.115 | 0.100 | 0.089 |
|  | 8.8 | 0.09 | 30 | 0.1039 | 7.7218 | 0.147 | 0.126 | 0.109 | 0.095 | 0.084 |
|  | 8.8 | 0.08 | 30 | 0.1056 | 7.8329 | 0.138 | 0.117 | 0.099 | 0.085 | 0.075 |
|  | 8.8 | 0.08 | 32 | 0.0853 | 7.0392 | 0.124 | 0.108 | 0.095 | 0.084 | 0.076 |
| 1971-1975 | 9 | 0.09 | 30 | 0.1058 | 7.7932 | 0.156 | 0.134 | 0.115 | 0.100 | 0.089 |
|  | 8.4 | 0.09 | 30 | 0.1002 | 7.5617 | 0.131 | 0.112 | 0.097 | 0.085 | 0.077 |
|  | 8.4 | 0.07 | 30 | 0.1030 | 7.7552 | 0.112 | 0.093 | 0.077 | 0.065 | 0.057 |
|  | 8.4 | 0.07 | 32.5 | 0.0798 | 6.8479 | 0.100 | 0.087 | 0.075 | 0.067 | 0.06 |
| 1976-1979 | 9 | 0.09 | 30 | 0.1051 | 7.7431 | 0.155 | 0.133 | 0.115 | 0.100 | 0.089 |
|  | 7.9 | 0.09 | 30 | 0.0955 | 7.3573 | 0.112 | 0.097 | 0.084 | 0.074 | 0.069 |
|  | 7.9 | 0.06 | 30 | 0.0995 | 7.6297 | 0.083 | 0.067 | 0.054 | 0.044 | 0.038 |
|  | 7.9 | 0.06 | 33 | 0.0742 | 6.6320 | 0.076 | 0.065 | 0.056 | 0.050 | 0.046 |

Table 3 contd.

Age, yrs

| Age, yrs |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
| 0.082 | 0.079 | 0.082 | 0.090 | 0.104 | 0.125 | 0.154 | 0.191 | 0.238 |
| 0.107 | 0.095 | 0.090 | 0.090 | 0.097 | 0.111 | 0.133 | 0.164 | 0.206 |
| 0.136 | 0.126 | 0.120 | 0.120 | 0.126 | 0.139 | 0.161 | 0.191 | 0.232 |
| 0.082 | 0.079 | 0.082 | 0.090 | 0.104 | 0.126 | 0.155 | 0.193 | 0.240 |
| 0.100 | 0.091 | 0.088 | 0.090 | 0.099 | 0.115 | 0.140 | 0.174 | 0.218 |
| 0.120 | 0.111 | 0.108 | 0.110 | 0.119 | 0.135 | 0.158 | 0.191 | 0.234 |
| 0.119 | 0.111 | 0.108 | 0.111 | 0.118 | 0.133 | 0.154 | 0.184 | 0.224 |
| 0.082 | 0.079 | 0.082 | 0.090 | 0.104 | 0.126 | 0.154 | 0.192 | 0.239 |
| 0.093 | 0.086 | 0.085 | 0.090 | 0.101 | 0.119 | 0.145 | 0.180 | 0.226 |
| 0.103 | 0.097 | 0.095 | 0.100 | 0.111 | 0.129 | 0.155 | 0.189 | 0.234 |
| 0.102 | 0.097 | 0.096 | 0.100 | 0.109 | 0.124 | 0.146 | 0.175 | 0.212 |
| 0.082 | 0.079 | 0.082 | 0.090 | 0.104 | 0.125 | 0.154 | 0.191 | 0.239 |
| 0.084 | 0.081 | 0.083 | 0.090 | 0.103 | 0.124 | 0.152 | 0.188 | 0.235 |
| 0.086 | 0.083 | 0.084 | 0.090 | 0.101 | 0.116 | 0.138 | 0.167 | 0.203 |
| 0.082 | 0.079 | 0.082 | 0.090 | 0.104 | 0.126 | 0.154 | 0.192 | 0.239 |
| 0.078 | 0.077 | 0.081 | 0.090 | 0.105 | 0.127 | 0.157 | 0.195 | 0.243 |
| 0.069 | 0.067 | 0.071 | 0.080 | 0.095 | 0.118 | 0.148 | 0.187 | 0.236 |
| 0.072 | 0.071 | 0.073 | 0.080 | 0.091 | 0.107 | 0.129 | 0.157 | 0.191 |
| 0.082 | 0.079 | 0.082 | 0.090 | 0.104 | 0.126 | 0.154 | 0.192 | 0.239 |
| 0.073 | 0.074 | 0.079 | 0.090 | 0.104 | 0.130 | 0.161 | 0.201 | 0.250 |
| 0.053 | 0.053 | 0.059 | 0.070 | 0.087 | 0.112 | 0.143 | 0.184 | 0.234 |
| 0.058 | 0.059 | 0.062 | 0.070 | 0.082 | 0.098 | 0.120 | 0.147 | 0.180 |
| 0.082 | 0.079 | 0.082 | 0.090 | 0.104 | 0.125 | 0.154 | 0.191 | 0.239 |
| 0.067 | 0.070 | 0.077 | 0.090 | 0.109 | 0.134 | 0.166 | 0.207 | 0.257 |
| 0.036 | 0.039 | 0.047 | 0.060 | 0.079 | 0.106 | 0.139 | 0.182 | 0.234 |
| 0.045 | 0.046 | 0.051 | 0.060 | 0.072 | 0.089 | 0.110 | 0.137 | 0.169 |

Table 3 presents the variation of $M$ in cod at ages 3 to 16 due to change in the mean age composition of catches by 5-year periods (Table 4) and due to the possible variation of parameters $\bar{t}_{s}, t_{e}$ and $M_{t m}$. The arithmetic mean of $\bar{E}_{s}$ in each 5year period pertained to the middle of interval and was then redetermined by the linear regression equation

$$
\bar{t}_{s}=-0.436 x+10.971
$$

where $x$ is number of consecutive 5-year periods. The graph of the equation is presented in Fig. 5.

As for parameters $t_{e}$ and $M_{t m}$ it is supposed that from one period of fishery to another the first increases by 0.5 years beginning from the age of 30 years and the second decreases by 0.01 beginning from 0.12 .

It follows from the Table that existing variations in the age composition of mean cod catches in 5-year periods at constant $\bar{t}_{s}=9$ yrs, $t_{e}=30 \mathrm{yrs}$ and $\mathrm{M}_{\mathrm{tm}}=0.09$ do not lead to a marked change in the behaviour of the $M(t)$ function. It has a pronounced minimum range and is asymmetrical as before. At points $\bar{t}_{s}+i$ where $i=1,2, \ldots, \bar{t}_{s}-t_{r}$, its absolute values and rate of change are higher than at points $\bar{E}_{s}-i$ (Fig. 6). The parameter $M$ remains constant in cod of the same age with an accuracy of 0.01. Both the simultaneous change in age composition of the catch and in parameters $\bar{t}_{s}, t_{e}$ and $M_{t m}$ lead to the decrease in natural mortality rate of fish of the same age. The decrease is especially significant in young cod (Fig. 8).

