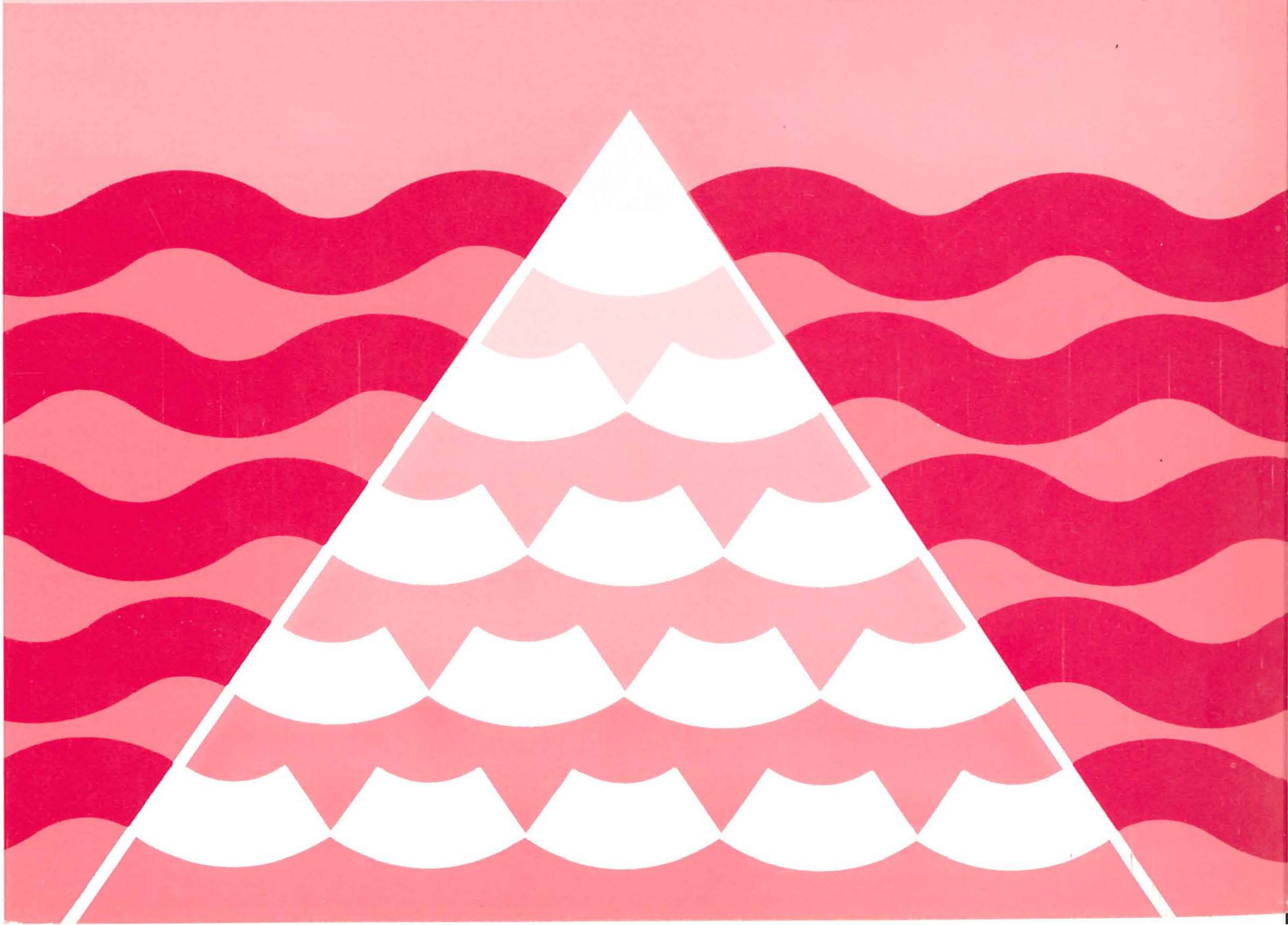
The Effect of Oceanographic Conditions on Distribution and Population Dynamics of Commercial Fish Stocks in the Barents Sea

Proceedings of the third Soviet-Norwegian Symposium

Murmansk, 26-28 May 1986



Polar Research Institute of Marine Fisheries and Oceanography (PINRO),
Murmansk

Institute of Marine Research
Bergen

THE EFFECT OF OCEANOGRAPHIC CONDITIONS ON DISTRIBUTION AND POPULATION DYNAMICS OF COMMERCIAL FISH STOCKS IN THE BARENTS SEA

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Edited by
Harald Loeng

Institute of Marine Research, Bergen
1987

Earlier Soviet-Norwegian Symposia:

Reproduction and recruitment of Arctic cod, Leningrad 26-30 September 1983
Proceedings edited by O.R. Godø and S. Tilseth (1984)

The Barents Sea Capelin, Bergen 14-17 August 1984
Proceedings edited by H. Gjøsæter (1985)

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FOREWORD

Nearly all the fish resources in the Barents Sea are shared between the Soviet Union and Norway. Both countries accomplish scientific investigations on the fish stocks in this area. To be able to coordinate this work, the two principal institutions involved, the Polar Research Institute of Marine Fisheries and Oceanography (PINRO) in Murmansk and the Institute of Marine Research in Bergen are developing, under the aegis of the Mixed Soviet-Norwegian Fisheries Commision, a programme of close cooperation. As a part of this programme a series of symposia have been planned, dealing with important aspects of the fish stocks in the Barents Sea and their environment.

With exception of two Norwegian contributions which are published elsewhere, this volume presents the contributions presented to the third of these symposia, which was held in Murmansk 26-28 May 1986, and dealt with the effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks. The two previous symposia focused on the Arctic cod and the Barents Sea capelin.

In addition to this version in the English language, the contributions will also appear in a version in the Russian language published by PINRO, Murmansk. The editorial changes in this version were all approved by the authors. The editing of English for all papers was attempted in such a way as not to alter the original grammatical style or scientific content of the contributions.

The editor is indebted to Christopher D. Hewes for review and revision the English grammar of the manuscripts.

The Norwegian Fisheries Research Council (NFFR) has kindly supported the printing of this proceedings.

Bergen, May 1987

The editor

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"It is to be expected that variations in the physical conditions of the sea have great influence upon the biological conditions of the various species of fishes living in the sea, and it might therefore also be expected that such variations are the primary cause of the great and hitherto unaccountable fluctuations in the fisheries. It is therefore obvious that it would be of very great importance, not only scientifically but also practically, if the relation between the variations in the physical conditions of the sea and the variations in the biological conditions of the various food-fishes could be discovered."

B. Helland-Hansen and F. Nansen (1909): The Norwegian Sea (p 204).

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Edited by H. Loeng. Institute of Marine Research, Bergen, 1987.

CLIMATIC VARIATIONS IN HYDROMETEOROLOGICAL PROCESSES IN THE BARENTS SEA AND THEIR BIOLOGICAL CONSEQUENCES

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The problem of studying the climate and registration of its variations for national economy is one of the primary scientific and practical problems on the world scale. Such investigations are especially urgent for geographic regions with extreme climatic conditions, to which the Barents Sea also belongs.

In the investigated, relatively shallow area, one finds the boundary of interacting warm Atlantic and cold Arctic waters. Besides the advective oceanographic factors, a great effect on the formation of a hydrographical regime is also produced by the processes of the heat exchange with the atmosphere. As a result the basin of the sea has a complex and dynamic nature of seasonal and year-to-year variations of water circulation, that is the pattern of the frontal zones, water temperatures and ice conditions.

All these large scale variations of hydrometeorological processes have important consequences upon the biology and fisheries of the studied region. The result of many years of investigations, made both by Russian and Norwegian scientists, starting with the classic works by Knipovich, Berg, Helland-Hansen, Nansen, Vize, Derjugin, Hjort, Wiborg and Maslov, bear out convincingly the significance of abiotic factors for both the formation of the year class strength and commercial stocks, their feeding, wintering and spawning conditions, as well as of seasonal migrations of the main commercial fish species in the Barents Sea. It is understandable that great attention was paid to the problems of studying the oceanographical basis for the formation of abundance and distribution dynamics of the main fish species, at Soviet/Norwegian Symposia of 1983 and 1984. Under conditions of northerly distribution of the main commercial fishes - cod, haddock, capelin, herring - it is of vital importance for the fisheries to detect correctly the general features of the present climatic variations, and consequently solve the problem of forecasting the climatic changes in the Barents Sea.

The frequency structure of the long-term fluctuations of hydrometeorological processes in the studied area is characterized both by

- manifestation of a number of statistically reliable large scale cyclic oscillations of 2-3, 5, 7-8, 10-16 years, as well as by

- the trend component which forms the investigated climatic variations of hydrometeorological processes in the Barents Sea (BOCHKOV, SMIRNOV and SARUKHANYAN 1968, BOCHKOV 1977, 1979).

Furthermore, such frequency structure as a whole corresponds to modern scientific ideas of the perennial variability of the atmosphere cryosphere-hydrosphere system on the Earth.

The trend component forming the climatic variations in the Barents Sea plays an important part in the long-term variability of hydrometeorological processes. These climatic changes approximate 20 to 40% of the long term variations of the main factors of hydrometeorological regime (cyclonic activity, water and air temperature, ice coverage etc.). The insufficient duration of these scientific observations do not permit, as yet, to estimate accurately the parameters of climatic varation. However, in numerous works dealing with the climate, the so-called secular (80-100 years) cycle of climatic changes is considered.

The investigations carried out by BOCHKOV (1964, 1972) and BOCHKOV, BOYTSOV and ERGAKOVA (1986) demonstrated that climatic changes in the Barents Sea are very significant and have the following periods:

i) The onset of the 20th century (1900-1918) is characterized by severe climatic conditions. During this period, negative air and water temperature anomalies dominated in the Barents Sea, and heavy ice conditions were observed in seventeen out of the nineteen years. The recurrence of deep cyclons moving from the Atlantic to the Barents Sea declined, and the severest climatic conditions were observed during 1900-1903 and 1915-1918.

ii) The next period, (1919-1929), is of relative stabilization of the climate with a slightly warmer period of 1920-1925 and an insignificantly cold one of 1926-1929.

iii) During the 1930s, a long warm period commenced (1930-1964) in the Barents Sea. During this time positive air and water temperature anomalies and light ice conditions prevailed. Only during 1940-1942 and 1956-1958 brief cold periods were registered.

As to the end of the warm period in the Barents Sea, different points of view are reported in literature. Investigations by BOCHKOV (1964, 1972) and TRESHNIKOV (1973) indicate that the warm period in the Barents Sea did not end in the 40s but had been consistent until the 1960s.

Comparing the 10-year means of air and water temperatures during 1931-1940 and 1951-1960, to the total ice coverage of the Barents Sea, the indices are similar and show that ice conditions in the Barents Sea during 1951-1960 were easier than in the 1931-1940 period. Compared to the 30-years period of 1900-1929, the climatic rise during 1930-1961 amounted to $1^{o}C$ in the air temperature, $0.5^{o}C$ in the water temperature, and the ice coverage was declined by 16%. Consequently a long warm period in the Barents Sea did not end in the early fourties, but continued until the early sixties.

From the mid-60s and up till present day the tendency towards climatic cooling appeared again in the Barents Sea. This certainly should not be treated as a systematic decline in the thermal state of the climatic system. In this case the prevalence of negative water and air temperature anomalies, as well as of heavy ice conditions were postulated. Thus, short warm periods 1972-1976 and 1983-1984 were also recorded against a general background of the cooling of the Barents Sea.

According to a series of investigations, the major reason for the observed climatic changes may possibly lie in the variability of solar activity, in particular its secular (80-90 years) cycle. Thus, MAKSIMOV (1970) and BOCHKOV (1979) found empirically the correspondence between secular changes of the solar activity and climatic variations of water temperature and ice coverage of the Barents Sea. The above sharp increase in recurrence of negative water temperature anomalies since mid-60s is interpreted as the effect of the solar activity at the minimum phase of its secular cycle.

Climatic changes of the atmosphere-cryosphere-hydrosphere system have biological and fishing consequences in the Barents Sea.

In particular, climatic variations in the thermal state of the Barents Sea in 1900-1985 was the main reason for notable changes in the composition and size of biomass for different species of benthos organisms, as well as in their distribution in the area. The results of investigations (BOCHKOV and KUDLO 1973, ANTIPOVA, DEGTEREVA and TIMOKHINA 1974, GALKIN 1976) state uniformly the following peculiarities in variations of the bottom fauna of the Barents Sea related to the changes in the climate:

- During the cold period of 1900-1918 the most important bottom fauna in the southern part of the sea (except in south-west) were the boreal arctic species.

- The warm period in the Barents Sea (1930-1964) was characterized by a notable extension of the range and growing abundance of boreal species, and the corresponding retreat of both the arctic and the boreal arctic forms.

There are reasons to believe that an increasing amount of boreal species of the Barents Sea bottom fauna was a consequense of the climate getting milder in this area, reaching its maximum rather in late 50s - early 60s than in the 30s. Thus, a warm-water mollusc Cardium legantulum was found on the northern slope of the Goose Bank (at the position 72°N, 46°E) in 1959 while in 1933-1938 the range of this species was limited by the coastal 100-120 mile zone at the Murman coast and did not extend eastwards beyond 41°E (GALKIN 1976). At the same time in the 50s - early 60s arctic and boreal arctic species were found farther to the east and north than in the 30s. Such northward distribution of boreal species and increase in their abundance and the simultaneous decline in abundance of the boreal Arctic and Arctic forms from the 1930s to the 1960s, bears out the conclusion that the warm period in the Barents Sea did continue till early 1960s. A new cycle of falling temperatures in the Barents Sea, commenced in the mid-60s, and greatly changed the ratio of warm-water and cold-water species; the range of boreal forms was reduced and the boreal arctic and arctic species of benthos population grew in significance.

It is also noteworthy that according to numerous literature sources, climatic changes of hydrometeorological processes in the Barents and Norwegian Seas actually produced corresponding variations in abundance and composition of the nutritive base of fishing objects, the location of feeding, wintering and spawning ranges of the main commercial fishes, their spawning intensity and fluctuations in recruitment, and production. The data presented at the Soviet/Norwegian Symposia of 1983 and 1984 provide the evidence for this.

The analysis of climatic variations of the hydrosphere-biosphere system made by BOCHKOV et al. (1986) indicates a close correlation between long-period variations in cod and herring year class strength and climatic changes of hydrometeorological processes in the Barents Sea. The results obtained demonstrate that the ratios of poor and rich year classes of cod and herring appearing in climatically cold and warm periods differ greatly. For example, during cold periods (1900-1918, 1965-1984) the recurrence of poor year classes of cod averaged 54% compared to 18% for abundant ones, i.e. it was three times as low. In the period of climatic temperature rise of the Barents Sea waters (1930-1964) these values were 23% and 40%, respectively, i.e. the number of abundant year classes were almost twice the number of poor ones. As for herring, in the warm period of 1930-1964 the recurrence of poor year classes declined by a factor of 3, and that of abundant ones increased by a factor of 2.8. Thus, climatic changes of hydrometeorological processes in the Barents Sea determine directly and uniformly the long term variations in the year class strength, and hence, in the commercial stock of species such as cod and herring. Based on the data for 1929-1984 specification of the degree and nature of the effect produced by oceanographic conditions on the year class abundance of commercial fishes in the Barents and Norwegian Seas indicate a correspondence between strong year classes of cod, haddock and herring and the increase in the heat content of the water masses and of lower ice coverage. Thus, the probability for appearance of strong year classes of cod, haddock and herring in abnormally cold and cold years is extremely low and averages 12% for cod, 8% for haddock and 2% for herring.

In correspondance with this, during abnormally warm and warm years the probability for appearance of highly abundant and abundant year classes of cod, haddock and herring averages 66% for cod, 70% for haddock and 81% for herring, i.e. it is 6-fold for cod, 9-fold for haddock and 40-fold for herring as compared with abnormally cold and cold years. This corresponds with the opinions of SÆTERSDAL and LOENG (1984).

However, we are not apt to relate the year class abundance of these species only to variations in feeding ranges generated by climatic fluctuations. The results of long term complex oceanographic, hydrobiological and ichthyological observations made by PINRO and generalized in the papers by KISLYAKOV (1964), BARANENKOVA (1968), PONOMARENKO (1973) etc. indicate that the most prominent effect on the formation of the year class abundance of cod and haddock at early stages of fish development is produced by oceanographical factors.

In conclusion it should be mentioned that the appearance of rich year classes at a certain historic stage depends not only on the environmental factors, but also on the anthropogenic factor, i.e. on human activity. Particularly during unfavourable climatic conditions and with the low spawning stock of the main commercial fishes in the Barents Sea, it is extremely necessary to support the spawning stocks and above all, those year groups which recruit to these stocks, to maintain a level needed for normal reproduction. This should be of constant concern for all organizations dealing with fisheries and its management in the Barents Sea.