The last two circumstances are not unexpected. They show a natural homeostasis of the population which, under the longterm intensive exploitation, withstands the decrease in numbers. Among homeostatic mechanisms of negative feedback of fishcannibals such as Arcto-Norwegian cod (competition, predation, diseases etc.) a far less extent of eating of the young seems to be of greater importance.

Table 4. Arithmetic mean of catches of Arcto-Norwegian cod at different ages taken in various periods of fishery ( $\mathrm{x} 10^{3}$ ).

| Age, yrs | Period of fishery |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 1946-1950 | 1951-1955 | 1956-1960 | 1961-1965 | 1966-1970 | 1971-1975 | 1976-1979 |
| 3 | 1426 | 24315 | 25869 | 24422 | 20717 | 94938 | 53008 |
| 4 | 9043 | 99822 | 73497 | 96423 | 85123 | 137568 | 103903 |
| 5 | 31622 | 127497 | 88109 | 134499 | 127239 | 106016 | 88658 |
| 6 | 54065 | 87656 | 96554 | 72642 | 98144 | 41552 | 66077 |
| 7 | 56516 | 46866 | 50762 | 29529 | 53191 | 23322 | 38691 |
| 8 | 23738 | 24252 | 30451 | 14639 | 23789 | 21788 | 19713 |
| 9 | 25498 | 16788 | 15286 | 7081 | 10079 | 11736 | 7986 |
| 10 | 18978 | 10966 | 9063 | 3682 | 3164 | 3733 | 1461 |
| 11 | 17232 | 5813 | 3745 | 2226 | 974 | 1342 | 626 |
| 12 | 8831 | 2276 | 1110 | 931 | 303 | 373 | 325 |
| 13 | 5938 | 776 | 500 | 451 | 131 | 185 | 274 |
| 14 | 2801 | 917 | 230 | 209 | 36 | 64 | 56 |
| 15 | 2535 | 412 | 161 | 136 | 42 | 44 | 59 |
| 16 | 850 | 245 | 26 | 32 | 18 |  |  |
| 17 | 539 | 204 | 14 | 18 | 3 |  |  |
| 18 | 194 | 114 | 1 | 21 | 2 |  |  |
| 19 | 90 | 65 | 3 | 1 |  |  |  |
| 20 | 81 | 69 | 7 | 1 | 2 |  |  |



Fig. 8. Change in natural mortality rate of Arcto-Norwegian cod with age under different age composition of catches and various values of parameters $\bar{E}_{s} r M_{t m}$ and $t_{e}: 1$ - mean age composition of catch for $1946-1950, \bar{E}_{s}=10.5 \mathrm{yrs}, M_{t m}=0.12$, $t_{e}=30$ yrs; 2 - mean age composition of catch for 1976-1979, $\bar{t}_{s}=7.9 \mathrm{yrs}, M_{t m}=0.06, t_{e}=30 \mathrm{yrs}$.

## CONCLUSIONS

1. The suggested method allows estimation of natural mortality rates of all fish age groups in the commercial stock.
2. In contrast to existing methods this one may be used for both intensively fished and unexploited species.
3. The long-term intensive exploitation of Arcto-Norwegian cod leads to a decrease in natural mortality rate of fish of a given age. The decrease is especially significant in young fish.
4. The mean value of the natural mortality rate of ArctoNorwegian cod at ages 3 to 16 is equal to 0.12 which is 1.7 times less than the generally accepted estimate.

## REFERENCES

Babayan, V.K., 1978. Determination of some population parameters and possible catches of cod from the South Barents sea. Trudy VNIRO, 128: 44-51.

Bajkov, A., 1933. Fish population and productivity of lakes. Trans. Am. Fish. Soc., 62: 307-316.

Baranov, F.I., 1918. On the question of the biological basis of fisheries. Izv. otdela rybovodstva i nauchno-promyslovykh issledovanij, l(I): 21 p.

Beverton, R.J., MS 1960. Second Progress Report of the Working Group on Arctic Fisheries, ICES C.M. 1960, Gadoid Fish. Comm., No. 133,8 p. (Mimeo).

Beverton, R.J. \& Holt, S.J., 1956. A review of methods for estimating mortality rates in fish populations, with special reference to sources of bias in catch sampling. Cons. Int. Explor. Mer., No 140, p. 6783.

Beverton, R.J. and Holt, S.J., 1957. On the dynamics of exploited fish population. Fish. Inv., ser. 2, v. 19, 533 p.

Blinov, V.V., 1977. Modelling of natural mortality in fishes of younger age groups. Vopr.ikht., vol. 17, vyp. 3 (104), p. 572-578.

Blinov, V.V., 1979. Relationship between the natural mortality rate of fish and their age. Ryb.khoz, 1: 14-16.

Borisov, V.M., 1976. Results of the application of P. V. Tyurin's method to estimate natural mortality of ArctoNorwegian cod Gadus morhua L. Vopr.ikht., vol. 16, vyp. 5 (100), p. 889-898.

Borisov, V.M., 1978. The selective effect of fishery on the population structure of long-cycle fish. Vopr.ikht., vol. 18, vyp. 6(113): 1010-1019.

Borisov, V.M. and Shatunovsky, M.I., 1973. On the possibility of using the moisture content index in the assessment of natural mortality of cod from the Barents Sea. Trudy VNIRO, 93: 301-321.

Bukhanevich, I.B., 1973. A particular case of the fish natural mortality calculated by means of computer. Trudy Atlant NIRO, 51: 186-189.

Bulgakova, T.I. and Efimov, Yu.N., 1982. A method for calculating the possible catch incorporating relationship between natural mortality and age of the fish. Vopr.ikht., 22(2): 200-206.

Carscadden, J.E. and Miller, D.S., MS 1980. Estimation of natural mortality of Newfoundland capelin using the Icelandic method. NAFO, SCR Doc. No. NO77, 8 p. (Mimeo).

Dorovskikh, R.S., 1981. On determination of the index of natural and fishing mortality with the Beverton and Holt method. In: Sostojanie zapasov i osnovy ratsional'nogo rybolovstva v Atlanticheskom okeane. Kaliningrad, p. 30-34.

Fridgeirsson, E., MS 1979. Natural mortality of the Icelandic capelin. ICES CM 1979, NO27, 6 p. (Mimeo).

Fry, F.E., 1949. Statistics of a lake trout fishery. Biometrics, 5: 27-67.

Garrod, D.J., 1967. Population dynamics of the ArctoNorwegian cod. Fish.Res.Board of Canada, 24: 145190.

Gulimov, A.V., Maleeva, E.N., Ponomarenko, V.P. and Tretyak, V.L., 1977. The estimate of vulnerability coefficients for the fishing of the Lofoten-Barents Sea cod. Trudy PINRO, 38: 82-89.

Gulin, V.V., 1967. Differentiated estimate of the total, fishing and natural mortality of fish depending on their sex and age with regard for specific character of inland water bodies. In: Sbornok nauchno-tekhnicheskoi informatsii o dostizhenijakh rybnoi promyshlennosti. Moscow, vyp. 11, p. 53-64.

Gulin, V.V. 1971. Theoretical basis and practical development of methods for estimating the total, fishing and natural mortality of fish in inland water bodies. Izv. GosNIORKh, 73: 33-74.

Gulin, V.V. and Rudenko, G.P., 1973. A contribution to the methods of assessing fish production in lakes. Vopr.ikht., $13(6)$, p. 977-989.