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CLIMATIC VARIATIONS IN THE BARENTS SEA

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ABSTRACT

The circulation system of the Barents Sea is described. Warm water flows into the sea from west and is gradually transformed into Artic waters flowing out from the sea, partly as surface currents, partly as dense bottom water. The climatic conditions of the Barents Sea are determined both by effects from variation in the inflow and by processes taking place in the sea itself. The large variations observed in temperature and salinity from standard sections through the inflowing watermasses are examined and possible explanations are discussed.

INTRODUCTION

Although the main purpose of this paper is a presentation and discussion of the rather large climatic variations observed in the Barents Sea, it is found worthwhile first to give a short description of the circulation system as far as this is known from the literature.

Based on early observations, KNIPOWICH (1905) gave a description of the water masses of the Barents Sea and NANSEN (1906) devized theories on the formation of bottom water in the northern seas including the Barents Sea. Nansen also believed that dense water formed in the eastern Barents Sea could supply the bottom water of the Arctic Ocean through the channel between Novaya Zemlya and Franz Josef Land as indicated by Admiral Makaroff's temperature observations in that area. Recently MIDTTUN (1985) has confirmed Nansens hypothesis. MOSBY (1938) studied the waters between Svalbard and Franz Josef Land. This area is mainly dominated by Atlantic water masses although some outflow from the Barents Sea may take place near Franz Jozef Land.

The majority of the contributions to the oceanography of the Barents Sea are presented by scientists from USSR. TANTSIURA (1959) made a comprehensive analyses of the currents in the Barents Sea. AGENEROV (1946) studied a large number of current observations. The detailed work by NOVITSKIY (1961) delt with the currents of the northern Barents Sea. SARYNINA (1969) was concerned with the bottom water of the Bear Island Channel, and

KISLYAKOV (1964) studied the conditions at the western inlet to the Barents Sea.

Naturally, the southern part of the Barents Sea has been the most intensively studied area, and where several standard sections have been established in order to investigate variations in the inflowing water masses. Measurements in the Kola section were started as early as 1900 by dr. N. Knipowich and have been regularly continued since 1920. BOCHKOV (1976) has studied the observed temperature variations in relation to the solar activity. Three sections observed by IMR have been analysed by BLINDHEIM and LOENG (1981) and later by LOENG and MIDTTUN (1984). The section Fugløya-Bjørnøya (Bear Island) has been studied by DICKSON and BLINDHEIM (1984). Varialbility in the fixed station Nordkapp was analysed by MIDTTUN (1969), while BLINDHEIM, LOENG and SÆTRE (1981) compared the climatic variations in Norwegian coastal water with the observations from the Kola sections. DICKSON, MIDTTUN and MUKHIN (1970) have presented results from the hydrographic work done during the joint 0-groups fish surveys i Barents Sea 1965-69.

Mainly based on the above mentioned literature, LOENG (1987) gave a brief rewiew of the main circulation and water masses of the Barents Sea.

GENERAL DESCRIPTION OF THE PHYSICAL CONDITIONS

The current systems

Fig. 1, which shows a simplified picture of the surface current system, is based mainly on current maps made by TANTSIURA (1959) and NOVITSKIY (1961). Only minor corrections have been made on the basis of some recent observations. The map indicates two main current directions. In the southern part, the currents are towards the east, while the current direction in north is westwards and southwestwards.

The Norwegian Coastal Current flows along the western and northern coast of Norway. Outside, and parallel to the coastal current flows the Norwgian Atlantic Current along the Norwegian continental shelf. Off the coast of northern Norway the Atlantic current splits in two branches, one continuing northwards along the continental slope as the West-Spitsbergen Current, and the other entering the Barents Sea along the Bear Island Channel as the Nordkapp Current.

The southern part of this current continues eastwards together with the Norwegian Coastal Current and proceeds along the Murman coast as the Murman Current. The northern part of the Nordkapp Current divides along three major routes at about 30°E. One arm turns northwards between Hopen Island and the Great Bank where it submerges under the lighter Arctic water. The second branch continues eastwards in the deeper area between the Great Bank and the Central Bank as an intermediate current. The third part turns southeastwards, south of the Central Bank, and flows parallel to the Murman Current, turning northeastwards along the axis of the eastern basins. A much less important inflow of Atlantic water to the Barents Sea takes place along the Storfjordrenna between Bjørnøya and Spitsbergen.

The influx of Artic water to the Barents Sea takes place along two main routes: firstly, between Spitsbergen and Franz Josef Land, and through the opening between Franz Josef Land and Novaya Zemlya (DICKSON et al. 1970).

The main part of the first mentioned current flows as the East Spitsbergen Current southwards along the coast of Spitsbergen. The current flowing southwestwards south of Franz Josef Land, called the Persey Current, splits north of the Central Bank. According to TANTSIURA (1959), one branch turns southwards to the Central Bank, but this part is probably small. The main part of the Persey Current goes southwestwards along the eastern slope of the Svalbard Bank as the Bear Island Current. The current turns around Bear Island and goes northeastwards around the Storfjordrenna.

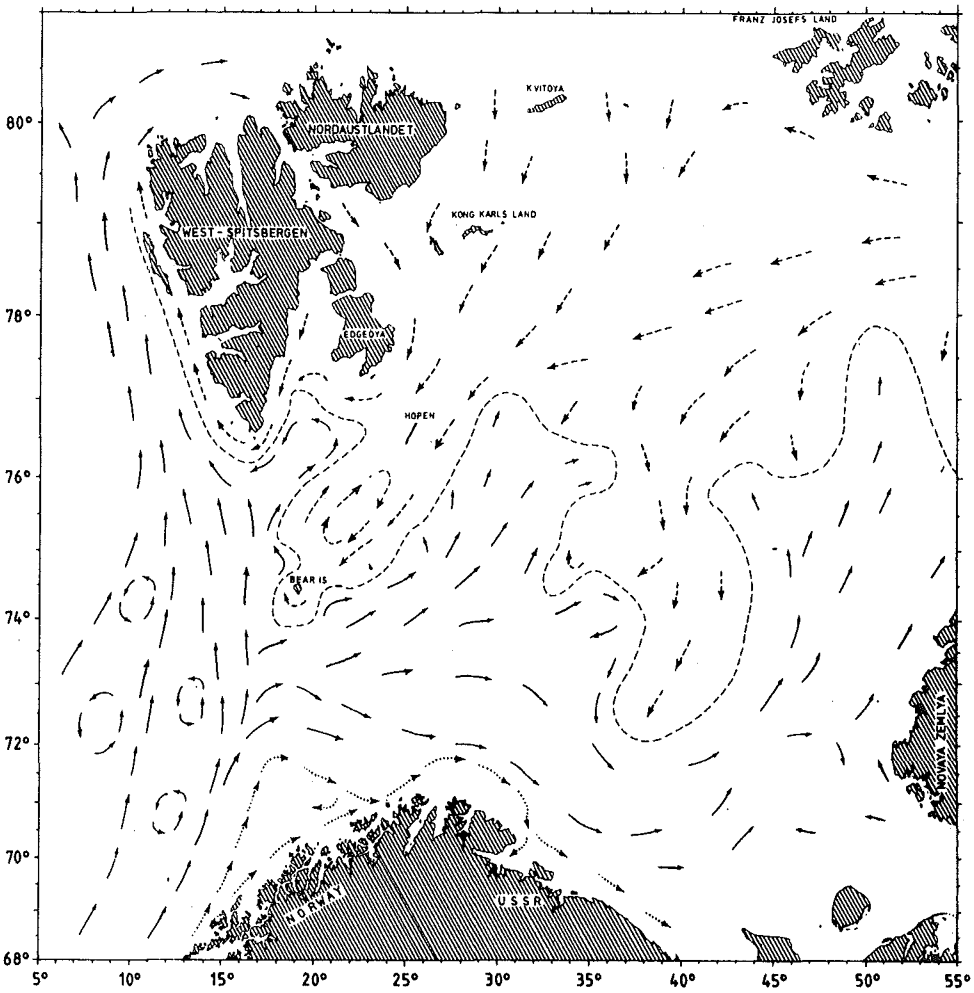

Fig.1. Surface currents in the Barents Sea. Arctic currents (– – ➔), Atlantic currents (——➔) and Coastal currents (·····➔). (Simplified after TANTSIURA 1959, NOVITSKIY 1961).

The details of the current system are poorly known. Hydrographic observations indicate an anticyclonic vortex above some of the bank areas, such as the Central Bank and probably also the Svalbard Bank. This implies a long resident time of the water masses and possibilities for vertical mixing during the winter season (NANSEN 1906). Current measurements indicate almost the same current direction from surface to bottom in areas with only one water mass (BLINDHEIM and LOENG 1978, HELLE 1979). However, in areas where the Atlantic water submerges the lighter Arctic water, as west and south of the Great Bank, one must expect different current direction with depth. Also in areas with outflowing dence bottom water, the current direction is probably different from surface to bottom. Therefore, Fig. 1, only to some extent represents the current systems in intermediate and bottom layers.

Water masses.

Following HELLAND-HANSEN and NANSEN (1909), Atlantic water is defined by salinity, higher than 35.0 °/oo. At the entrance to the Barents Sea, the mean salinity and temperature in the core in autumn during the period 1966-77 was 35,13 and 6.2°C, respectively (BLINDHEIM and LOENG 1981). Further east in the Barents Sea the characteristics change to lower salinity and temperature as shown in Fig. 2,and also clearly demonstrated by LOENG ans MIDTTUN (1984). As will be discussed later, there are also great long-term variations in the properties of the Atlantic inflow to the Barents Sea, which again may influence the properties of the locally formed water masses.

The coastal water is characterized by low salinity (S < 34.7 o/oo) and relatively high temperature (t > 3°C). This water mass is also most easily traced by the salinity (Fig. 2). The light coastal water spreads out in a wedge form above the heavier Atlantic water. The seaward extent of this wedge of Coastal water varies seasonally and has its minimum in the winter (SÆTRE and LJ0EN 1971).

The Arctic water (or Barents Sea winter water) is during summer mainly found in the intermidiate layer, between 20-150 m, in the northern Barents Sea. The core is usually found between 30-60 m with temperature below -1.5°C and salinity between 34.4-34.6 o/oo. In the horizontal map (Fig. 2) most of the water with temperature below 0°C is Arctic water.

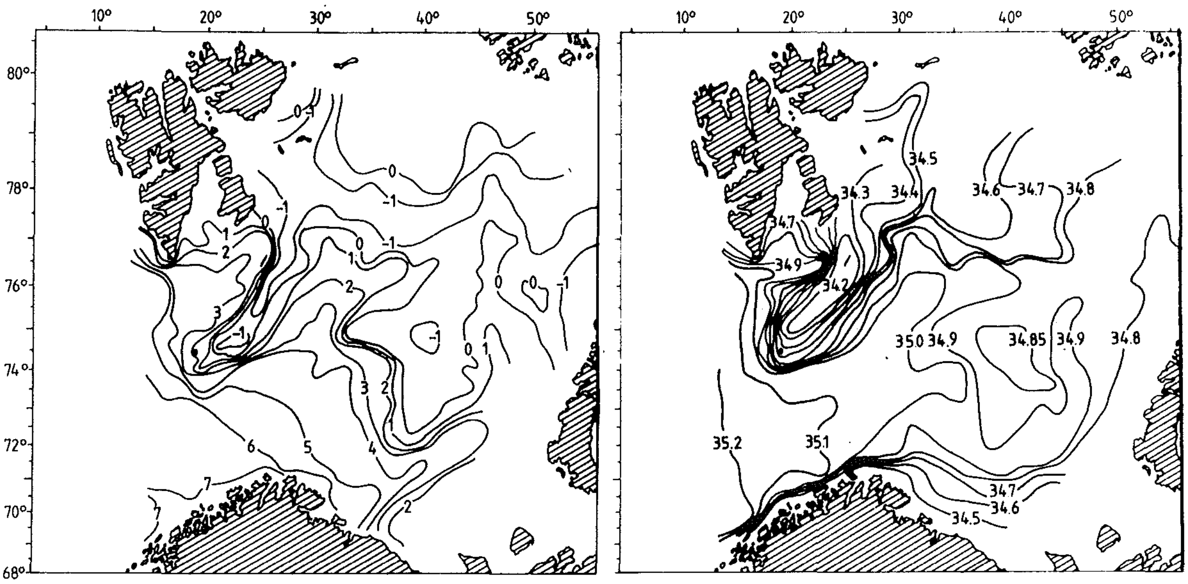

Fig. 2. Distribution of temperature (left) and salinity (right) at 100 m depth, autumn 1984.

The area between the Atlantic and the Arctic water masses is called the Polar front. In this area Arctic and Atlantic water mix. In the area west of the Central Bank, the Polar front is sharp and follows typical features of the bottom topography. In the eastern Barents Sea the front area is less distinct, and a mixed water mass cover great areas.

Bottom water of different kinds may be formed at various places in the Barents Sea. Dense bottom water is formed through rejections of brine during ice freezing and is a more or less regular phenomenon, particularly on the shelf of Novaya Zemlya, but sometimes also on the Svalbard Bank (MIDTTUN 1985).

Bottom water with a somewhat lower salinity is formed on the Central Bank during the winter season. The bottom water of the Bear Island Channel, however, is formed in the frontal zone (Polar front area) during the period of vertical winter circulation on the southeastern slope of the Svalbard Bank (SARYNINA 1969). This bottom water may have temperatures higher than 1°C.

The winter and summer situations differ most clearly in the vertical structure of the water masses. During winter, vertical mixing takes place all over the Barents Sea. Over shallow bank areas, convection may reach down to bottom and contribute to bottom water fomation as already mentioned. In the deeper areas, the water masses may be homogeneous down to more than 200 m. In the ice-covered areas, the temperature will be homogeneous, while a salinity gradient will maintain a weak vertical stability. Ice-freezing with rejection of brine will break down the salinity gradient.

Sea ice conditions.

The variation in the position of the ice edge, based on satellite images from a period of 10 years,(1971-1980), is shown in Fig. 3 for the months February, April, June, August, October and December. The figure shows considerable variations in ice extension, which may take place from year to year. Some months, especially in summer and autumn, these variations may exceed 500 km. In spite of this, the seasonal variations of the sea ice extension is, in its broad features, similar from one year to another with maximum and minimum extension in March-May and August-September, respectively (LOENG 1979, LOENG and VINJE 1979). The formation of ice usually starts in late September or in October, and the ice border moves rapidly southwards to the Polar front during November and December. The melting of ice starts in May-June, but in the beginning the melting is very slow. The retreat of the ice border is usually most rapid in July and in early August.

Fig. 4 shows the variations of maximum ice coverage in the years 1979-1985. In the vicinity of Bear Island, there is almost no variations from one year to an other. In the eastern Barents Sea, however, the variations are considerable.

As seen in Figs 3 and 4, the year-to-year variations may be considerable. Some authors have proposed cyclic variations in the sea ice conditions of 3-5 years (KISSLER 1934, LUNDE 1965). Long-term variations, not necessarily of cyclic nature, are also well known from other marginal areas of the Arctic, e.g., on the west coast of Greenland (DUNBAR 1972).

CLIMATIC VARIATIONS

General description

Climatic variations can be recorded in sections crossing the inflowing water masses. At the entrance, between Fugløya and Bjørnøya (along 19°30'E), temperature and salinity have been observed each autumn since 1964, while the Kola-section (along 33°30'E), with exceptions of two periods, 1906-1920 and 1941-1944, has been observed by the Russians back to 1900.

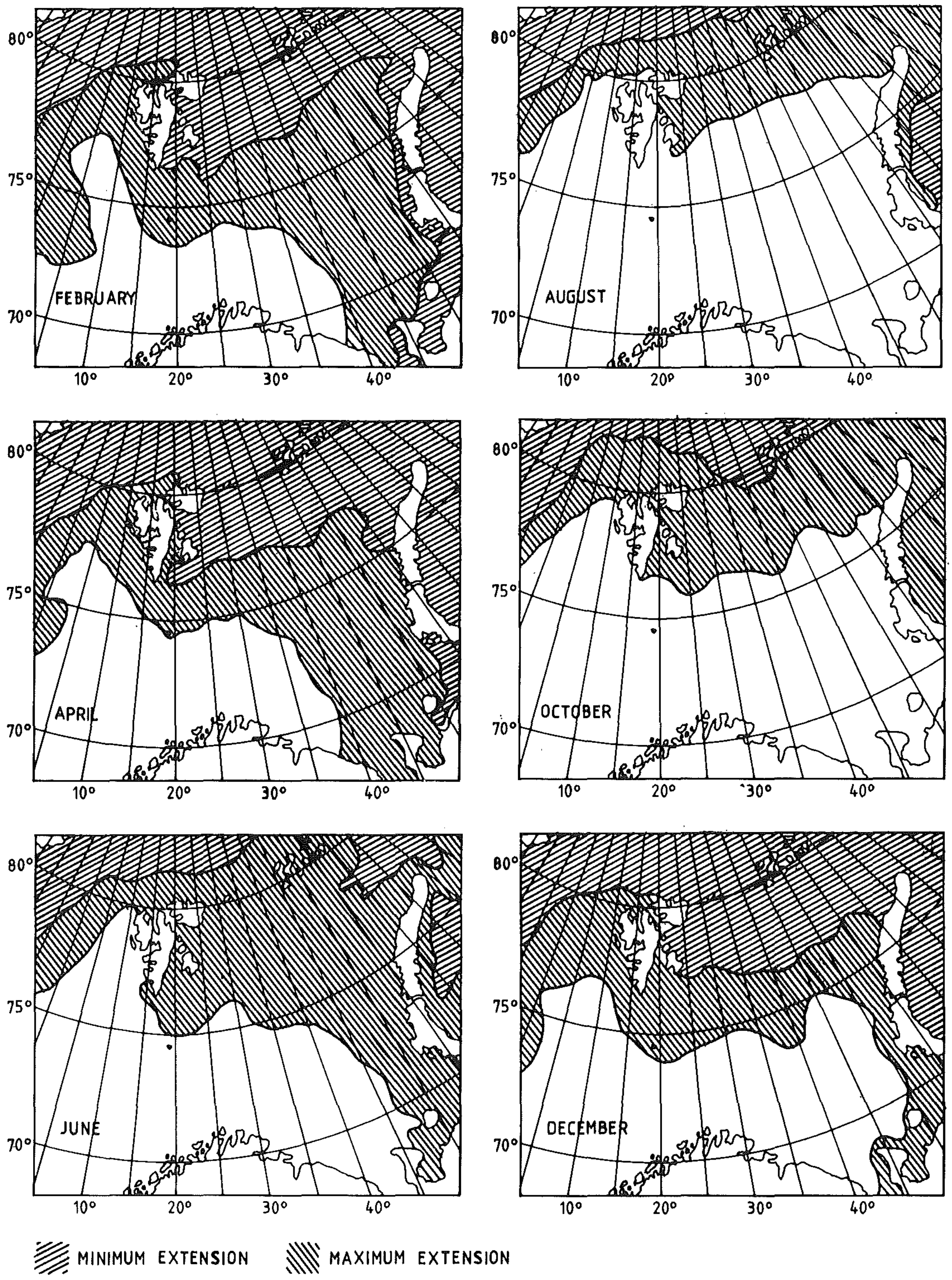

Fig. 3. Southern limit of sea ice at the end of the months February, April, June, August, October and December during the period 1971-1980 (after VINJE 1983).

MIDTTUN et al. (1981) using the Kola-section, calculated monthly mean temperatures on the basis of the period 1921-1980 and anomalies from those means have been calculated for the whole period up to 1985 (Fig.5).

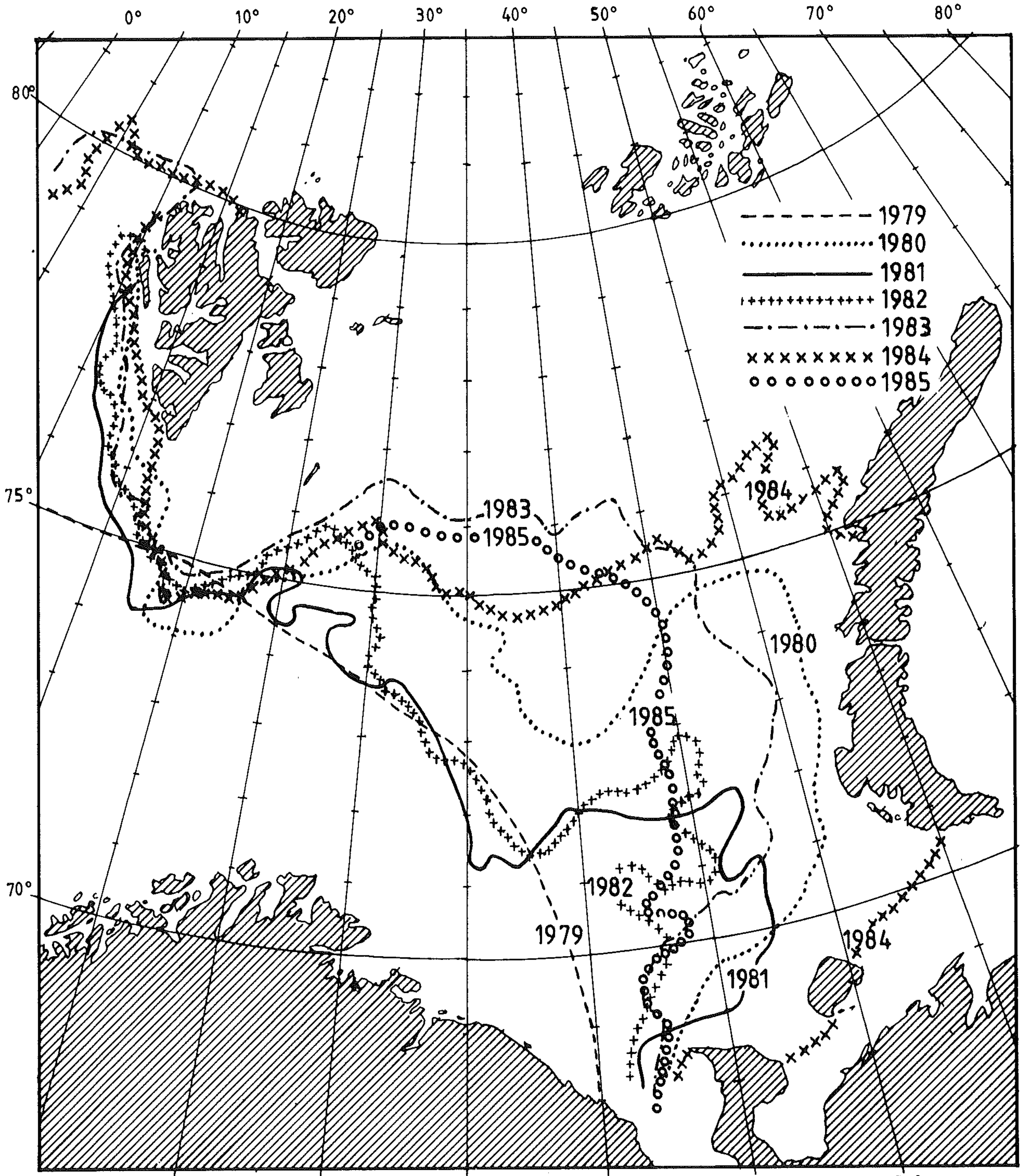

Fig. 4. Maximum ice coverage in the Barents Sea during winter in the period 1979-1985.

Fig. 5 shows that the years up to 1906 were cold. According to SÆTERSDAL and LOENG (1984), almost the whole missing period, 1907-1920, also was cold. After some years with higher temperatures in the beginning of the 1920's, the years up to 1930 had lower temperatures than normal. The longest period of a warm regime was between 1930-1939, with maximum in 1938. The years after 1945 are characterized by fluctuations of duration 3-5 years. These periods

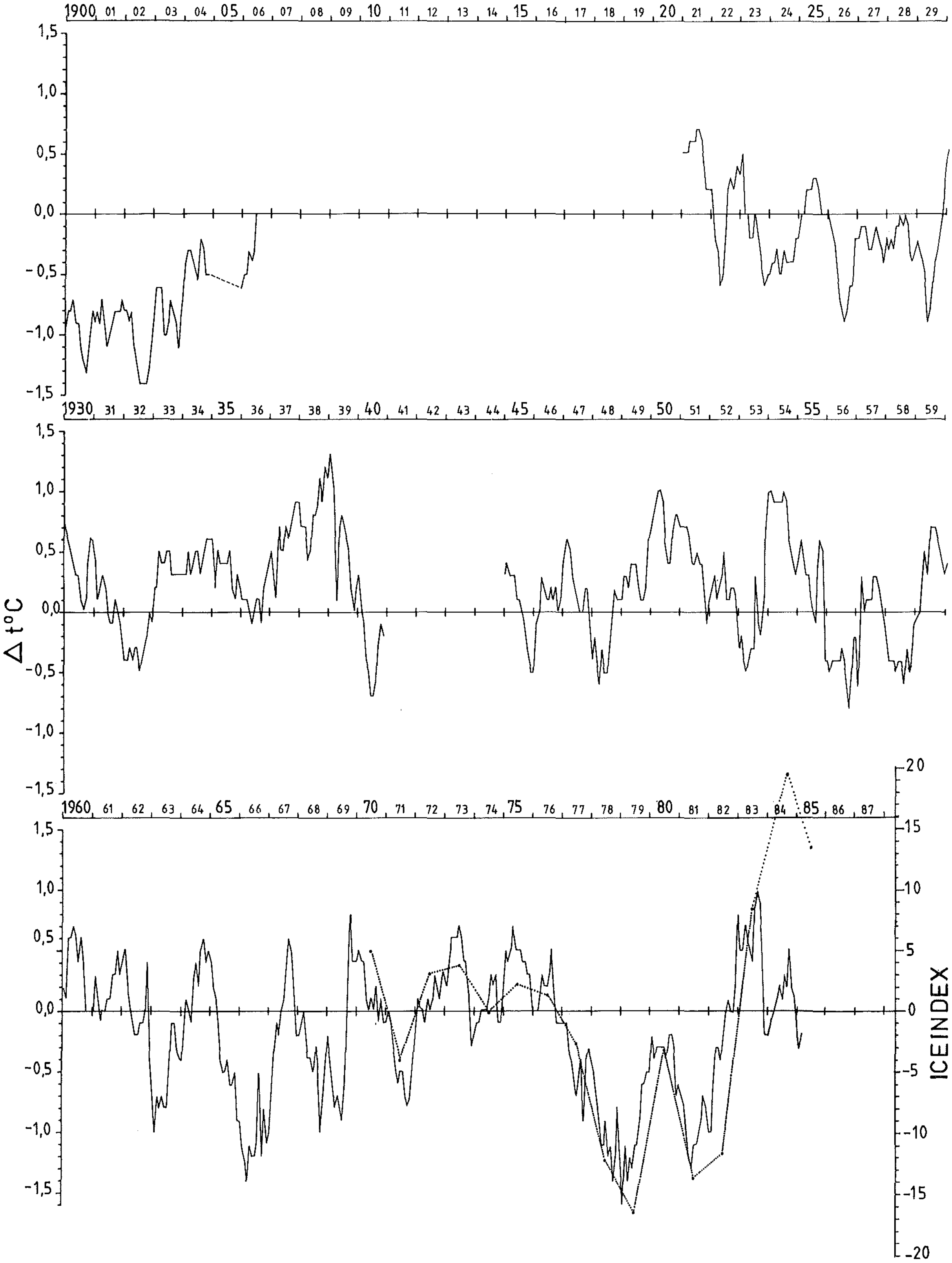

Fig. 5. Temperature anomalies in the Kola section for the period 1900-1985 (continuous line) and ice index for the Barents Sea (dotted line).

coincide with cyclic variations in sea ice condtions, as proposed by KISSLER (1934) and LUNDE (1965). A period of 11 years, which coincides with the solar activity cycle, has also been suggested both for temperature and ice conditions (BOCHKOV 1976).

During the 1970's, large variations have been observed in climatic conditions in the Barents Sea. The period 1970-1976 was warm, while the second half of the decade was charcterized by low temperatures (Fig. 5). Through the beginnings of the 1980's, temperatures were increasing. An ice index for the period after 1970 shows similar trends, indicating a close relationship between variations in sea temperature and ice conditions (Fig. 5).

The salinity also shows great variations after 1970. Fig. 6 shows temperature and salinity variations between 50 and 200 m at a section between Fugløya and Bjørnøya (BLINDHEIM and LOENG 1981, LOENG and MIDTTUN 1984). The temperature variations are equal to those in the Kola-section. The most striking feature in the salinity curve is the decrease, which started in 1969 and lasted until 1979. The minimum in 1978-1979 is characterized by the lowest salinity values ever observed in this section, and the salinity of the Atlantic inflow was below 35.0 ^{0}/oo. Since then the salinity has been increasing towards the mean values for the period 1966-77, given by BLINDHEIM and LOENG (1981).

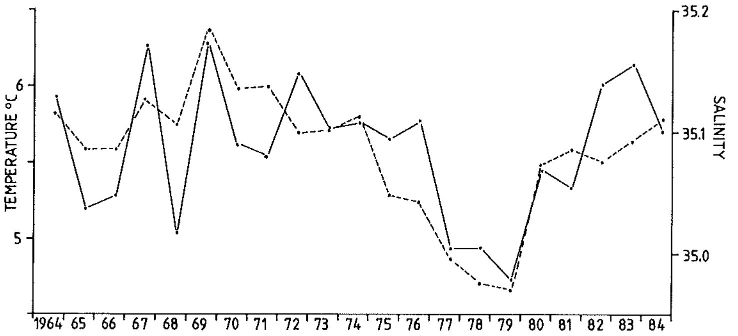

Fig. 6. Mean temperature (continuous line) and mean salinity (broken line) of the Atlantic inflow to the Barents Sea in autumn during the period 1964-1985.

Already in 1909 HELLAND-HANSEN and NANSEN (1909) suggested that climatic variations in the Barents Sea probably are of advective nature. They observed a time lag of one year between Lofoten and the Kola-section. LOENG, NAKKEN and RAKNES (1983) showed that temperature changes in the eastern part will most often occur about one year later than in the western part. Also in the Norwegian Sea, climated variations seem to be due to advective processes in the Atlantic inflow (BLINDHEIM 1987).

Discussion of possible causes

As shown by the majority of the other contributiones to this Symposium, the rather large variations observed in the physical environment of the Barents Sea exercise great effects on biological conditions in the large fish stocks of the sea. It is therefore felt important to discuss possible explainations and try to understand the physical causes behind the climatic variations observed in the inflowing watermasses. The variations are described by the long series of temperature observations in the Kola section crossing the main branch of the Murman Current (Fig 1). The temperature is alternating with warm and cold periods in succession with lenghts of 3-5 years (Fig. 5). Similar variations are observed in other sections further west in the Barents Sea, and are also reflected in the ice coverage. It can be seen from Figs. 3 and 4 that the ice coverage in winter has the greatest variations over the Central Bank and in the eastern part of the Barents Sea.

The variations may be hypothetically explained as caused by similar variations in the property of the inflowing water, that is, the current system of constant velocity and volume is bringing in a watermass with changing temperature and salinity. But the variations may as well be a result of variations in the current system itself. Since both temperature and salinity increase in countercurrent directions, high velocity should result in high temperature and salinity, low velocity in low temperature and salinity. In the last case the variation of the current system has to be explained. Again, the variation in the current activity could be forced upon the sea from outside, but may as well be a result of processes taking place in the Barents Sea itself.

Water of high density is formed during the winter as a result of cooling and ice formation and drained out from the sea as bottom currents. The process of ice formation is also the source to formation of the light surface water brought out by the Arctic currents. The process is described in detail by MIDTTUN (1985) and can be regarded as a separator transferring salt from surface water to deep water and in this way gradually building up dense bottom water and light surface water. The bottom water forms bottom currents along the righthand side of channels leading out from the Barents Sea to the Norwegian Sea through the Bear Island Channel and to the Polar Sea through the Novaya Zemlya-Franz Josef Land Channel. The water volume, which in this way leaves the sea, has to be replaced by inflowing water from west. The activity in building up dense bottom water may vary from one year to another followed by variations in the outflow with corresponding change in the inflow as reaction. After a great inflow it may take more than one year to again build up the required conditions to initate the next dense water outflow. To some degree the rate of dense water formation will depend on the salinity of the inflowing water since density is a function of salinity.

Fig 7 shows that the areas with high density water formations are located over the Central Bank and on the Novaya Zemlya Bank. This is the same area where the winter ice coverage changes (Fig. 4). Fig. 8 shows the effect of the large water exchanges between 1982 and 1983. The inflow and outflow from the Norwegian Sea to the Barents Sea has been measured in the section between Fugløya and Bjørnøya from a series of anchored current metres. The results are presented in Fig. 9. Transport calculations indicate about 3 Sv. in and around 1 Sv out through the section. This would require another outflowing current, most likely located in the channel between Novaya Zemlya and Franz Josef Land. Outflow of high density water in this area has been recently described by MIDTTUN (1985).
The above considerations lead us to formulate the following tentative conclusions:

1. The mechanisms behind the climatic variations in the Barents Sea can be described as the result of dense water formation during winter cooling and ice formation. This process transforms the inflowing water mass into two outflowing waters, viz. bottom water of high density and surface water of low density.