Gulin, V.V. and Rudenko, G.P., 1975. Ecological conditions in a water body and the value of natural mortality in fish. Izv.GosNIORKh, 99: 239-251.

Gulland, J.A., 1968. Recent changes in the North Sea plaice fishery. Cons.Int.Explor.Mer., 31: 305-322.

Hylen, A., MS 1965a. Arctic Fisheries Working Group. Report of meeting in Hamburg. ICES CM 1965, Gadoid Fish. Comm, 3, 10 p. (Mimeo).

Hylen, A., 1965b. Report of meeting on the Arctic Fisheries Working Group in Hamburg. Coop.Res.Rep., Ser.B, p. 15-32.

Jensen, A.J., 1939. On the laws of decrease in fish stocks. Cons.Int.Explor.Mer, ll0: 85-96.

Kennedy, W.A., 1953. Growth, maturity, fecundity and mortality in the relatively unexploited whitefish, Coregonus clupeaformis, of Great Slave Lakes. Fish.Res.Board of Canada, 10: 413-441.

Kennedy, W.A., 1954. Growth, maturity and mortality in the relatively unexploited lake trout Cristivomer Namaycush, of Great Slave Lake. Fish.Res.Board of Canada, ll: 827-852.

Mankevich, E.M., 1965. Soviet investigations on the age and length compositions of cod in the Barents Sea in 1963. Annls.biol., 20: 126-127.

Mankevich, E.M., 1966. Soviet researches on the age and length composition of cod in the Barents Sea in 1964. Annls.biol., 2l: 80-83.

Mankevich, E.M., 1967. Soviet investigations on the age and length composition of cod stocks in the Barents Sea in 1965. Annls.biol., 22: 78-82.

Mankevich, E.M., 1970. Structure of the stock of the ArctoNorwegian cod in 1969 according to the samples obtained off the north-western coast of Norway. Annls. biol., 26: 123-125.

Mankevich, E.M., 1972. Age structure of the Arcto-Norwegian cod stock off the northwest coast of Norway in January to May 1970. Annls.biol., 27: 123-125.

Mankevich, E.M., 1973. Age composition of biological groups of the Arcto-Norwegian cod stock off the northwest coast of Norway in 1971. Annls.biol., 28: 90-92.

Marti, Yu. Yu., 1961. State of adult Arctic cod stock. Ryb.khoz., 7: 7-9.

Nikolsky, G.V., 1974. Theory of the fish stock dynamics. Pishchevaja Promyshlennost' Press, Moscow. 447 p.

Odum, E.P., 1975. Fundamentals of ecology. Mir Press, Moscow. 740 p.

Paloheimo, J.E., 1958. A method of estimating natural and fishing mortalities. J. Fish. Res. Board of Canada, 15(4): 749-758.

Pauly, D., MS 1978. A discussion of the potential use in population dynamics of the interrelationship between natural mortality, growth parameters and mean environmental temperature in 122 fish stocks. ICES CM 1978/G:2, 10 p. (Mimeo).

Pauly, D., 1980. On the interrelationships between natural mortality growth parameters and mean environmental temperature in 175 fish stocks. Cons.Int.Explor.Mer., 39(2): 175-192.

Pianka, E.R., 1981. Evolutionary ecology. Mir Press, Moscow. 399 p.

Poluektov, R.A., Pykh, Yu.A. and Shvytov, I.A., 1980. Dynamic models of ecological systems. Gidrometeorologicheskoe Izdatel'stvo, Leningrad. 280 p.

Ponomarenko, V.P., 1969. Biological substantiation of optimum fishing intensity in the cod fishery of the Barents Sea. Trudy VNIRO, $67(1): 114-132$.

Ponomarenko, V.P., Ponomarenko, I.Ya. and Yaragina, N.A., MS 1980. Growth and maturation of the Lofoten-Barents Sea cod. ICES Doc. CM 1980/G:25, 28 p. (Mimeo).

Ponomarenko, I.Ya. and Yaragina, N.A., MS 1981. Relation between mature and immature specimens among cod of different ages and sizes in 1978-1980. ICES Doc. CM 1981/G:22, 20 p. (Mimeo).

Rastrigin, L.A., 1974. Extremal control systems. Nauka Press, Moscow. 630 p.

Ricker, W.E., 1945. Abundance, exploitation and mortality of the fishes of two lakes. Invest. Indiana Lakes Streams, 2: 345-448.

Ricker, W.E., 1949. Mortality rates in some little exploited population of freshwater fishes. Trans.Am.Fish.Soc, 77: 114-128.

Ricker, W.E., 1958. Handbook of computations for biological statistics of fish populations. Fish.Res.Board of Canada, 119, 300 p.

Ricker, W.E., 1970. Biostatistical method of A.N. Derzhavin. Ryb.khoz., 10: 6-9, 1l: 5-7.

Rikhter, V.A. and Yefanov, V.N., l977. On one of the approaches to the estimate of fish population natural mortality. Trudy AtlantNIRO, iss.LXXIII, p. 77-85.

Rollefsen, G., 1954. Observation on the cod and fisheries of Lofoten. Rapports et proces-verbaux des rèunions, 136: 40-48.

Rudenko, G.P., 1967. From the experience of determining number, ichthyomass and output of fish in a roach-perch lake. Izv. GosNIORKh, 64: 19-38.

Sætersđal, G. and Hylen, A., 1959. Skreiundersøkelsene og skreifisket. Fisken og Havet, l, 20 p.

Sergeev, Yu.S., 1979. Theoretical bases of fishing with trap nets. Pishchevaja Promyshlennost', Moscow. 143 p.

Severtsov, S.A., 1941. Dynamics of population and adaptive evolution of animals. Akademija Nauk SSSR Press, Moscow. 168 p.

Silliman, R.P., 1943. Studies on the Pacific pilchard or sardine (Sardinops caerulea). 5. A method of computing mortalities and replacements. U.S.Fish and Wildlife Service Spec.Sci.Rep., 24, 10 p.

Smirnov, I.V. and Dunin-Barkovsky, I.V., 1969. A course on probability law and mathematical statistics. Nauka Press, Moscow. 511 p.

Sokolovsky, A.S., 1973. On methods of determining the fish natural mortality. Trudy PINRO, 4: 142-148.

Suvorov, B.K., 1948. Fundamentals of ichthyology. 2nd ed. Sovetskaja Nauka Press, Leningrad, 580 p.

Svetovidov, A.N., 1948. Gadiformes. A new series, MoscowLeningrad, 9(4): 221 p .

Tester, A.L., 1955. Estimation of recruitment and natural mortality rate from age composition and catch data in British Columbia herring populations. J. Fish. Res. Board of Canada, 12: 649-681.

Thompson, W.F. and Herrington, W.C., 1930. Life history of the pacific halibut. l. Marking experiments. Rep.Int. Fish. (Pacific halibut), comm. 2, 137 p.

Tjurin, P.V., 1972. "Normal" curves of survival and natural mortality rates in fish as the theoretical basis for fishing regulation. Izv. GosNIORKh, 71: 71-127.

Tomlinson, J.K. and Abramson, V.J., 1961. Fitting a von Bertalanffy growth curve by least squares. Calif. Dept.Fish and Game Fish, ll6: 69 p.

Tretyak, V.L., 1976. Method of estimation of the parameters of the Schaefer model. Trudy PINRO, 37: 170-178.