2. The transforming process is time dependent on the property and quantity of the influx. After a period of high influx, the transformation requires

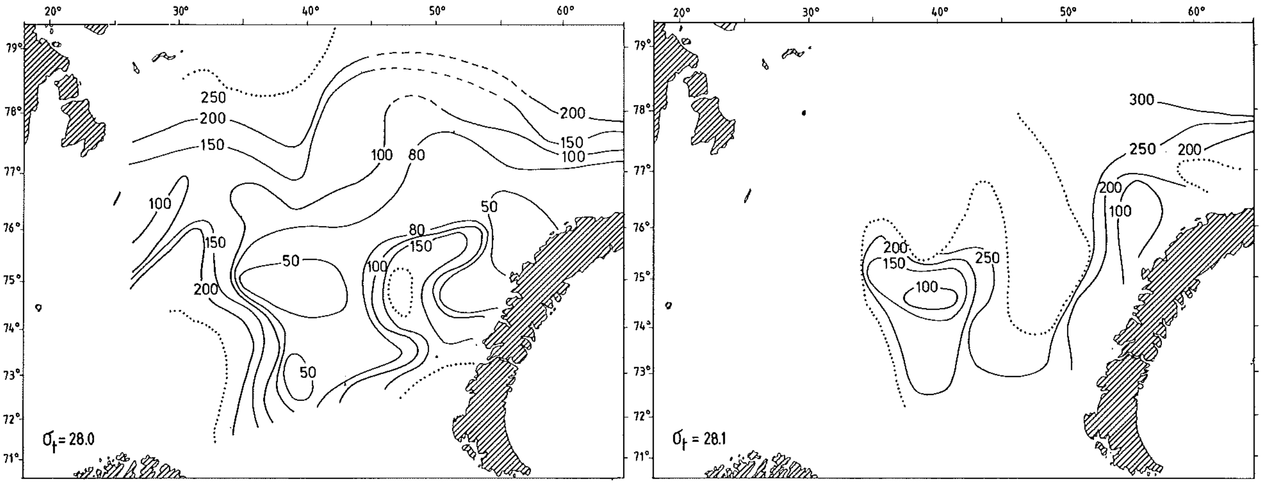

Fig. 7. Depth of the σ_t surfaces 28.0 and 28.1 in 1977. Dotted lines indicate area limitations.

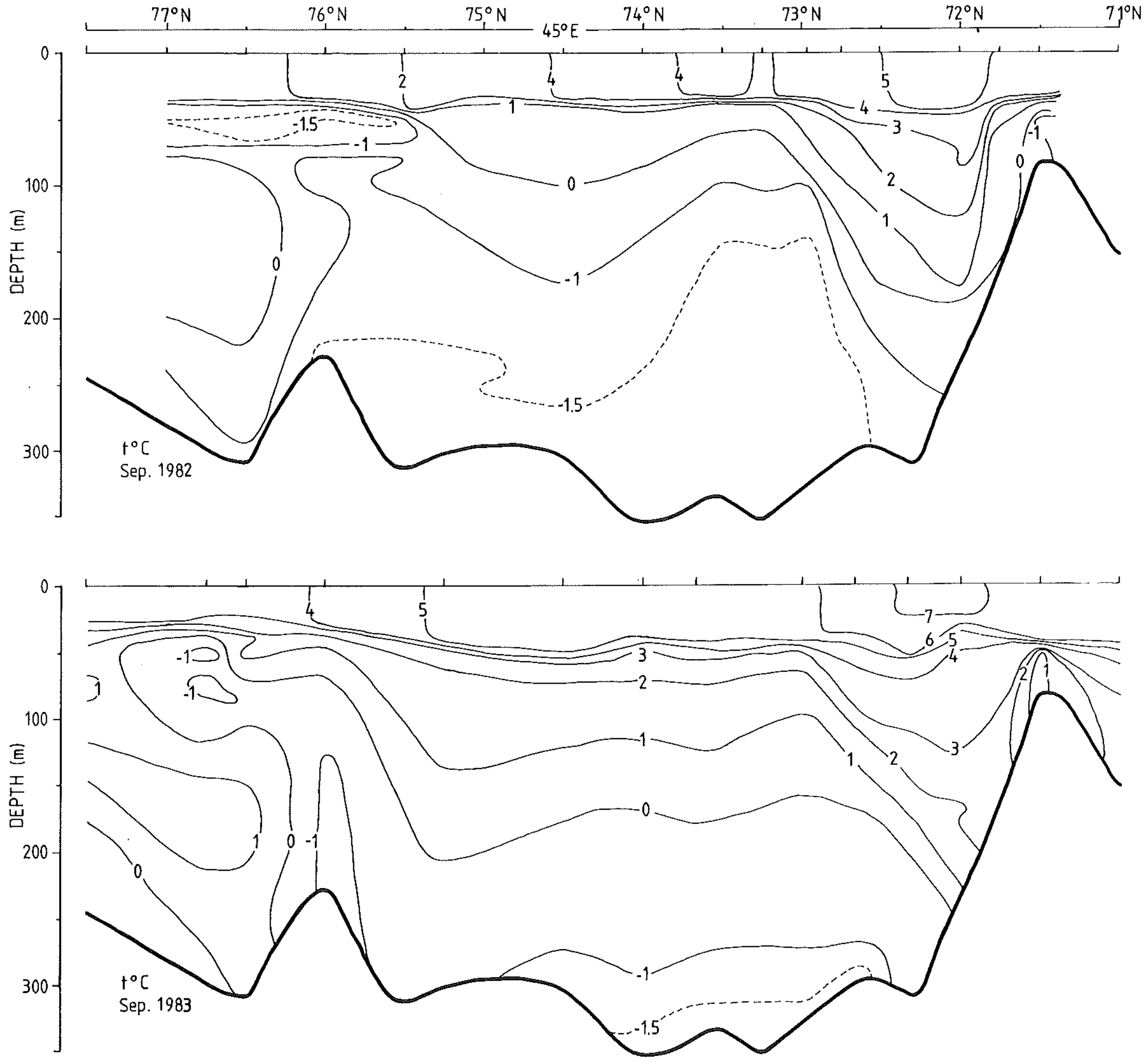

Fig. 8. Temperature in the meridional section of 45°E in September 1982 and 1983.

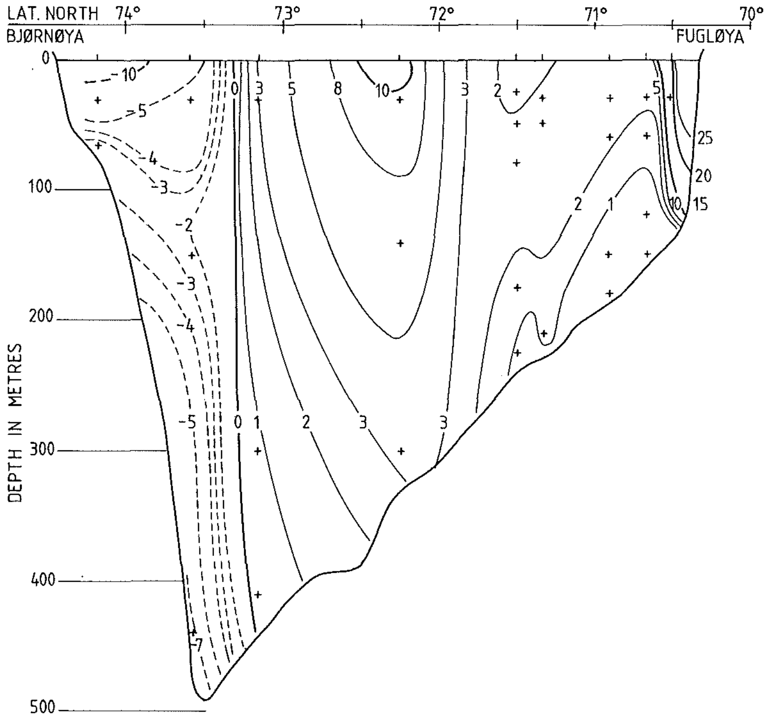

Fig. 9. Mean current component ($cm \cdot s^{-1}$) through the Fugløya-Bjørnøya section from measurements at mooring stations in September-October 1978. The observation depths are indicated by +. (BLINDHEIM, personal communication).

more than a one year's winter cooling to build up the bottom water density high enough to initiate a new outflow.

3. The bottom water outflow takes place mainly in the northern Bear Island Channel and along the southern part of the Novaya Zemlya - Franz Josef Land Channel.

4. To confirm this hypothesis direct current observations in the above mentioned areas of outflow are strongly recommended.

ACKNOWLEDGEMENTS

We wish to express our appreciation to Mr. H. Kismul for preparing the figures and to Ms. I. Byrkjedal and I. Mæland for typing the manuscript.

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THE EFFECT OF OCEANOGRAPHIC CONDITIONS ON DISTRIBUTION AND POPULATION
DYNAMICS OF COMMERCIAL FISH STOCKS IN THE BARENTS SEA
Proceedings of the third Soviet-Norwegian Symposium, Murmansk, 26-28 May 1986
Edited by H. Loeng. Institute of Marine Research, Bergen, 1987.

PRIMARY PRODUCTION IN RELATION TO CLIMATIC CHANGES IN THE BARENTS SEA

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ABSTRACT

The Barents Sea is characterized by extreme environmental conditions that have considerable influence on the biological development, especially during spring. Based on physical and biological observations obtained during a six years period and a mathematical model for phyto- and zooplankton, we have examined the biological development in relation to the climatic changes which occurred during this period. The main effect of climatic variations is in determining the timing of the phytoplankton spring bloom in the different water masses. Warm years are characterized by a delayed phytoplankton bloom and an earlier stage development of zooplankton in Atlantic waters, apparently resulting in a higher proportion of the spring bloom being grazed and channelized to higher pelagic trophic levels. Cold years, on the contrary, can result in earlier ice-edge spring bloom and late development of zooplankton, causing a significant portion of the primary production to be left ungrazed and to sediment out to the deeper water layers and the bottom.

INTRODUCTION

The influence of ice and hydrographical conditions on the biological production of the Barents Sea has been described based both on field observations (MARSHALL 1957, REY and LOENG 1985) and on simulations with a mathematical phytoplankton model (SLAGSTAD 1985). The start of the spring phytoplankton bloom in the central part of the Barents Sea is closely related to water column stabilization, as described by SVERDRUP (1953). The timing of the bloom can be quite variable depending on the specific physical factors that are responsible for stabilization (REY and LOENG 1985). In waters that have been covered by ice, the necessary stability for the spring bloom is produced by melting of the ice. As a general rule, the bloom will take place earlier here than in more southern areas with Atlantic waters not covered by ice, where the vertical stability is due to warming of the upper layer (SKJOLDAL, HASSEL, REY and LOENG 1987).

As the ice recedes northwards, it is followed by a phytoplankton bloom at its edge. The marked pycnocline formed by the meltwater will effectively isolate the surface layer from the deeper water layers below it. Following nutrient depletion by the spring bloom, this upper layer can be characterized as oligotrophic water, where most of the biological production is supported by remineralization of nutrients, either through zooplankton grazing or bacterial activity.

Since the phytoplankton production processes are closely related to the physical environment, changes in hydrographical and ice conditions from year to year will undoubtedly have an effect on the temporal development of the spring bloom and possibly also on the overall production of the Barents Sea. Here we examine the possible effects of such climatic changes by using data obtained in late spring or early summer through 6 years, from 1979 to 1984. The basic data are presented in SKJOLDAL *et al.* (1987) and analysed there with respect to the timing of the bloom development and zooplankton reproduction and development. In the present paper, we analyse these data further, emphasizing the quantitative and vertical aspects of primary production. For this purpose we have also included results from a mathematical simulation model (SLAGSTAD 1981, 1982).

MATERIAL AND METHODS

The present investigation is mainly based on observations made during late spring or early summer at a south-north section, section I, in the central Barents Sea (REY and LOENG 1985, SKJOLDAL *et al.* 1987) each year in the period 1979-1984. Sampling and analytical procedures have been previously described (ELLERTSEN, LOENG, REY and TJELMELAND 1981, ELLERTSEN *et al.* 1982, GJØSÆTER, HASSEL, LOENG and REY 1983a, GJØSÆTER *et al.* 1983b, HASSEL, LOENG, REY and SKJOLDAL 1984, REY and LOENG 1985). A short overview of the methods is also presented by SKJOLDAL *et al.* (1987).

A phytoplankton model was used to follow the dynamics of phytoplankton and nutrients as functions of the seasonal light intensity, vertical mixing, ice cover and zooplankton grazing (SLAGSTAD 1982). The equation describing the growth, sinking and turbulent mixing of phytoplankton is given by:

$$\frac{\delta P_{(t,z)}}{\delta t} = -W \frac{\delta P}{\delta z} + \frac{\delta}{\delta z} \left(D_z \frac{\delta P}{\delta z}\right) + f \text{ biol} \qquad (1)$$

where z is depth, t is time, and P(t,z) is the concentration of phytoplankton. The first term on the right hand side of the equation represents the vertical transport (sinking), whereas the second term represents the vertical turbulent mixing. The biological term, f biol, describes how respiration, light, nutrients and grazing affect the phytoplankton production:

$$f \text{ biol} = P_{max} f_1(I_z) G_N P - \phi_r P - qI(P) \qquad (2)$$

The first term on the right hand side of the equation represents growth and the second term represents respiration and mortality of the phytoplankton. The last term gives the effect of the grazing pressure from zooplankton. P_{max} is the maximum growth rate or uptake rate of nitrogen (which is assumed to be the limiting nutrient) and is a function of temperature. $f_1(I_z)$ gives the effect of light on the growth rate (SLAGSTAD 1982). G_N is a Michaelis-Menten expression to account for reduced growth rate when concentration of nitrogen is reduced (SLAGSTAD 1985).

A mathematical model was also used to calculate production of zooplankton as a function of the concentration of phytoplankton and temperature. This model is described in detail by SLAGSTAD (1981) and only a brief outline is given here. The zooplankton biomass was assumed to be dominated by *Calanus finmarchicus* and the model parameters were adjusted accordingly. The zooplankton model is made up of three sub-models. The population sub-model calculates growth and reproduction rates as functions of the biological state. The biological state, which is calculated in the second sub-model, is again a dynamic function of the environment (available food concentration and temperature) and animal size. The third sub-model calculates the vertical migration of the animals as a function of the biological state, food concentration and light intensity.

The zooplankton model is coupled to the phytoplankton model in order to represent this dynamics as a function of physical conditions and grazing.

RESULTS

The position of the ice edge from January to September in the years 1979-1984 is shown in Fig. 1. It is seen that 1979 and 1981 were years when the ice was distributed south of 75°N. In contrast, in 1983 the ice edge barely extended south of 77°N.

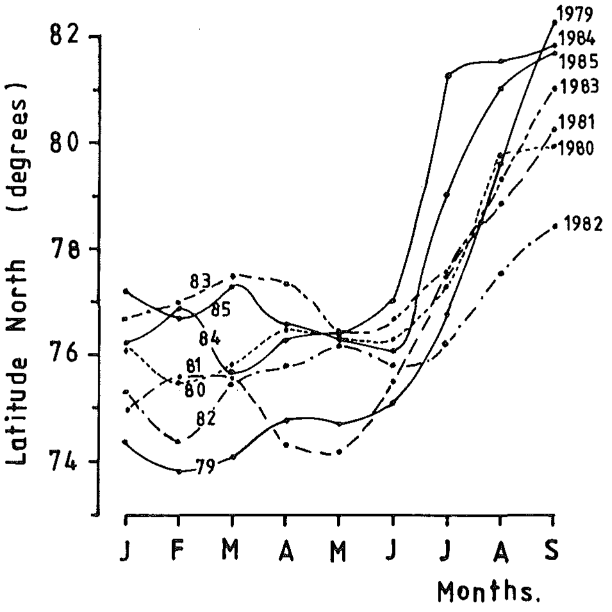

Fig. 1. Monthly mean position of the ice border between 30 and 35°E from January to September in the years 1979-1985.

A summary of positions of the ice-edge and the melt water front at different times of the year is presented in Table 1. The ice recedes in general fairly slowly from April to June, whereas its receding speed increases markedly up to September when it usually reaches its northernmost extension. The melt water front, on the contrary, recedes northwards much less than the ice edge (Table 1). The recession of the melt water front is mainly the result of erosion by mixing with Atlantic water. As can be seen from Table 1, all the area north of about $76^{\circ}30'$N remains covered by melt water. The strong pycnocline associated with this layer effectively limits the input of nutrients to the upper mixed layer, resulting in an oligotrophic surface layer that remains throughout the summer. This is an important feature which influences the overall productivity of this region.

Table 1. Positions of ice edge and melt water front and extension of the melt water area in the years 1979-1984.

Year	Average ice edge position			Postition of melt water front		Extension of melt water area in September	
	April	June	Sept.	June	Sept.	Eroded	Not eroded
1981	74°12'N	75°30'N	80°15'N	75°05'N	76°10'N	118 nm	245 nm
1979	74°42'N	75°05'N	82°10'N	75°20'N	75°50'N	68 nm	380 nm
1982	75°48'N	75°50'N	78°25'N	76°10'N	76°50'N	62 nm	95 nm
1980	76°10'N	76°18'N	79°55'N	75°55'N	76°30'N	20 nm	205 nm
1984	76°35'N	77°05'N	81°50'N	76°00'N	76°50'N	15 nm	300 nm
1983	77°25'N	76°42'N	81°00'N	76°15'N	76°50'N	8 nm	250 nm

The stage of development of the hydrographical and biological conditions at the time of coverage of section I in each of the years 1979-1984 can be observed in Figs 2 to 4 which show the vertical stability of the water column, the chlorophyll _a_ concentration, and nitrate utilized, respectively. The stability in the upper 100 m was always higher in the area that had been covered by ice than in the Atlantic water not influenced by ice (Fig. 2). The stability in the melt water area was mainly the result of a decrease in salinity, while in the southern part of the section it was due to an increase in temperature. The vertical stability of the water column south of the melt water front was lowest in 1982, higher in 1983 and 1984 and highest in 1980. The position of the meltwater front, which at this time of the year reflects quite well the southernmost extension of the ice-edge, also indicates that 1979 and 1981 were cold years.

The time of coverage has varied somewhat, and this must be taken into account when comparing the bloom developments in the different years. The section was covered on 11-12 July in 1979, in late June in 1980 and 1981, and in early June in 1982, 1983 and 1984 (SKJOLDAL _et al._ 1987). In the cold years 1979 and 1981, the low concentrations of chlorophyll _a_ north of the melt water front both in the upper mixed and deeper layers, together with the high nitrate utilization, indicate that long time had elapsed since the spring phytoplankton bloom at the ice edge. However, in the Atlantic water not covered by ice in 1981, relatively high average concentrations of chlorophyll _a_ in the upper layer indicate that the spring bloom had taken place more recently.

The high chlorophyll _a_ concentrations found during late June in 1980, especially south of the melt water front, indicate that the spring phytoplankton bloom took place much later than in 1979 and 1981 (Fig. 3). The average nitrate utilization in the upper layer in these three years varied from about 10 to 12 µM nitrate, indicating nitrate depletion of the upper layer by phytoplankton (Fig. 4). The relatively high nitrate utilization below the upper mixed layer is due mainly to the conspicuous chlorophyll _a_ maximum that develops below the pycnocline towards the end of the spring bloom (REY and LOENG 1985). A trend of lower nitrate utilization towards the north can also be observed; this could reflect a trend in the spring phytoplankton bloom development, with the youngest stage of the bloom to the north. The same trend can be observed in the depth stratum from 100 to 200 m, although the decrease in nitrate concentration in this layer reflects upwards transport by vertical mixing and subsequent utilization in the euphotic zone.

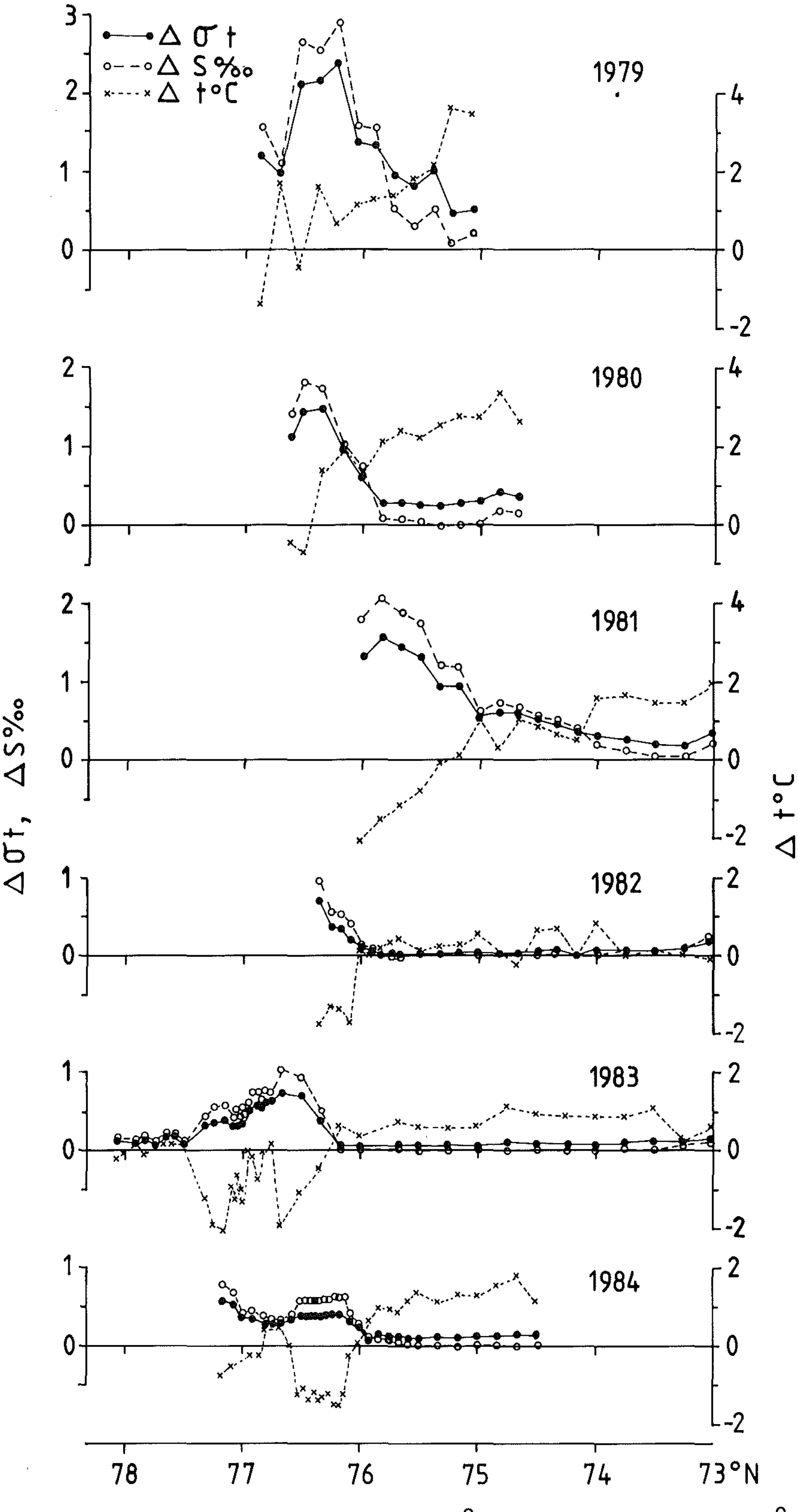

Fig. 2. Density (Δ σt), salinity (Δ S^o/oo) and temperature (Δ t^oC) gradients in the upper 100 meter water column at different latitudes in the main section during 1979-1984.

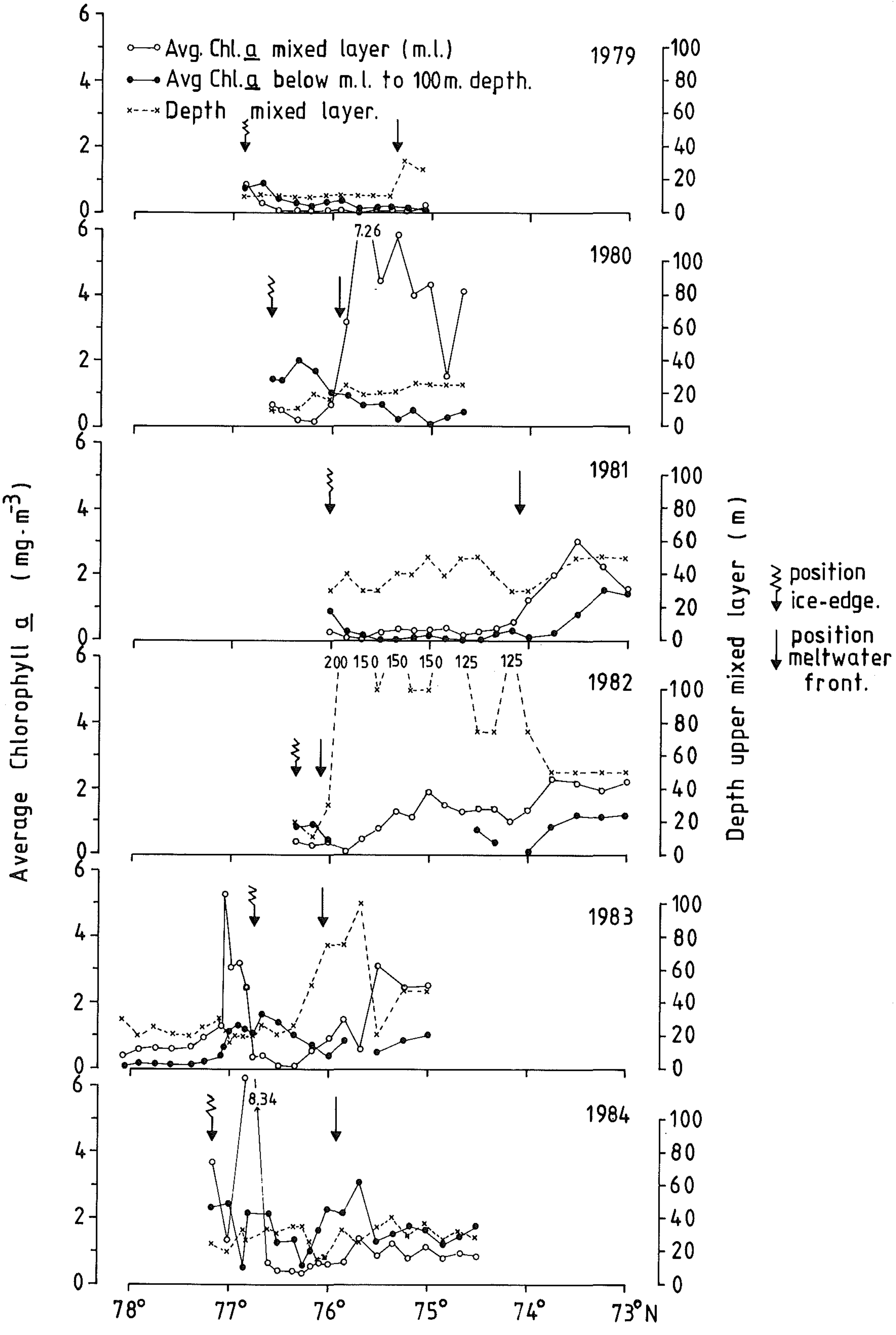

Fig. 3. Average chlorophyll a at different depth layers and depth of the mixed layer at different latitudes in the main section during 1979-1984.

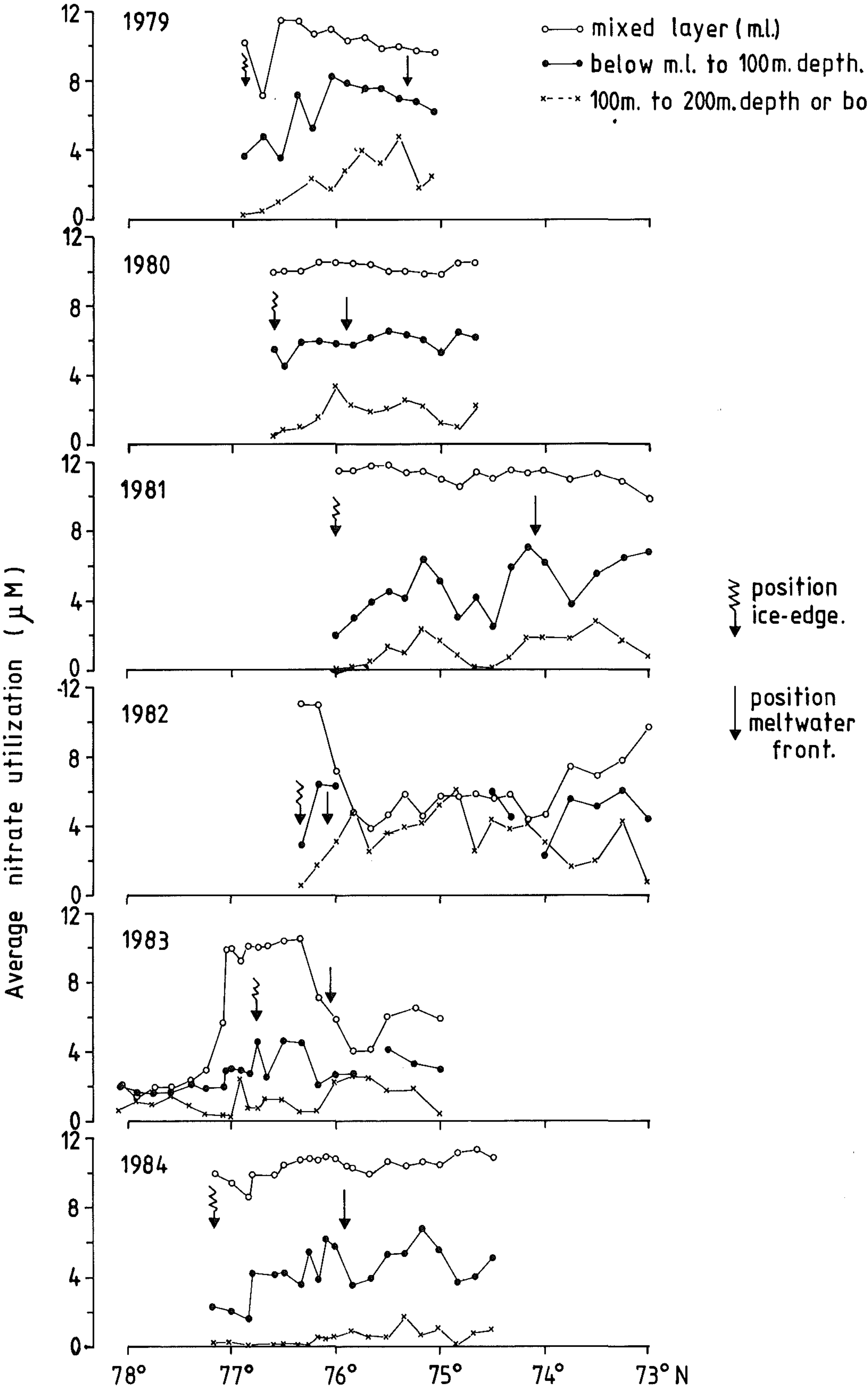

Fig. 4. Average nitrate utilization at different depth layers and at different latitudes in the main section during 1979-1984.

In 1982, the phytoplankton bloom had already taken place at the ice edge. In the Atlantic water that had not been covered by ice, the low vertical stability of the water column (Fig. 2) had delayed the spring bloom, although a noticeable phytoplankton growth could be observed (Fig. 3). The upper mixed layer was very deep, up to 200 m, which resulted in a fairly large consumption of nitrate in the 100 to 200 m layer (Fig. 4). In the southernmost part of the section which was influenced by the Norwegian Coastal Current, the upper mixed layer was about 50 m deep, and the spring bloom was more progressed than in the homogenous Atlantic water further north. In 1983, the situation was more or less similar to that in 1982, but slightly higher vertical stability in the Atlantic water had resulted in a somewhat earlier spring bloom (Figs 2 and 3). In this year, sampling was extended to ice covered regions and this allowed a more complete description of the spring bloom in the marginal ice edge zone (Figs 3 and 4). Some growth, indicative of a prebloom phase, was observed further into the ice to the north. In 1984, a marked spring bloom was observed near the ice edge, but in the remaining part of the melt water areas the bloom was already over. The higher vertical stability in the Atlantic water in 1984 (Fig. 2) caused the spring bloom to take place earlier than in 1982 and 1983, and most of the chlorophyll a was found below the pycnocline (Fig. 3).

The distribution of zooplankton biomass along the section during the six years is shown in Fig. 5. In 1979 to 1981 zooplankton biomass values were quite high at the middle of the section and decreased towards the ice edge. In 1982 the zooplankton biomass was lower than in the previous years, but it was still relatively high. The grazing pressure on phytoplankton combined with the low stability and the deep mixed layer could together have been responsible for the delayed phytoplankton bloom in the Atlantic water in 1982. In 1983 and 1984 the zooplankton biomass decreased drastically along the whole section. Reduced grazing pressure could have resulted in more massive sinking of phytoplankton from the euphotic zone due to nutrient depletion and explain the relatively large concentrations of chlorophyll a found below the upper mixed layer down to 100 m depth (Fig. 3).

Looking at the investigated period as a whole, relatively large variations in the development of the spring phytoplankton bloom were observed, depending mainly on the degree of vertical stability of the water column. The peak and culmination of the bloom varied by as much as 4-5 weeks in the period 1979-1984 in a given area. An attempt to date the timing of the spring bloom development is given in an accompanying paper (SKJOLDAL et al. 1987).

Fig. 6 shows the integrated content of chlorophyll a in the upper 100 m plotted against the vertical stability of the same layer. In the Atlantic water where the stability is regulated by the warming of the upper layer, the integrated content of chlorophyll a increased with increasing values of the vertical stability (Fig. 6A). In the areas covered by melt water where the stability is stronger and mainly due to a decrease in salinity, the relationship was not so obvious because of the wide range in seasonal phytoplankton development. The highest chlorophyll a contents were found at moderately high stability values (Fig. 6B). The chlorophyll content decreased as the stability increased further, reflecting the culmination of the bloom and disappearance of chlorophyll from the water column.