Vilee, C.A. and Dethier, V.G., 1974. Biology (Principles and processes). Mir Press, Moscow, 823 p.

Watt, K.E., 1959. Studies on populations productivity. II. Factors governing productivity in a population of smallmouth bass. Ecol.Monogr., 29: 367-392.

## SECTION III <br> Population structure

# GENETIC STUDIES ON EGGS, LARVAE AND 0-GROUP OF THE ARCTIC COD STOCK 

by

Knut E. Jørstad Institute of Marine Research


#### Abstract

Genetic analyses have been performed on samples of spawning cod (March), a large number of eggs and yolk sac larvae (May, postlarvae (July) and 0 -group cod (August-September). The distribution of eggs and larvae at different stages as well as biological and genetic data were in accordance with earlier observations on larval drift from the main spawning grounds. Some samples drawn from localities on the coast or in fjords differed, however, significantly from samples in the open sea. The genetic analyses of these samples, as observed in analyses of the LDH-3 locus, confirm the existence of locally spawning groups of coastal cod. The genetic data are discussed in relation to stock structure of cod, the significance of genetic variation within stocks and the problem of concervation of genetic resources.


INTRODUCTION

The early genetic studies on cod (Sick, 1961; Sick, 1965a,b; Frydenberg et al., 1965; Moller, 1968) suggested a complex population structure for this species. In these investigations the genetic variation seen in blood proteins was used as well
as immonogenetic methods (Mф1ler, 1967). At present, however, polymorphic enzymes expressed in different tissues are more applied in studies of population structure of fish species (Allendorf and Utter, 1979).

Extensive studies of natural populations have revealed a large amount of genetic variation (Powell, 1975). Genetic differentiated populations of valuable fish species represent unique biological resources (Soulé, 1981) which should be managed according to the genetic characteristics of the population, environmental preference, migration behaviour and general life history.

A number of studies (for review see Soulé, 1980) also suggest that the amount of genetic variation within a population plays a key role both for short term fitness and long term evolution. Due to these observarions, concervation genetics (Frankel and Soulé, 1981) predict that as much genetic variation as possible should be preserved within populations and species.

With respect to the north-east arctic cod, proper management of this important stock should be based on genetic data as well as biological information. Genotype distributions and allele frequencies for a large number of loci are needed for identification of subpopulation structures. To evaluate possible genetic effects due to increased fishing pressure, environmental changes and pollution, genetic baseline information is essential. Impacts on the gene pool are likely to take place in the early stages of the development. For this reason genetic data at different stages during the recruitment process will provide basic knowledge for detection of unwanted changes in the gene pool in the future.

## MATERIALS AND METHODS

The sampling programme in different years and stages of development are summerized in Table 1 and the sampling areas are shown in Fig, 1 and Fig. 3. As a reference sample we have used arctic cod caught on the spawning ground in Lofoten in March-

April 1981. From these fish, samples of white muscle were taken from each individual fish on which biological information (length, sex, maturity, age, otolith type) also were recorded. The tissue samples were kept frozen until analyses on the research vessel or in the laboratory.

Table 1. Sampling program in different years.

| Year | Month | Stage of development | Area | Research <br> vessel |
| :---: | :---: | :---: | :---: | :---: |
| 1981 | March | Spawners | Lofoten | "Djupaskjær" |
|  | May | Eggs, yolk sac larvae | Lofoten- <br> Vesterålsfjord | "M. Sars" |
|  | July | Postlarvae | Norwegian Sea | "J. Ruud" |
|  | AugustSeptember | 0-group | Barents Sea-Vest-Spitsbergen | "J. Hjort" <br> "G.O. Sars" <br> "M. Sars" |
| 1982 | May | Eggs, yolk sac larvae | Lofoten- <br> Vesterålsfjord | "J. Hjort" |
|  | July | Postlarvae | Norwegian Sea | "J. Ruud" |
|  | August- <br> September | 0-group | Barents Sea-Vest-Spitsbergen | "J. Hjort" "G.O. Sars" "M. Sars" |

Samples of eggs and yolk sac larvae were collected in May in the Lofoten and Vesterålen area by using Juday nets. Eggs in early stages were kept alive in seawaters and incubated at $6{ }^{\circ} \mathrm{C}$ until hatching. The samples were then analysed on the boat following the methods described by Jørstad, Solberg and Tilseth (1980).

In July the most concentrated areas of postlarvae were found in the open sea north-west of Torsvag-S申r申ya. Only the main larvae distributions which have been taken in the open sea are indicated in the figures. In August-September the 0-group is found distributed in the area Bear Island-Vest-Spitsbergen and in the Barents Sea. The postlarvae and 0 -group cod were


Fig. 1. Sampling areas in 1981.
a. Postlarvae

## 




LENGTH IN
b. o-group



MILLIMETER

Fig. 2. Length distribution of postlarvae and 0-group in 1981.
sampled by pelagic trawl and the main areas in open sea are indicated in Fig. 1 and Fig. 3. In addition to tissue samples for genetic analyses, the length of each fish was recorded, and the length distributions of postlarvae and 0 -group cod in different years and for the most concentrated areas are given in Fig. 2 and Fig. 4.

a. Eggs/yolk sac larvae

A limited number of sampling stations in the fjords were also included in the sampling programme of postlarvae. Two fjord localities are shown in Fig. 5, and the length distribution of


Fig. 4. Length distributions of postlarvae and 0 -group in 1982.
these larvae samples are given in Fig. 6. For comparison, data from control samples are included.

All samples were analysed by using starch gel electrophoresis and selective staining methods (Harris and Hopkinson, 1976). Several polymorphic enzymes were investigated. These included lactate dehydrogenase (LDH), phosphoglucose isomerase (PGI) and


Fig. 5. Fjord localities of postlarvae.


Fig. 6. Length distributions of fjord samples of postlarvae.
phosphoglucomutase (PGM). The different loci and alleles have been described elsewhere (Cross and Payne, 1978; Jørstad et al., 1980, Mork et al., 1982). Designation of enzyme loci and alleles followed the recommendations of Allendorf and Utter (1979). In this paper, only the results obtained from analyses of the LDH-3 locus are presented.

In the statistical comparisons between different areas and stages of development a G-test described by Sokal and Roh1f (1969) were used. The P-values given in some of the tables are the probability obtained from a G-test asking if the sample collection is genetically homogeneous. The test is based on the distribution of genotypes in the different samples, and significant heterogeneity is obtained for $P$-values $<0.05$.

## RESULTS

The results from the analyses of the 1981-material are summerised in Table 2. For the LDH-3 locus three alleles, designed 70 , 100 and 150 were found in all samples. Some rare heterocygotes in LDH-2 locus were also observed but are not considered here.

The catches of cod in Lofoten during the spawning season consist of a mixture of arctic and coastal cod. In Table 2 only individuals classified as arctic cod according to otolith structure (Rollefsen, 1933) have been used and constitute about $90 \%$ of all cod specimens in the samples which were analysed for genetic characters. In this reference sample of arctic cod several year classes were present, and due to the sample design, comparisons between biological and genetic data could be performed. No significant differences were found, however, between the two sexes, different year classes or length groups. The distribution of genotypes were also consistant with HardyWeinberg's expectations tested as described by Christiansen et al. (1976).

As shown in Table 2 the allel frequencies were nearly identical for the spawning stock in Lofoten and the eggs and yolk sac

Table 2. Allelfrequencies of LDH-3 in different samples in 1981.

| Sample no. | Month | Stage of development | Area | No. of fish | Allele |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  | 70 | 100 | 150 |
| 1 | March | Spawners | Lofoten | 383 | . 410 | . 582 | . 008 |
| 2 | May | Eggs/yolk sac larvae | Lofoten | 749 | . 407 | . 588 | . 005 |
| 3 | May | Eggs/yolk sac larvae | Vesteråsfjord | 407 | . 425 | . 572 | . 002 |
| 4 | July | Postlarvae | Norwegian Sea | 232 | . 412 | . 586 | . 002 |
| 5 | July | Postlarvae | Norwegian Sea | 100 | . 450 | . 550 | . 000 |
| 6 | July | Postlarvae | Norwegian Sea | 383 | . 410 | . 582 | . 008 |
| 7 | Aug.-Sept. | 0-group | V.Spitsbergen | 69 | . 406 | . 587 | . 007 |
| 8 | Aug. -Sept. | 0-group | Barents Sea | 109 | . 367 | . 628 | . 005 |

Homogeneity test based on distribution of genotypes: $P=.132$
larvae found a month later in Lofoten-Vesterålen. No genetic differences seem to exist between the two main hatching areas.

With respect to the postlarvae sampled in July in the areas shown in Fig. 1, no variation in allele frequencies were detected. In addition, the analyses of 0 -group cod in the Barents Sea and Spitsbergen area in August-September reveal no significant variation. As the data indicate, noe significant differences were found in the total material analysed, covering the spawning stock of arctic cod in Lofoten, different stages of development, different sampling time and geographic distribution. A homogeneity test based on the distribution of genotypes in the different samples in Table 2 , revealed no heterogeneity ( $\mathrm{P}=0.132$ ) within the sample collection. When performing a test between the different samples, one sample of postlarvae (sample no. 4) seemed to be different ( $\mathrm{P}=0.02$ ) from the 0 -group sample from Spitsbergen (sample no. 7). The allele frequencies were approximately identical for the two samples, but a closer examination showed that the distribution of genotypes in the 0 -group sample differed significantly from the
values expected from Hardy-Weinberg's law. This is possibly the reason for the observed heterogeneity between those two samples.

A similar picture was obtained in the analyses of the 1982material summerized in Table 3. This year the spawning stock of arctic cod in Lofoten was not sampled, but the data on eggs and yolk sac larvae found in May in Lofoten and Vesterålen corresponded well to the data on the spawning stock the preceding year as well as data on juvenile and mature fish sampled in Barents Sea and Spitsbergen (Jørstad, unpublished). As shown in Fig. 3, a similar distribution of postlarvae and 0 -group cod was observed except for the 0 -group this year was much more abundant in the Barents Sea compared to 1981.

Table 3. Allelfrequencies of LDH-3 in different samples in 1982.

| Sample no. | Month | Stage of development | Area | No. of fish | Allele |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  | 70 | 100 | 150 |
| 1 | May | Eggs/yolk sac larvae | Lofoten | 79 | . 430 | . 563 | . 006 |
| 2 | May | Eggs/yolk sac larvae | Vesterålsfjord | 70 | . 443 | . 550 | . 007 |
| 3 | July | Postlarvae | Norwegian Sea | 63 | . 396 | . 590 | . 015 |
| 4 | July | Postlarvae | Norwegian Sea | 112 | . 375 | . 607 | . 018 |
| 5 | Aug.-Sept. | 0-group | V.Spitsbergen | 162 | . 407 | . 590 | . 003 |
| 6 | Aug.-Sept. | 0-group | Barents Sea | 145 | . 434 | . 562 | . 003 |
| 7 | Aug.-Sept. | 0-group | Barents Sea | 230 | . 448 | . 550 | . 002 |

Homogeneity test based on distribution of genotypes: $\mathrm{P}=.172$

As seen from Table 3, testing for homogeneity in the sample group showed no heterogeneity ( $\mathrm{P}=0.172$ ). A homogeneity test between the samples suggested that one of the postlarvae samples (sample no. 4) was different from the 0-group cod found in the Barents Sea (sample no. 7). As discussed above, also this difference is possibly due to the uneven distribution of
genotypes in the two samples. In addition, the postlarvae sample was taken near the coast and could be mixed with other more locally spawning groups of cod.

The length distributions of postlarvae and 0 -group for the two years are shown in Fig. 2 and Fig. 4. The postlarvae taken in the open sea have a larger mean length compared to samples taken near the coast. Further, the postlarvae were significant larger in July 1982 compared to the larvae found at the same time in 1981. In spite of this difference, the 0 -group sampled in August-September have similar mean length for the two years. Significant differences were detected between the samples from the Barents Sea and the Spitsbergen area. In 1981 the 0 -group cod found at Spitsbergen have a mean length of 63.4 mm compared to 55.4 mm in the Barents Sea, while the largest 0 -group cod in 1982 was found in the Barents Sea.

In contrast to the genetic uniformity observed in the spawning stock of arctic cod, the different stages of development and the geographic distribution as described above, some fjord samples of postlarvae (Fig. 5) have different allele frequencies and genotype distribution. The two samples shown are both taken from fjord localities and have a relatively high frequency (0.69) of LDH-3(100) allele.

In Table 4 the fjord samples are compared to reference samples of arctic cod and the homogeneity test demonstrated a very heterogeneous sample group $(\mathrm{P}=0)$. Homogeneity tests between the samples showed that both samples were different from the spawning stock in Lofoten (Eidsfjord, $\mathrm{P}=0.003$; Porsangerfjord, $\mathrm{P}=0.04$ ) .

As shown in Fig. 6, both samples clearly differed in length distribution and mean length compared to postlarvae found in the open sea. The differences in geographic distribution and biological as well as genetic characters suggest other spawning groups than the arctic cod stock. The observation give evidence for the existance of genetic distinct stocks of coastal cod in the area. This conclusion have been further supported

Table 4. Allelfrequencies of LDH-3 in two fjord samples of postlarva

| Sample no. | Year | Month | Stage of development | Area | No. of fish | Allele |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  | 70 | 100 | 15 |
| 1 | 1981 | March | Spawners | Lofoten | 356 | . 397 | . 598 | . 00 |
| 2 | 1982 | May | Eggs/yolk sac larvae | Lofoten | 79 | . 443 | . 550 | . 00 |
| 3 | 1981 | July | Postlarvae | Eidsfjord | 138 | . 304 | . 692 | . 00 |
| 4 | 1982 | July | Postlarvae | Porsangerfjord | d 54 | . 306 | . 694 | . 00 |

Homogeneity test based on distribution of genotypes: $P=0$
by analyses of cod sampled in the Porsangerfjord during the spawning season (Jørstad, 1983).

DISCUSSION

Due to the extensive sampling programme focused on the northeast arctic cod stock it was possible to carry out detailed genetic studies at different stages of development for several year classes of this important cod stock. The genetic data so far demonstrate a very close agreement between the spawning stock in March and eggs/yolk sac larvae found in the main hatching areas in May. These data document the correlation between the spawning population and offspring. Further, this observation points to the possibility of sampling and analyses of eggs and yolk sac larvae on or near spawning grounds for identification of genetically differentiated spawning groups. As indicated, such methods offer a valuable tool in studies of stock structure of fish in general.