The degree of vertical stability is important in determining the extension of vertical mixing and consequently the magnitude of input of nutrients from the deeper layers to the euphotic zone. This can be illustrated by Fig. 7 where the decrease in nitrate concentration in the 100 to 200 m depth layer has been plotted against the degree of vertical stability in the upper 100 m. Low stability resulted in a large decrease in nitrate in this layer due to deep mixing. The degree of apparent nitrate utilization decreased rapidly with increasing stability.

Nitrate is the main nitrogen source for phytoplankton growth during the spring bloom. One way to compare the nitrate utilization is to relate it to a

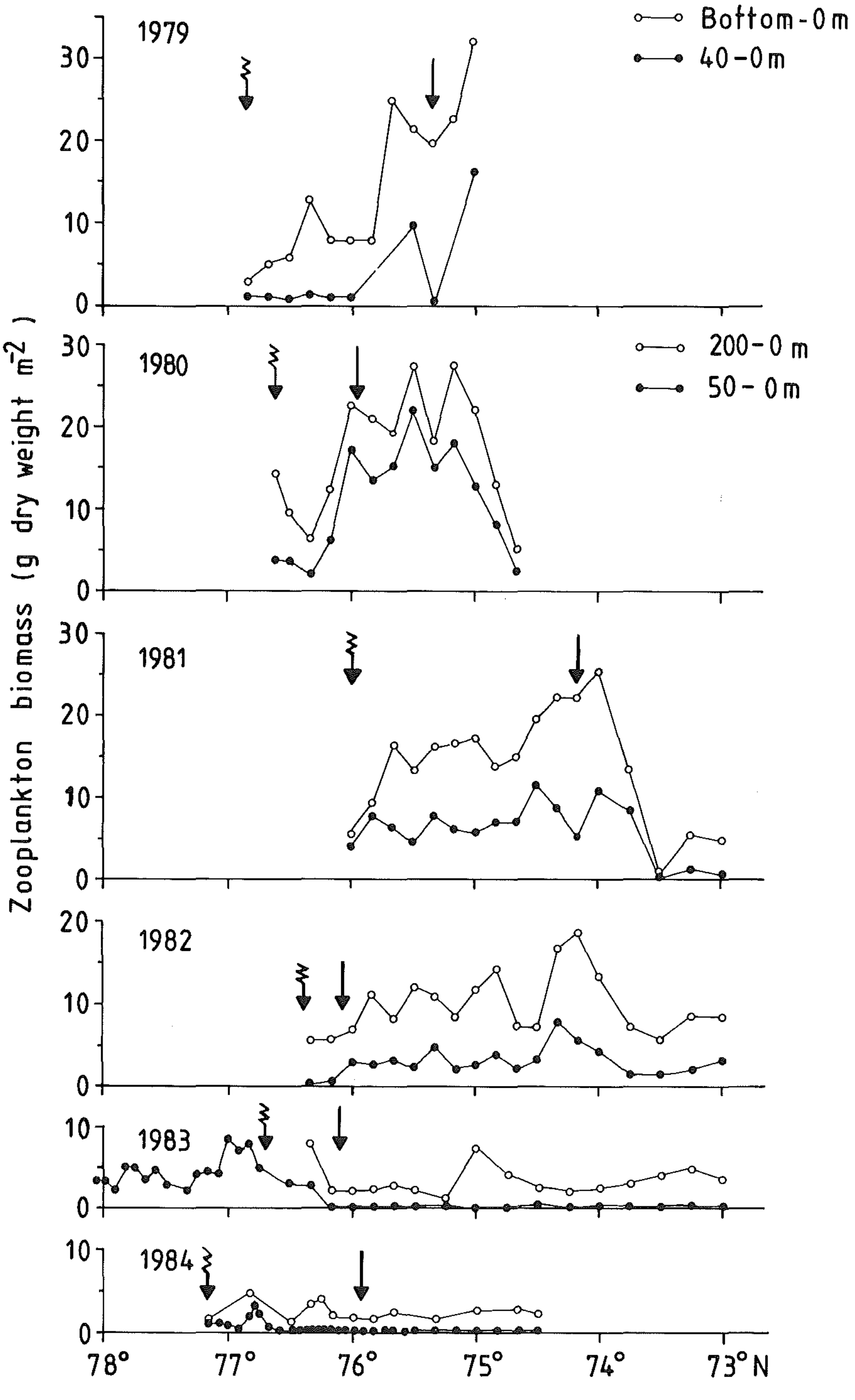

Fig. 5. Zooplankton biomass at different latitudes in the main section during 1979-1984.

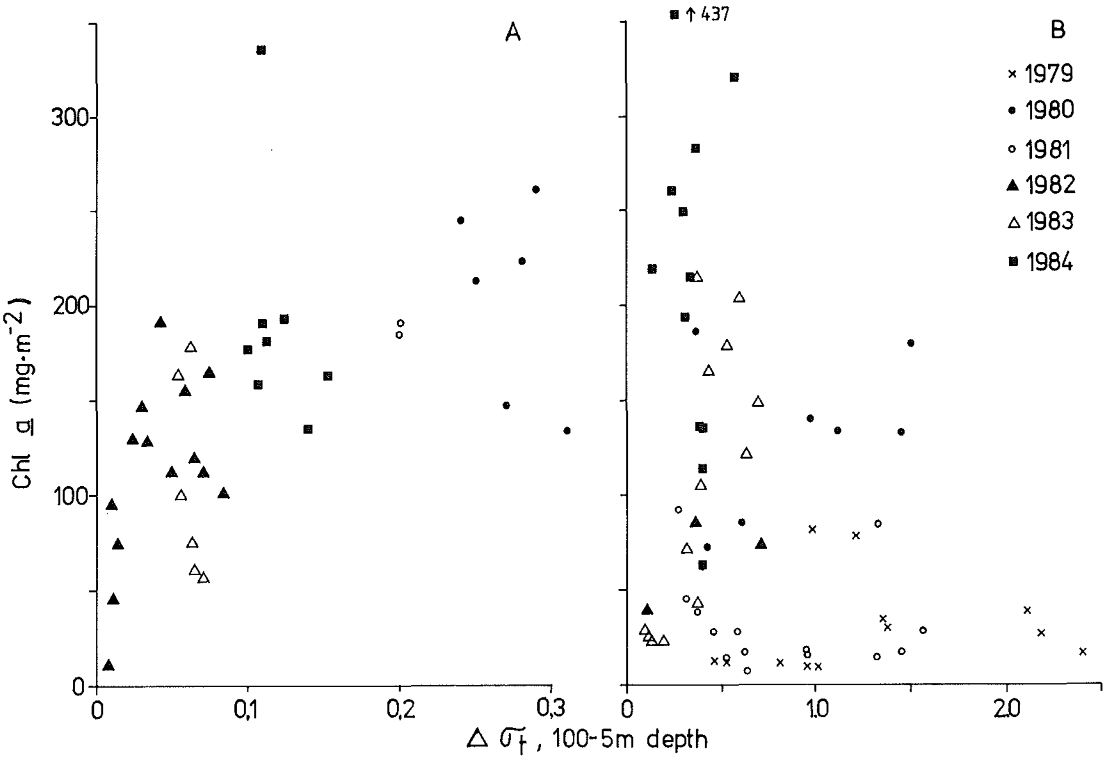

Fig. 6. Integrated chlorophyll a as a function of the degree of vertical stability in the upper 100 meters for A) stations that have not been covered by ice and B) stations with a melt water upper layer.

biomass parameter such as chlorophyll a. This has been done for the whole investigated period, separating the values for the upper mixed layer from those from the deeper layer down to 100 m depth (Fig. 8). The main disadvantage with such a comparison is that chlorophyll a in late phases of the spring bloom can be removed from a certain layer by grazing, sinking or natural degradation, and will therefore not be representative of the biomass produced during the bloom.

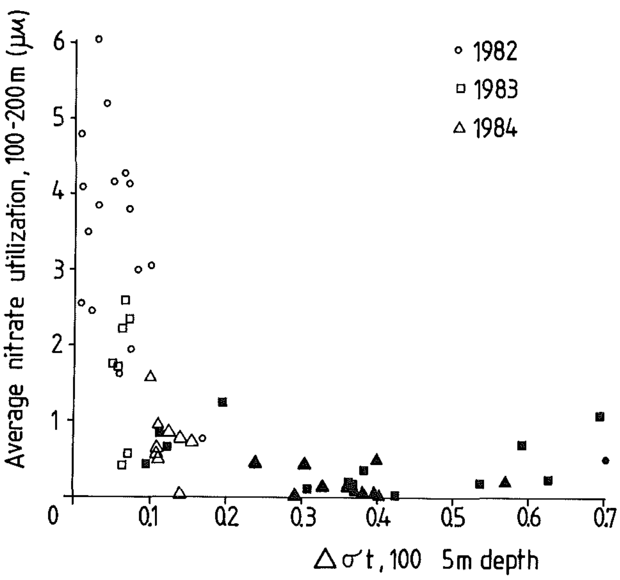

Fig. 7. Average nitrate utilization between 100 and 200 meter depth as a function of the degree of vertical stability in the upper 100 meters.

The solid line in Fig. 8 corresponds to 0.84 mg chlorophyll a m^{-3} per 1 µM nitrate. This can be taken as an estimate of the amount of chlorophyll produced per unit nitrate consumed, in the absence of any losses of chlorophyll. The data points closest to this line are from 1984 and 1983, which were the years when the zooplankton biomass and assumedly also the grazing pressure were lowest (Fig. 5). If we assume a mean weight ratio of chlorophyll a/phytoplankton carbon of 0.017 (n=46) (REY, unpublished observations) for phytoplankton during the spring bloom both at the ice edge and in Atlantic waters, then 1 µM nitrate should result in a biomass of about 50 mg C • m^{-3}. Since the mean particulate atomic N/C ratio of the same samples was 0.189, it seems that most of the phytoplankton nitrogen (78% or more) originated from winter nitrate. Taking 10 and 11.5 µM as winter concentrations of nitrate for ice-covered and not ice-covered waters, respectively, then 635 and 730 mg C • m^{-3} would be produced until the upper mixed layer became depleted of nitrate. In the Arctic waters when a shallow melt water layer is formed (about 20 m), the total amount of carbon produced will be approximately 13 g C • m^{-2}. In Atlantic water with an upper mixed layer 30-40 m deep, the carbon produced will be between 22 and 29 g C • m^{-2}. It has been shown that nitrate can become depleted well below the pycnocline (REY and LOENG 1985) and that a reduction in nitrate concentration can be observed as deep as to 200 m (Figs 4 and 7). Usually, a noticable reduction in nitrate occurs down to about 100 m. From the nitrate utilization values for the upper 100 m shown in Fig. 4, the total production can be calculated to be on the average 49 and 54 g C • m^{-2} for the Arctic and Atlantic waters, respectively.

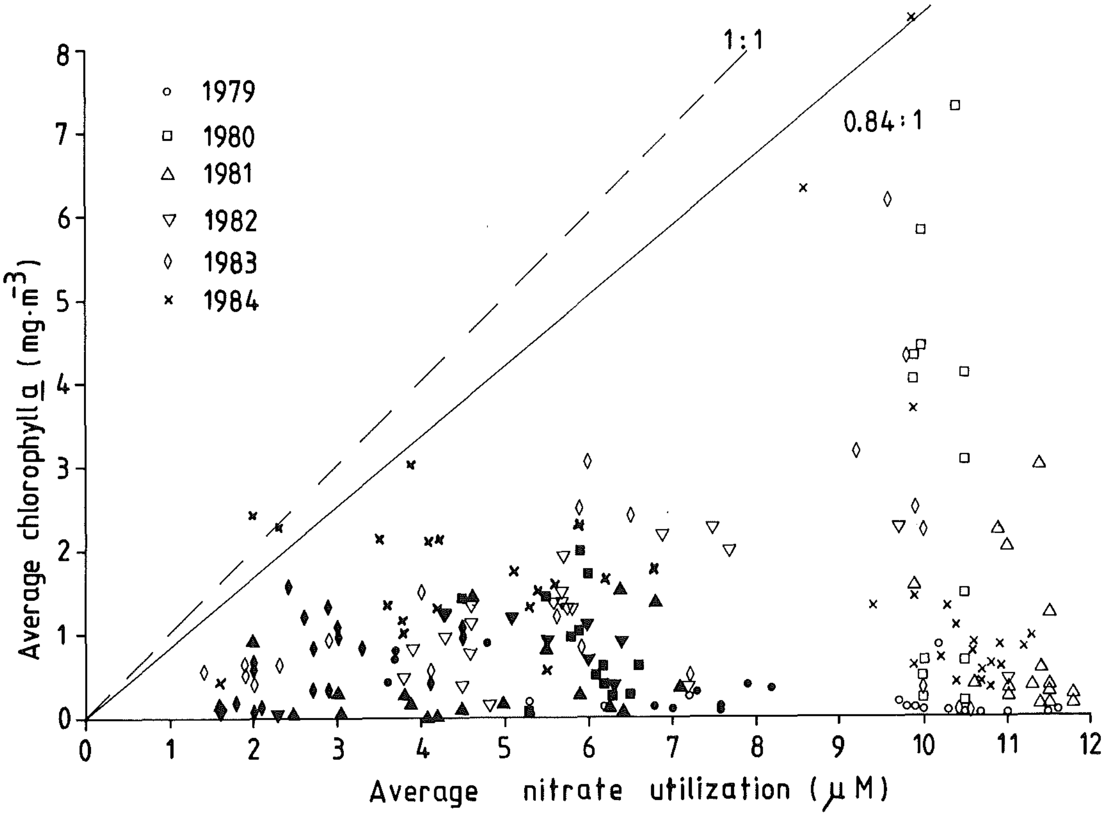

Fig. 8. Average chlorophyll a as a function of average nitrate utilization at the upper mixed layer (open symbols) and below the upper layer and down to 100 meter depth (filled symbols).

These values compare quite well with estimates of the primary production of the spring bloom based on measurements of radiocarbon uptake (REY, unpublished data). During the prebloom situation, when chlorophyll a levels are about 0.5 mg • m^{-3}, the primary production ranges from 100 to 400 mg C • m^{-2} • day^{-1} and then rapidly increases in the spring bloom to values usually about 2 g C • m^{-2} • day^{-1}. This period of the bloom with very high production rates is short-lived, since later on the large amount of organic material produced effectively reduces the penetration of light, limiting high production rates only to the surface layers. So, primary production rates decrease rapidly again to more stable and moderate rates during summer. The culmination of the bloom is usually reached when nutrients become depleted, and thereafter most of the phytoplankton growth is based on remineralized nutrients. The biological conditions during summer are more stable in the sense of phytoplankton growth, and average primary production rates are in the range of 400 to 600 mg C • m^{-2} • day^{-1} in June-July, decreasing gradually to between 200 and 250 mg C • m^{-2} • day^{-1} in August. Fig. 9 shows the development of the primary production from spring to autumn based on average values of measurements taken at different seasons during the period 1979-1984, thus representing an "average" year. The amount of carbon produced during the bloom and until 1 June is 39 g C • m^{-2}, a value that is fairly similar to the estimates based on nitrate utilization. The annual production is 69 g C • m^{-2} • $year^{-1}$.