The data presented are obtained from samples which covered a large geographic area as well as different stages of development. With the exception of two samples of postlarvae, which deviations can be explained by some other reason, all the samples taken in the open sea at any stages in 1981 and 1982 are very similar in allele frequencies and phenotype distribu-
tion of the LDH-3 locus. This locus have been informative with respect to stock structure of cod in other area (Moth-Poulsen, 1982; Jørstad, 1983) as well as this study (e.g. coastal cod groups). The results obtained are in accordance with the present recruitment model of this cod stock concerning spawning area, main hatching area and drift/distribution of postlarvae/ 0 -group cod to the feeding area in the Barents Sea and the Spitsbergen area.

The length distributions of 0 -group cod in these two areas are different in the two years investigated. This is possibly due to the differences in the geographic distribution of postlarvae in July. In 1981 the largest postlarvae were found SW of Bear Island and far from the Norwegian coast. This larvae are likely to follow a more western drifting route. As expected, this year the 0 -group cod in Spitsbergen area have a significantly higher mean length compared to the Barents Sea. In 1982, however, the largest postlarvae were found SSE of Bear Island and more close to the Norwegian coast compared to the distribution in 1981. These larvae are more likely to be distributed in the more eastern area in the Barents Sea. It must be pointed out, however, that the length data shown only represent the fish which have been analysed for genetic characters and do not reflect the total material of 0 -group in the areas.

The genetic data presented suggest no differences between the two main areas in which the 0 -group cod were distributed. In this work, however, data from only one polymorphic locus have been presented and a definite conclusion about possible subpopulation structure of the arctic cod in this area cannot be made. Investigations including larger number of polymorphic loci will possibly offer more detailed information. With regards to the importance of this cod stock, the recruitment problems during the last years and the problems of concervation of genetic resources in fish (FAO/UNEP 1981), basic information of the genetic structure of this stock is necessary for both short time management and for long term preservation of this fish resource.

As recommended by the FAO expert team on concervation of genetic resources in fish, genetic monitoring programmes should be established for important fish stocks to detect any genetic changes due to overexploitation and/or pollution. For the north-east arctic cod stock genetic monitoring on the early stages and during the recruitment process is very desirable.

## ACKNOWLEDGEMENT

This work has received financial support from Norwegian Council for Fisheries Research.
I appreciate the technical assistance of O.I. Paulsen running a large number of starch gel electrophoresis, and the suggestions and critical comments made by G. Nævdal. I will also thank the staff at the Institute of Marine Research who have been involved in the sampling programme.

## REFERENCES

Allendorf, F.W. and Utter, F.M., 1979. Population Genetics. S. 407-454 in Hoar, W.S. and Randall, D.J. (Ed.). Fish Physiology VII. Academic Press, New York.

Christiansen, F.B., Frydenberg, O., Hjort, J.P. and Simonsen, V., 1976. Genetics of Zoarces populations. IX Geographic variation at the three phosphoglucomutase 1oco. Hereditas, 83: 245-256.

Cross, T.F. and Payne, R.H., 1978. Geographic variation in Atlantic cod. Gadus morhua, off eastern North America: a biochemical systematics approach. J. Fish. Res. Bd. Can., 35: 117-123.

FAO/UNEP, 1981. Concervation of the genetic resources in fish: problems and recommendations. Report of the Expert Consultation on the genetic resources in fish. Rome, 9-13 June 1980. FAO Fish Tech. Pap. (217): 43 p.

Frankel, O.H. and Soule, M.E., 1981. Conservation and Evolution. Cambridge University Press.

Frydenberg, O., Møller, D., Nævdal, G. and Sick, K., 1965. Haemoglobin polymorphism in Norwegian cod populations. Hereditas, 53: 257-271.

Harris, H. and Hopkinson, D.A., 1976. Handbook of enzyme electrophoresis in human genetics. North-Holland, Amsterdam.

Jørstad, K.E., Solberg, T. and Tilseth, S., 1980. Enzyme polymorphism expressed in newly hatched cod larvae and genetic analysis of larvae exposed to hydrocarbons. Coun. Meet. int. Coun. Explor. Sea, 1980 (F:22): 1-16. Mimeo.

Jørstad, K.E., 1983. Genetic analyses of cod in Northern Norway. Flфdevigen rapportser. 3, 1983. ISSN 03332595.

Mork, J., Reüterwall, C., Ryman, N. and Ståh1, G., 1982. Genetic variation in Atlantic cod (Gadus morhua L.): A quantitative estimate from a Norwegian coastal population. Hereditas, 96(1): 55-61.

Moth-Poulsen, T., 1982. Genetic variation of cod from the Danish sound: Interrelations of stock from adjacent waters. Coun. Meet. int. Coun. Explor. Sea, 1982 (G:46): 1-19.

M $\phi 1$ ler, D., 1967. Red blood cell antigens in cod. Sarsia, 29: 413-430.

Mø1ler, D., 1968. Genetic diversity in spawning cod along the Norwegian coast. Hereditas, 60: 1-32.

Powell, J.R., 1975. Protein variation in natural population of animals. In Evolution Biology, vol. 8, ed. T.

Dobzhansky, M.K. Hecht and W.W. Steere, pp. 79-119. Plenum Press, New York.

Sick, K., 1961. Haemoglobin polymorphism in fishes. Nature, Lond., 192: 894-896.

Sick, K., 1965a. Haemoglobin polymorphism of cod in the Baltic and Danish Belt Sea. Hereditas, 54: 19-48.

Sick, K., 1965b. Haemoglobin polymorphism of cod in the North Sea and North Atlantic Ocean. Hereditas, 54: 49-69.

Sokal, R.R. and Rohlf, F.J., 1969. Biometry. W.H. Freeman and Co., San Fransisco, Calif.

Soulé, M.E., 1980. Thresholds for survival: maintaining fitness and evolutionary potential. In Conservation Biology: An Evolutionary-Ecological Perspective, ed. M'E. Soulé and B.A. Wilcox, pp. 151-70. Sinauer Associates, Sunderland, Mass.

# MIGRATION, MINGLING AND HOMING OF NORTH-EAST ARCTIC COD FROM TWO SEPARATED SPAWNING GROUNDS 

By

Olav Rune God $\phi$
Institute of Marine Research


#### Abstract

\section*{ABSTRACT}

Migration of mature North-east Arctic cod tagged in 1975 and 1979-81 on two different spawning areas were studied. The numbers tagged were 11,500 in Lofoten and 3,350 off More, of which 1,088 and 476 recaptures are reported respectively.

During the feeding periods in the Barents Sea and the Bear Island - Spitsbergen area mature cod from the two spawning areas intermingle, although the More cod have a more westernly and southernly distribution than cod from Lofoten.

Returns from the experiments clearly indicate homing to the spawning area where tagging occured. Whether this is homing in the strict sense of the word, i.e. return to birth area, can not be answered from these tagging results. The results show that cod spawning off More and in Lofoten do not randomly interbreed during repeated spawnings, and a possible division into separate spawning populations is discussed.


The North-east Arctic Cod is treated as one management unit, with the main spawning areas along the Norwegian coast and nursery and feeding areas in the Barents Sea and the Bear Island - Spitsbergen area. A subdivision into an eastern and a western component according to the location of the nursery areas has been discussed by various authors.

Meek (1916) inferred fish migration from information available on their spawning localities and the distribution of their eggs and larvae. He suggested that the spawning on the two main spawning grounds, Lofoten and Møre, probably resulted in recruits to the eastern and western fisheries off the northern Norwegian coast respectively.

Trout (1957) showed that otolith pattern could be used to seperate the two components. From tagging experiments he also found that cod tagged in the Bear Island - Svalbard area were recaptured to a greater extent in the western and southern spawning localities. This was in contrast to those tagged in Lofoten and in the Barents Sea which were mainly caught in Lofoten.

Tagging experiments carried out in Lofoten in March-April indicated only sporadic migration to the More spawning ground (Dannevig 1953, Hylen og Sætersdal 1959); however, cod tagged on the banks northwest of Lofoten in January and February were caught to a greater extent off the More coast (Hylen og Sætersdal 1959).

The relationship between the More and Lofoten cod has till now not been extensively studied. In the present paper migration, mingling and homing will be discussed on the basis of recent tagging experiments carried out on the spawning grounds in Lofoten and off Møre.

## MATERIAL AND METHODS

Tagging experiments were carried out on both the Lofoten and the Møre spawning grounds during the spawning season in 1975, 1979, 1980 and 1981. The cod used in these experiments were caught by purse seine in Lofoten and mainly by Danish seine and purse seine at the More coast (a few cod caught by gill net and hand Iine were released off Møre in 1975 and 1980). The tagging areas are shown in Fig. 1. The numbers of cod tagged and released from the More and Lofoten spawning grounds in the various years are given in Table 1 . All taggings were done in March and April with the hydrostatic Lea-tag fastened before the first dorsal fin. Reported recaptures are recorded according to the statistical areas used in the Norwegian fisheries (Fig. 1).

Table 1. Numbers of tagged and released cod caught by the various gears off the M $\phi$ re coast and in Lofoten from 1975 to 1981.

| Tagging <br> area | Year of <br> release | Tagging <br> gear | Number <br> tagged |
| :--- | :--- | :--- | ---: |
| Lofoten | 1975 | Purse seine | 2800 |
| Mфre | 1975 | Danish seine | 207 |
|  | 1975 | Gill net | 16 |
| Lofoten | 1979 | Purse seine | 3400 |
| Mфre | 1979 | Danish seine | 347 |
| Lofoten | 1980 | Purse seing | 1500 |
| Mфre | 1980 | Danish seine | 739 |
|  | 1980 | Hand line | 41 |
| Lofoten | 1981 | Purse seine | 3800 |
| Mфre | 1981 | Purse seine | 2000 |
| Lofoten total |  | 11500 |  |
| Mфre total |  | 3350 |  |

The designation "spawning season" will in this paper include the months January-April, while the rest of the year is called the "feeding period". The spawning areas Møre and Lofoten are covered by the statistical areas 07 and 28 and 00 respectively (Fig. 1).


Fig. 1. Norwegian statistical areas in the North-east Atlantic. Tagging areas are encircled.

Rollefsen (1933) distinguished between coastal cod (CC) and North-east Arctic cod (NAC) according to zonation of the otoliths. The CC comprises local cod resources along the coast and has limited migration. The CC as well as NAC spawn in the same areas (Hylen 1964, Godø 1981). In this paper only experiments where the percentage of NAC exceeds $70 \%$ of the total number of


Fig. 2. Recaptures from the Lofoten experiment in 1975. A) Feeding period B) Spawning season.


Fig. 3. Recaptures from the Møre experiments in 1975.
A) Feeding period B) Spawning season.
cod released are included. This percentage is based on samples of otoliths from catches of cod which are thought to be representative of the released cod.

The information from recaptures taken during the first month after release are considered to be biased due to changed behaviour and incomplete mingling. Recaptures during the spawning season of tagging are consequently not included in the presentation. Reported recaptures up untill June 1982 will be analyzed. Reports with imprecise date or area of recapture are excluded.

Tagging experiments have been carried out in Lofoten in every spawning season since 1948. In the present paper those experiments in Lofoten which were carried out in the same years as the experiments off M $\boldsymbol{M}$ re (1975, 1979-1981) will be considered.

## RESULTS AND DISCUSSION

The recaptures are divided into two categories:

- recaptures taken during the spawning seasons
- recaptures taken during the feeding period.

Reported recaptures during the two periods are shown in Figs. 2-9.

The feeding period

A substantial part of the recaptures in the feeding seasons came from the tagging area, particularly for those cod tagged off M M re (Figs. 2-9). Otoliths from 34 cod that were marked off M $\phi$ re and subsequently caught during the feeding periods were available. These were divided into three categories according to the otolith zonation: Coastal cod, North-east Arctic cod and a transition type,



Fig. 5. Recaptures from the Møre experiments in 1979. A) Feeding period B) Spawning season.

| Area | CC type | NAC type | Transition <br> type |
| :--- | :---: | :---: | :---: |
| From Lofoten and <br> northward | 0 | 15 | 3 |
| South of Lofoten | 11 | 5 | 0 |

The results indicate that the NAC do not necessarily migrate to the northern feeding areas immediately after the spawning season. Studies of otoliths from commercial catches has verified the presence of NAC on the M $\quad$ re coast in June. A higher share of CC in the tagged populations from Møre, or simply that the Møre cod feeds on more southerly locations, may explain the higher recapture frequency on the southern grounds from the Mфre experiments.

A comparison of the geographic distribution of recaptures from the two sets of experiments is impeded by the fact that the Mфre cod has to pass through the coastal area from More to Lofoten before possibly mingling with the Lofoten population. If it is assumed that the More and Lofoten cod completely intermingle on the feeding grounds north of Lofoten, the recapture frequency of the two sets of experiments in the various statistical areas should be roughly the same. Figs. 2-9 indicate that M Mre cod are more frequently caught in the western parts. To further analyze this, the results are summarized in Table 2. The eastern region covers the Barents Sea east of $30^{\circ}$ E including all area 03 (Fig 1). The western region comprises the areas west of $30^{\circ} \mathrm{E}$ and includes areas south to Lofoten. The 1979 experiments gave rather few recaptures in the northern areas compared with the others. In addition all recaptures were returned from the western region. All other experiments gave a higher recapture frequency in the western region from the M $\phi$ re releases than from the Lofoten ones. The possibility that this difference in geographic distribution is observed by chance, is less than one percent (Fisher-Irvin test (Hodges and Lehman 1970)). Taking together with the higher recapture frequency from the southern coastal areas of cod tagged in the Møre experiments (Figs 2-9), these results


Fig. 6. Recaptures from the Lofoten experiment in 1980.
A) Feeding period B) Spawning season.


Fig. 7. Recaptures from the Møre experiments in 1980.
A) Feeding period B) Spawning season.
indicate that the main feeding grounds of the M $\quad$ re spawning population tend to be more westernly and more southernly than those of the Lofoten cod.