The dynamics of the phytoplankton development for an average year have also been reproduced using the phytoplankton model. The vertical turbulent mixing in the model is given by the parameter Dz i equation (1). The representation of the mathematical model given by equation (1) in a digital computer makes it necessary to divide the water column into discrete layers of a certain depth. Each layer is considered to be well mixed whereas Dz gives

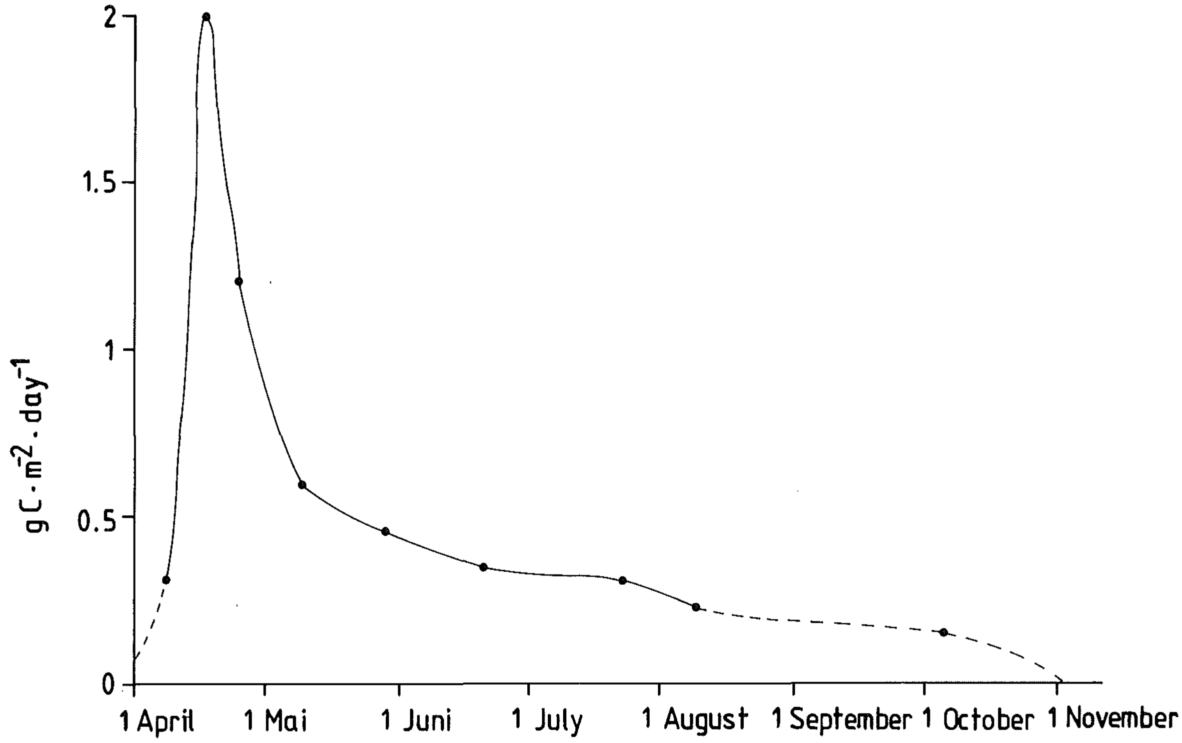

Fig. 9. Average primary production for the investigated period.

the degree of mixing between the layers. The variation of Dz with depth is given by four parameters (Fig. 10):

Dmix : vertical mixing in the upper layer
Dpycn: vertical mixing through the pycnocline
Ddeep: vertical mixing below the pycnocline
Zp : depth of the pycnocline

In the simulation runs the depth of the mixed layer for the case of Atlantic water with no influence of melt water was considered to be 75 m until 1 May, decreasing to 40 m during May. The coefficients of mixing were 150, 0.5 and 2 cm^2 • s^{-1} for Dmix, Dpycn and Ddeep, respectively. Fig. 11 shows the resulting vertical profiles of nitrate at different dates. The total phytoplankton production during the simulation period (1 March to 31 August) was 77 g C • m^{-2} and the average nitrate utilization in the upper 100 m was 8.1 μM.

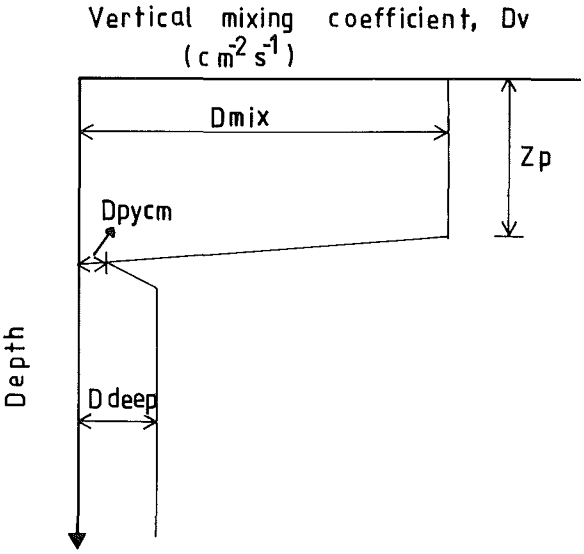

Fig. 10. Variations of the coefficient of vertical mixing with depth

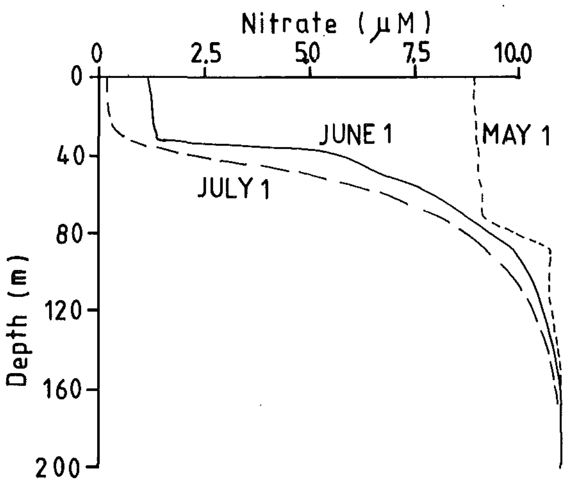

Fig. 11. Simulated nitrate vertical profiles at different dates for Atlantic waters that have not been covered by ice.

In a second case, representing Atlantic water covered by ice, the depth of the mixed layer was considered to be 50 m until 1 May, decreasing to 20 m at the beginning of June. The coefficients of mixing for Dmix, Dpycn and Ddeep were 150, 0.2 and 2 cm^2 • s^{-1}, respectively. Vertical distributions of nitrate at different dates are shown in Fig. 12. The total production during the simulation period was 70 g C • m^{-2} and the average nitrate utilization in the upper 100 m was 7.9 μM.

In a third case, representing Arctic waters, the water column was assumed to be well mixed down to 50 m during the winter. The coefficient of mixing was assumed to be less than in open Atlantic water due to the presence of ice. The pycnocline at 50 m was assumed to be strong, and we used 0.05 cm^2 • s^{-1} as the value for Dpycn. When the ice starts melting, the low salinity creates a strong pycnocline at 10-15 m. The mixing coefficient through this pycnocline was assumed equal to 0.03 cm^2 • s^{-1}. Below the pycnocline the mixing was set as 2.0 cm^2 • s^{-1}. This situation was assumed to remain for the rest of the simulation period. The date when the ice starts melting is probably variable from year to year. During the simulation the ice cover was assumed to be 7/10 in March and April. The ice was almost gone for a few days in early May. After this the water was covered by 5/10 of ice until 1 June, when the ice disappeared. Temperature was -1.8°C in the whole water column until 1 June, after which there was a gradual increase in temperature in the upper 20 m to 5°C in late August. Simulated vertical distributions of nitrate is shown in Fig. 13. The total production during the simulation period was 47 g C • m^{-2} and the average utilization of nitrate in the upper 100 m was 6.2 μM.

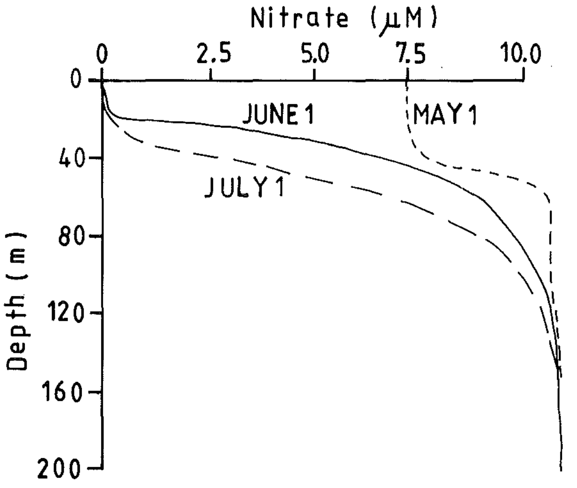

Fig. 12. Simulated nitrate vertical profiles at different dates for Atlantic waters that have been covered by ice.

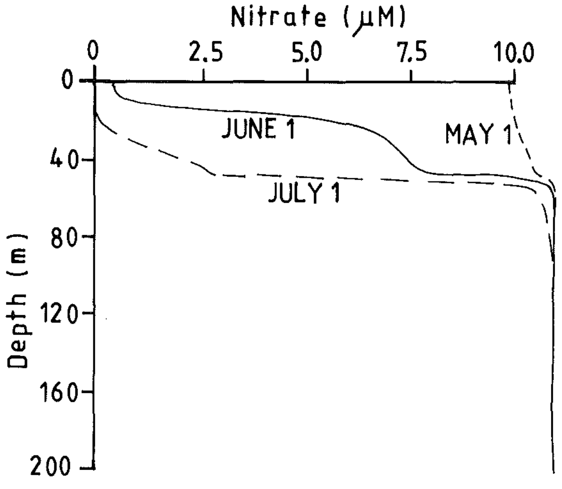

Fig. 13. Simulated nitrate vertical profiles at different dates for Arctic waters.

In all the simulation runs the N/C ratio for phytoplankton was 0.143. Using an N/C ratio of 0.189, as found in the spring bloom, the primary production in Atlantic water with no ice would be about 58 g C • m^{-2} as compared to 77 g C • m^{-2} estimated by the model.

According to the zooplankton simulation model (SLAGSTAD 1981), secondary production is very sensitive to variations in the overwintering stock of adult

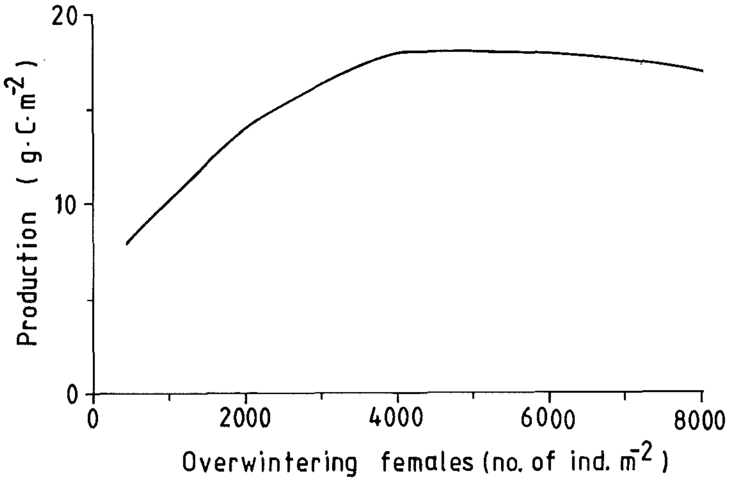

Fig. 14. Simulated production of zooplankton biomass as a function of the overwintering stock of C. finmarchicus females.

Table 2. Variations in primary and secondary production in relation to the overwintering stock of Calanus finmarchicus.

	Number of overwintering individuals					
	500	1000	2000	4000	6000	8000
Primary production ($g\ C \cdot m^{-2}$)	71	73	77	81	79	77
Secondary production ($g\ C \cdot m^{-2}$)	8.2	10.0	14.0	18.0	18.0	17.0
Utilization efficiency (%)	12	14	18	22	23	22

females (Fig. 14). This can also have an effect on the overall primary production. Table 2 shows the results of simulation runs using different overwintering stocks. As can be seen, the maximum variation in primary production due to differences in the overwintering zooplankton stock was 14%, while the secondary production varied by as much as 120%.

The zooplankton production along the main section has been simulated for each year in the period 1981-1984, based on temperature and ice data for those years. The stock of overwintering females was taken to be 2000 ind. • m^{-2}. The simulation results show fairly similar and high production in each year (Fig. 15). The low zooplankton biomass values observed in 1983 and 1984 (Fig. 5) can apparently not be related to unfavourable growth conditions in these years, as indicated by the high production potential revealed by the simulation results.

Assuming a growth efficiency of 20-30%, the simulated secondary production of Calanus finmarchicus indicates an efficient potential conversion from primary to pelagic secondary production (Table 2). The high zooplankton biomass values in 1979-1981 (about 20 g dry weight • m^{-2}; Fig. 5), the majority of

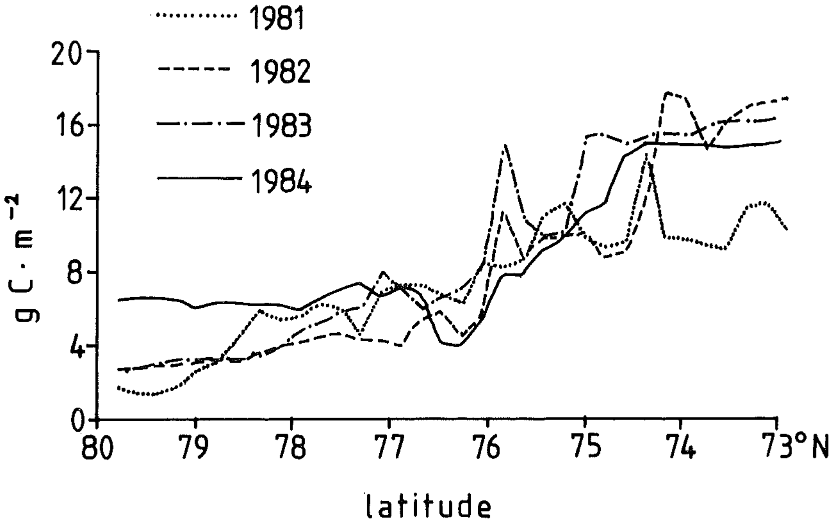

Fig. 15. Simulated production of zooplankton biomass along the main section for 1981-1984.

which represented biomass produced during the spring season (HASSEL 1986, SKJOLDAL et al. 1987), is evidence that this potential can be achieved in some years.

The reason for the apparently low zooplankton biomass produced in 1983 and 1984 could be due either to low standing stock of overwintering females (Fig. 14) or to heavy grazing by fish and other predators. Grazing could be a major factor in regulating the number of spawning females of Calanus finmarchicus, thereby potentially influencing the food supply for the predators in the following season. We have no data on the number of overwintering females for the years under consideration. In January 1985 the numbers of overwintering Calanus finmarchicus were about 5000 and 10 000 ind. $\cdot$ m^{-2} in Storfjordrenna and the Southeast Basin, respectively (HASSEL et al. 1986). Many of those were in stage CIII or CIV, particularly in the Southeast Basin, and the number of females developing to spawn the following spring is probably lower and may be in the sensitive region for production (Fig. 14).

DISCUSSION

The physical oceanographic conditions play a central role in the development of phytoplankton in the Barents Sea (REY and LOENG 1985). The formation of a stable upper mixed layer and the strength of the pycnocline, indispensable factors for the phytoplankton spring bloom to take place, varied significantly at the different main water masses present in the Barents Sea. The physical factors responsible for the formation of the upper mixed layer are the ice melting in ice covered water masses, either they are Arctic water or Atlantic water and the warming up due to an increase in atmospheric temperature and solar insolation in the water masses that have not been covered by ice, usually the Atlantic water. Climatic changes will, without doubt, have a key role in determining the magnitude of these two physical factors and the extension of the area affected by them. According to LOENG (1979) the winter extension of the sea ice is mainly controlled by the oceanographic conditions, in the sense that most of the ice in the Barents Sea is one year-old ice and its formation is strongly influenced by the water temperature. When the water temperature is low it will result in more ice. Warm years, characterized by high inflow of Atlantic water with high temperature into the Barents Sea, generally results in little ice, if any, south of the Polarfront, while cold years result in a more southern extension of the ice, some times well into the Atlantic waters. In warm years, since the ice reaches only to the polar front it does not come in contact with the Atlantic waters and its melting is mainly caused by solar or atmospheric heating, and will therefore be very dependent on local meteorological conditions. Cold north winds, for example, can effectively delay the ice melting. Usually, ice melting in the Arctic waters occurs during May. On the other hand, warm years are also characterized by a strong influx of warm Atlantic waters of very low vertical stability and quite often with not stability at all down to the bottom. In both cases the phytoplankton spring bloom will take place later than in cold years, but also the bloom in the Atlantic water will be delayed with respect to that at the ice edge. The development of the thermocline in the Atlantic waters will be slow, and the overall phytoplankton growth will be reduced due to the removal of it from the euphotic zone by vertical turbulence. However, the deep and weak thermocline permits the advective input of nutrients from layers below the thermocline and this can probably support a higher total primary production. Also the higher temperatures of the Atlantic water are favourable for an earlier development of Calanus finmarchicus to an stage where it can efficiently graze on the delayed phytoplankton bloom. This would lead to a major fraction of the primary production during spring being channelized to higher pelagic trophic food levels.

In cold years, when the ice extends south of the polar front into Atlantic waters, the melting will take place much earlier than in warm years and a strong pycnocline will be formed given place to an intense but short-lived spring bloom. The lower water temperatures will retard the stage development of Calanus finmarchicus in such a way that a great portion of the early bloom at the ice edge will remain ungrazed and will sink to deeper layers or to the bottom. In the areas that have not been covered by ice, the pycnocline will develop later than at the ice-edge, but somewhat earlier than in similar areas during warm years, so it is probably that a portion of the spring bloom will also end in the deeper layers.

With respect to the total primary production, it seems that in a given area only small variations in the yearly primary production occurs from year to year, since the amount of nitrate being removed from the upper 100 meters does not presented large changes during the investigated period. However, generally somewhat higher production would be expected from the Atlantic water than from the Arctic waters, because the deeper upper mixed layer will involve the utilization of larger amounts of nutrients. Also a south-north gradient in the total primary production in Arctic waters seems to be a general trend. This is due to the time-lag in the spring bloom produced by the receding of the ice. Observations of a ice edge bloom as far north as 79°N during August have been made (REY and LOENG 1985).

Summarizing, we can say that climatic changes will not cause very much impact on the total primary production of the Barents Sea, but it will have pronounced effects on the development in time of the spring bloom, especially in Atlantic waters and at the ice edge at the polar front or south of it. In warm years the primary production from the spring bloom available for zooplankton will be larger than in cold years and most of it will be channelized to the pelagic ecosystem. In cold years, on the contrary, the primary production available for secondary production will be lower as a part of it sinks to deeper layers in the water column or to the bottom.