Table 2. Geographic distribution of recaptures during the feeding period in the Barents Sea.

| Tagging year | Tagging area | $\begin{aligned} & \text { East of } \\ & 30^{\circ} \mathrm{E} \end{aligned}$ |  | West of$30^{\circ} \mathrm{E}$ |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | \% | N | \% | N |
| 1975 | Lofoten | 72 | 23 | 28 | 9 |
|  | Mфre | 0 | 0 | 100 | 5 |
| 1979 | Lofoten | 0 | 0 | 100 | 20 |
|  | Mфre | 0 | 0 | 100 | 1 |
| 1980 | Lofoten | 44 | 11 | 56 | 14 |
|  | M ¢ re | 17 | 2 | 83 | 10 |
| 1981 | Lofoten | 40 | 18 | 60 | 27 |
|  | Mфre | 13 | 3 | 87 | 20 |
| Total | Lofoten | 43 | 52 | 57 | 70 |
|  | Mфre | 12 | 5 | 88 | 36 |

The spawning season

Reported recoveries from the spawning seasons following the years of tagging are shown in Figs. 2-9 and are summarized in Table 3. From $71 \%$ to $92 \%$ of all recaptures reported during the spawning seasons following the years of tagging were taken in the spawning area of release. The basic data show that $9 \%$ of the recaptured More cod were caught in Lofoten, while only $1 \%$ of the spawning season recaptures from the Lofoten releases were caught off More. Most of the tags from the More experiments reported from Lofoten were found before March 15. In the 1981 M $\quad$ re experiment, which had the highest number of returns from Lofoten, 17 out of the 21 recaptured cod were caught

209


Fig. 8. Recaptures from the Lofoten experiment in 1981.
A) Feeding period B) Spawning season.



Fig. 9. Recaptures from the Møre experiments in 1981.
A) Feeding period B) Spawning season.
before this date. The highest spawning activity in Lofoten during the period 1976-81 has been recorded usually to be the first week of April (Solemdal 1981). The same peak spawning time has been shown for the M Mre area in resent investigations (Godø and Sunnana 1983). These results indicate that some of the Møre cod caught in Lofoten were probably on their spawning migration to Møre. The totals of $17 \%$ and $14 \%$ of the recaptures taken in other areas (Table 3), were mainly returned from north of Lofoten.

Table 3. Distribution of recaptures during the spawning seasons following the tagging years.

| Tagging <br> year | Tagging area | Number <br> marked | Place of recapture |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | Lofoten |  | M re |  | Others areas |  |
|  |  |  | \% | N | \% | N | \% | N |
| 1975 | Lofoten | 2800 | 82 | 244 | 1 | 2 | 17 | 52 |
|  | M ¢ re | 225 | 16 | 8 | 74 | 37 | 10 | 5 |
| 1979 | Lofoten | 3400 | 85 | 199 | 0 | 0 | 15 | 36 |
|  | M re | 350 | 0 | 0 | 92 | 36 | 8 | 3 |
| 1980 | Lofoten | 1500 | 88 | 127 | 1 | 1 | 11 | 16 |
|  | M $\mathrm{re}^{\text {e }}$ | 780 | 4 | 4 | 83 | 86 | 13 | 14 |
| 1981 | Lofoten | 3800 | 75 | 169 | 2 | 5 | 23 | 53 |
|  | M $\phi$ re | 2000 | 12 | 21 | 71 | 125 | 17 | 30 |
| Total | Lofoten | 11500 | 82 | 739 | 1 | 8 | 17 | 157 |
|  | M $\phi$ re | 3355 | 9 | 33 | 77 | 284 | 14 | 52 |

Results of former tagging experiments carried out in Lofoten have shown a high return frequency to Lofoten, while reports from More have been scarce (Dannevig 1953, Hylen og Sætersdal 1959, Hylen, Midttun og Sætersdal 1961). The present results from the Lofoten experiments support their earlier findings. In addition the Møre taggings indicate homing to the tagging area
during repeated spawning to nearly the same extent as that found for the Lofoten experiments.

CONCLUSIONS

Tag recoveries from the northern feeding areas indicate that the More cod is more southernly and westernly distributed than cod from Lofoten during the feeding period. Cod from both spawning populations pass through roughly the same localities on their southward bound spawning migration till they reach Lofoten. The area outside Lofoten seems to be the most likely area of separation.

The presented results clearly show that NAC from M $\quad$ re and Lofoten are not randomly interbreeding. It is thus indicated that the More and Lofoten cod belong to two more or less separated spawning populations of the NAC. Genetic studies have till now, however, not shown any differences between the two spawning groups (Reisegg and Jørstad 1983). Whether the return process is homing in the strict sense of the word, i.e. homing to the area of birth, cannot be answered with the data currently available.

The parallel tagging experiments off M $\phi$ re and Lofoten have been carried out through a limited period only and thus the persistence of the observed situation is unknown.

## REFERENCES

Dannevig, G. 1953. Tagging experiments on cod, Lofoten 1947-1952: Some Preliminary Results. J.Cons.int. Explor.Mer, 19: 195-203.

Godø, O.R. 1981. Vintertorskefisket på M $\quad$ re-S申r-Tr申ndelagskysten i 1980. Fisken Hav., 1981(1): 37-48.

Godø, O.R. and Sunnanå, K. 1983. Spawning area and distribution of larval and 0 -group cod, Gadus morhua $L$., at the Møre coast. International Symposium. "The

Propagation of Cod" Arendal, Norway. June 14-17 1983. Fl申devigen rapportser. 3, ISSN 0333-2594.

Hodges and Lehman, 1970. Basic Concepts of Probability and Statistics. Holden-Day San Francisco, Cambridge, London, Amsterdam. 441p.

Hylen, A. og Sætersdal, G. 1959. Skreiundersфkelser og skreifisket i 1959. Fisken Hav., 1959 (1): 1-20.

Hylen, A., Midttun, L. og Sætersdal, G. 1961. Torskeundersфkelser i Lofoten og Barentshavet 1960. Fiskets Gang 5(1961): 101-114.

Hylen, A. 1964. Coastal Cod and Skrei in the Lofoten area. FiskDir.Skr.Ser. HavUnders., 13(7): 27-42.

Meek. A. 1916. The Migration of Fish. Edward Arnold, London. 427p.

Reisegg, J. and Jørstad, K.E., 1983. Stock structure of cod in the Møre area. International Symposium. "The Propagation of Cod" Arendal, Norway. June 14-17 1983. F1ヵdevigen rapportser. 3, ISSN 0333-2594.

Rollefsen, G. 1933. The Otoliths of the Cod. FiskDir. Skr. Ser. HavUnders., 5(7):23-32.

Solemdal, P. 1981. The Spawning Period of Arcto-Norwegian Cod during the years 1976-1981. Contribution No. 2 in ANON (1982): Report of the Working Group on Larval Fish Ecology. Lowestoft, England 3-6 July 1981. Coun.Meet.Int.Coun.Explor.Sea 1982 (L:3): 70-78, 5 figs. (Mimeo).

Trout, G.C., 1957. The Bear Island Cod: Migration and Movements. Fish. Invest., Ser. II., (18), No. 3: 1-15.


[^0]:    * The yearclasses are considered extremely poor if their abundance indices obtained by the survey data at an age of $0+$ are below 0.5 individuals per trawling hour. For such yearclasses very high $R_{s}$ incomparable with other yearclasses are typical.

[^1]:    * The number of valid hauls by a trawl-attached net in autumn-winter 1952-1953 and 1953-1954 was insignificant.

[^2]:    * Few data (less than 150 indivs.)
    ** Very few data (less than 50 indivs.)