ACKNOWLEDGEMENT

This work has been partly supported by the Norwegian Fisheries Research Council (NFFR).

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THE EFFECT OF OCEANOGRAPHIC CONDITIONS ON DISTRIBUTION AND POPULATION
DYNAMICS OF COMMERCIAL FISH STOCKS IN THE BARENTS SEA
Proceedings of the third Soviet-Norwegian Symposium, Murmansk, 26-28 May 1986
Edited by H. Loeng. Institute of Marine Research, Bergen, 1987.

LONG-TERM VARIATIONS OF THE BIOGENOUS ELEMENTS CONTENT AND PRIMARY PRODUCTION IN THE BARENTS SEA WATERS

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ABSTRACT

On the basis of long-term data, a statistical analysis of seasonal and year-to-year variations for phosphate and oxygen in the Barents Sea was made. A variability for the initial concentrations of phosphate during the prevernal period and their relationship with temperature during the previous winter are discussed. The amount and rate of phosphate consumed by primary producers during different seasons were determined.

The absolute oxygen content was analyzed which permitted the periods of maximum and minimum concentration to be obtained. A correlation between oxygen concentration and the level and rate of primary production for waters having different origins was obtained. Data of the long-term mean vertical oxygen concentration (per cent) of the Barents Sea were analysed by months. The extent of influence of the vertical structure of Arctic and Atlantic water masses upon the strength of dominating phytoplankton species was also evaluated.

INTRODUCTION

Biogenic elements that are concerned in geochemical and biochemical processes are also the starting materials for biological production. The concentration of these elements and their spatial and temporal distribution, exert, along with other factors, a great influence upon the level of primary production, the first link of the trophic structure in the ocean.

It should be emphasized that a discussion upon one of the factors is reasonable, as a rule, only to obtain a more detailed estimate of its significance and also for revealing any extreme characteristics. In some cases the oceanographical factors should be considered not only as those which directly influence biological productivity, but also indirectly as a factor having special features, such as promoting the intensity and general direction of biological production.

From the above positions, the authors tried to regard chemical constituents as set of conditions that affected the level of primary production in the Barents Sea. Some indices of the vertical water structure which determine the development of phytoplankton in the Atlantic and Arctic water masses during spring and summer were also investigated.

MATERIAL AND METHODS

Results of hydrochemical and hydrobiological investigations of the Polar Institute in the Barents Sea during 1970-1985 form the basis of the present paper. The content of oxygen was determined using the Winkler method. The phosphate concentration was analysed by the method of Denigés-Atkins (ANON. 1978).

To evaluate both the relationships between hydrochemical and hydrographical parameters of the environment, and between hydrochemical and biological (cod larvae survival) indices, a method of linear correlation was used. Only true correlations estimated at the 0.95 significance level (MÜLLER, NEUMANN and STORM 1982) are discussed.

The historical data on phytoplankton for standard depths were sampled at 0, 10, 20, 50 and 100 m. Samples were analysed by the sedimentation method generally accepted in the USSR using x24-x800 magnification (USACHEV 1961). The examination of the whole sample at a low magnification was used to supplement the other methods, and permitted an estimate of the density of large species of single algae or rare colonial species. This was a time consuming method which did not allow information to be collected over vast areas during the year. The most essential information to be gained was to reveal some aspects of plankton algae ecology and, in particular, to find the factors of habitat which influenced their abundance. These samples were analysed with respect to thermohaline characteristics and were outlined by TSEKHOTSKAYA and ZLOBIN (1977). Hydrochemical and hydrobiological data were collected during spring (20 April to 10 May) and during summer (from 20 July to 5 September). In addition, a long series of hydrographical data (more than 2800 depths) were analysed to reveal some factors which formed a stratified phytoplankton biotope. These factors included the density gradient in the seasonal pycnocline layer, and degree of inhomogeneity of environment in the layer above pycnocline. This was estimated as the difference between density values between the pycnocline layer and the surface. Peculiarities of development for spring and summer phytoplankton groupings for each water mass were discussed. Thus during spring, diatoms and dinoflagellates were analysed. During summer Protoperidinum depressum and Ceratium longipes, which frequently occurred in Arctic waters, and P.depressum, C.longipes and C.fusus, which were common for Atlantic waters, were analysed.

The correlation of biological components in the pelagic ecosystem was calculated by a method of multiple regression (ABRAMOVICH 1983) using the "ES-1035" computer. The reliability of regression coefficients was estimated with Fisher's variance ratio.

RESULTS

Concentrations of phosphate, one of the main biogenic elements, were subject to great spatial-temporal variations in the Barents Sea (Fig. 1). A strong influence of the streamflow in coastal waters, peculiarities of the circulation of the water masses, effects of biological and physicochemical system, and the occurrence of upwellings resulted in the irregular distribution of phosphate, especially in the 0-50 m layer. However, for some years considerable anomalies were also observed in the near-bottom layers.

The relationships presented in Fig. 1 not only provide information on seasonal

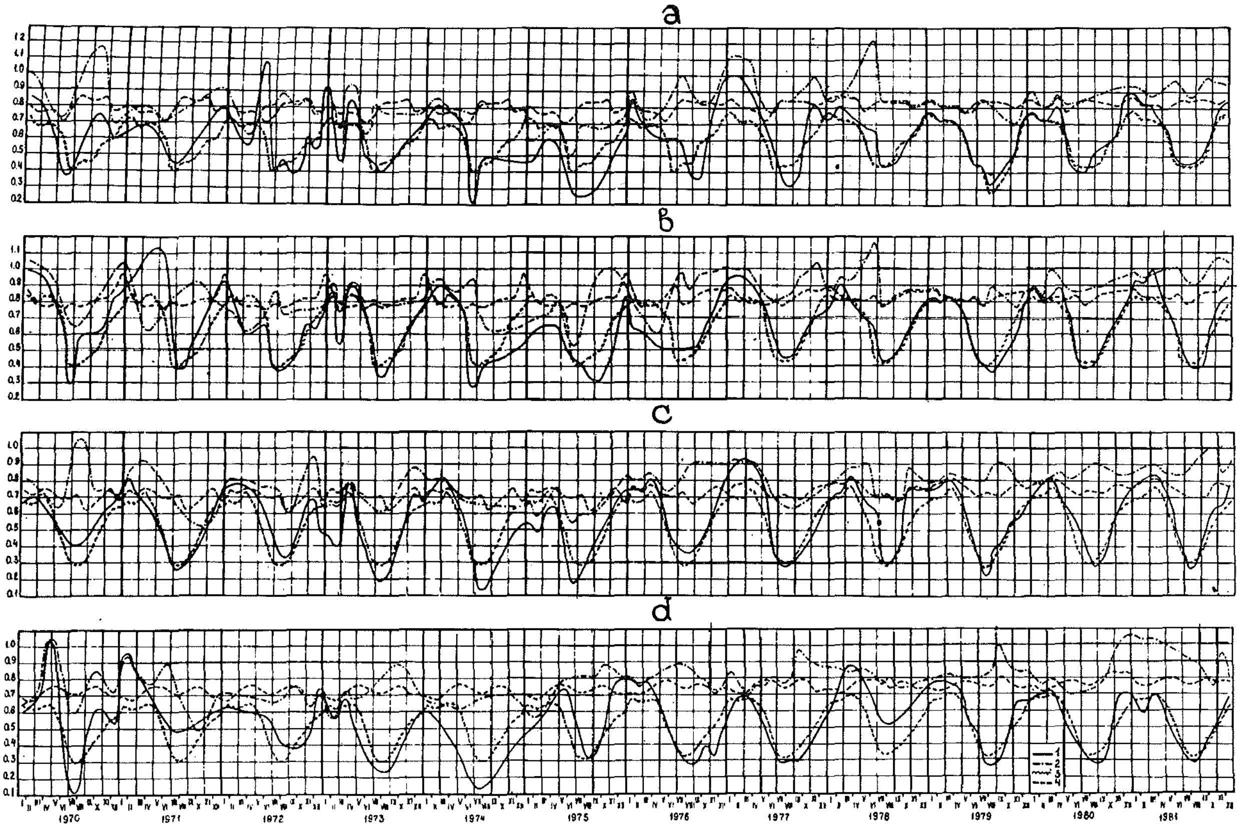

Fig. 1. Year-to-year and seasonal variations of phosphate content (µg-at•l^{-1}) in the Barents Sea:

a) southern (coastal) branch of the North Cape Current,
b) North Cape Current,
c) Murman Current,
d) transformed Atlantic waters of eastern areas.

1) 0-50 m layer,
2) 50 m bottom layer,
3) long-term means for the 0-50 m layer,
4) long-term means for the 50 m bottom layer.

and year-to-year variations of phosphate in different water masses of the Barents Sea, but also show the level and rate of their consumption for different years. The amount of phosphate which accumulated from the surface layer within a period of vegetation (excluding regeneration) is given in Table 1. Certain authors (KOCHERGIN and ASEEV 1983) used this amount as an indirect characteristic of the primary production level in the photic zone. According to CUSHING (1979), the existence of temporal relationship between the phosphorus content in water and the production value was confirmed by a conversion of biogenous elements into the tissues of plant and animal organisms. The results of our investigations on the influence of biogenous element content relative to the Barents Sea cod survival (SEREBRYAKOV, BORISOV and ALDONOV 1984) corroborated this. A positive correlation (r=0.58, n=12) was revealed between the survival rate of cod $^{2+}_{pf}$ (per cent of fishes which survived to age 2+ per the amount of eggs laid) and level of phosphate consumption within a period from the prevernal maximum to summer minimum in the feeding areas of young cod (Atlantic waters of eastern areas).

The seasonal and year-to-year fluctuations of phosphate (Fig. 1) indicate a significant variability of prevernal "starting" concentrations by years and

Table 1. Annual amplitude of variations of phosphate content (µg-at•l^{-1}) in the 0-50 m layer for different water masses of the Barents Sea.

Year	Southern branch of North Cape Current	Main branch of North Cape Current	Northern branch of North Cape Current	Murman Current	Transformed Atlantic waters of eastern areas
1970	0.50	0.69	0.55	0.30	0.92
1971	0.24	0.76	0.65	0.54	0.47
1972	0.69	0.54	0.44	0.45	0.25
1973	0.53	0.65	0.63	0.60	0.47
1974	0.60	0.63	0.76	0.68	0.47
1975	0.35	0.34	0.42	0.47	0.42
1976	0.49	0.32	0.56	0.46	0.52
1977	0.69	0.51	0.66	0.66	0.41
1978	0.38	0.47	0.63	0.54	0.41
1979	0.45	0.46	0.41	0.59	0.52
1980	0.41	0.51	0.45	0.53	0.46
1981	0.44	0.61	0.56	0.58	0.43

areas. The details of these fluctuations (Fig. 2) indicate a synchrony in the variations of prevernal maxima for different water masses of the Barents Sea. Atlantic waters of the eastern areas affected by the White Sea and Arctic waters were an exception. The variability in the phosphate concentration, along with other factors, was a result of the degree of severity of the previous winter. There was a good correlation between the temperature of the 0-50 m layer for the Murman Current and phosphate concentration during March/April (-0.69 at n=15). Thus, the more severe the winter was, the greater the amount of phosphate was carried up from deep layers to the surface. The results are similar to those of ROUKHIYAYNEN (1960).

The long-term mean dynamics of the vertical phosphate distribution for different water masses of the Barents Sea by months (Fig. 3) characterizes the degree of seasonal development of organisms at the first trophic level. It is found from Fig. 3 that the consumption of phosphates by primary producers started during April and finished during October. The consumption rate of phosphate by microplanton in the euphotic zone was one of the indices which was well correlated to the trophic level of waters (SOROKIN 1984).

The irregularity of the consumption of biogenous elements within a period of vegetation is typical for waters of the Barents Sea. At the beginning of the bloom, during the first third of April, the average daily rate of consumption of phosphate made up 0.004 - 0.006 µg-at/l per day at all the depths between 0-50 m. For May this value increased to 0.02 - 0.04 µg-at/l. For July the rate of phosphate consumption in western areas decreased again to 0.007 - 0.016 µg-at/l to reach the maximum value at the 20-50 m layer (the maximum was only recorded at 0-20 m in coastal waters). In the eastern regions, the rate of consumption in the layer of photosynthesis constituted 0.04 µg-at/l, and reached the highest values above the pycnocline (0.1 µg-at/l) at 20 m depth. During August, trace amounts of phosphate were found in the 0-20 m layer of the northern branch of the North Cape Current, while at the 50 m depth their consumption was continued at the rate of 0.02 µg-at/l.

For lack of synchronous observations, the data on phosphate consumption rates by seasons and areas could not be compared. The slope of the relationship for annual phosphate variations (Fig. 1) to the abscissa may

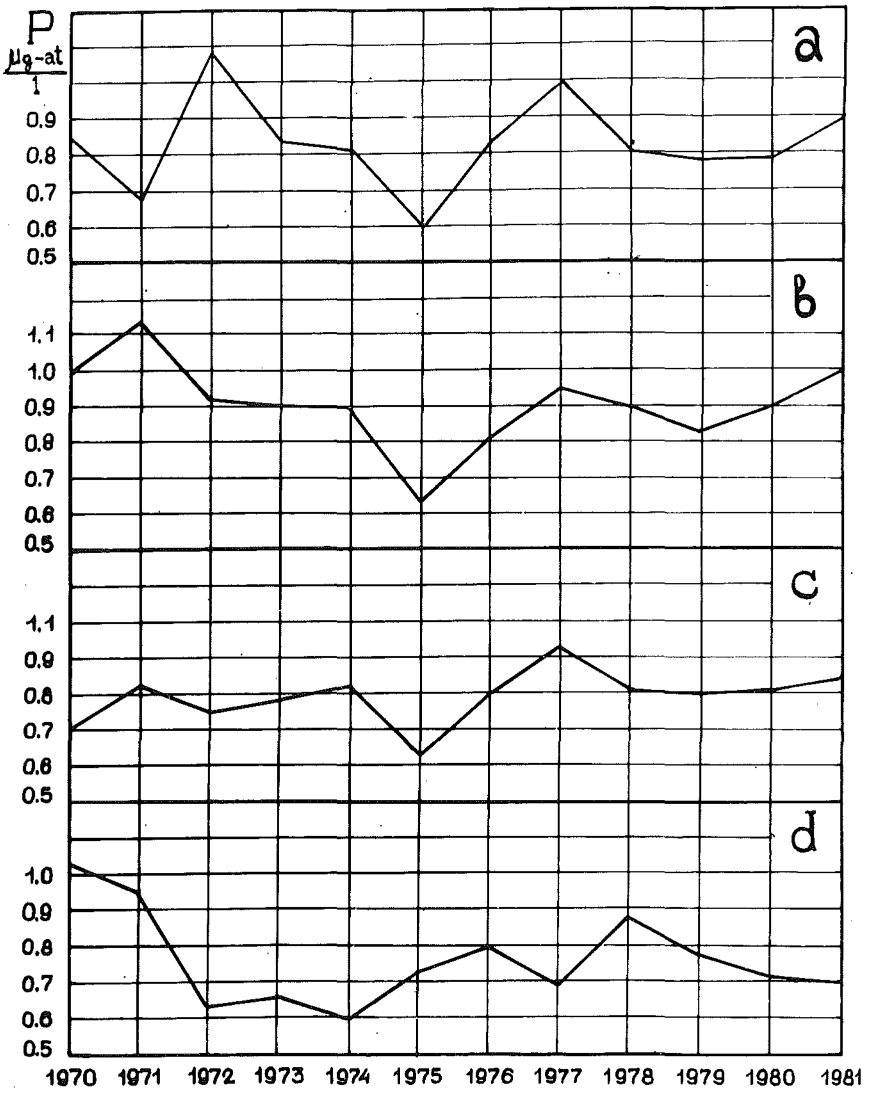

Fig. 2. Year-to-year dynamics of winter maxima of mineral phosphorus in the 0-50 m layer of the Barents Sea:
a) southern (coastal) branch of the North Cape Current,
b) North Cape Current,
c) Murman Current,
d) transformed Atlantic waters of eastern areas.

serve as an indirect characteristic of the process rate. In Fig. 4, year-to-year variations for the rate of the phosphate consumption during spring from different water masses of the Barents Sea are given. The analyses of these permitted estimation of the trophic level for waters during the course of spring vegetation by phytoplankton and to estimate the variability of this level for different regions of the sea. Thus, the highest variations of the phosphate consumption rate were observed in the deepwater of western areas (Fig. 4 b). The lowest variations occurred in the shallow eastern coastal areas (Fig. 4 a,e), waters of the Western Deep (Fig. 4 c) and Murman Current (Fig. 4 d).

Data on the spatial and temporal peculiarities of oxygen content for the Barents Sea are given in Fig. 5. The amount of oxygen and dynamics of its distribution differed in areas and by years. These resulted from the bottom morphology, depth and geographic position of an area, and level of seasonal

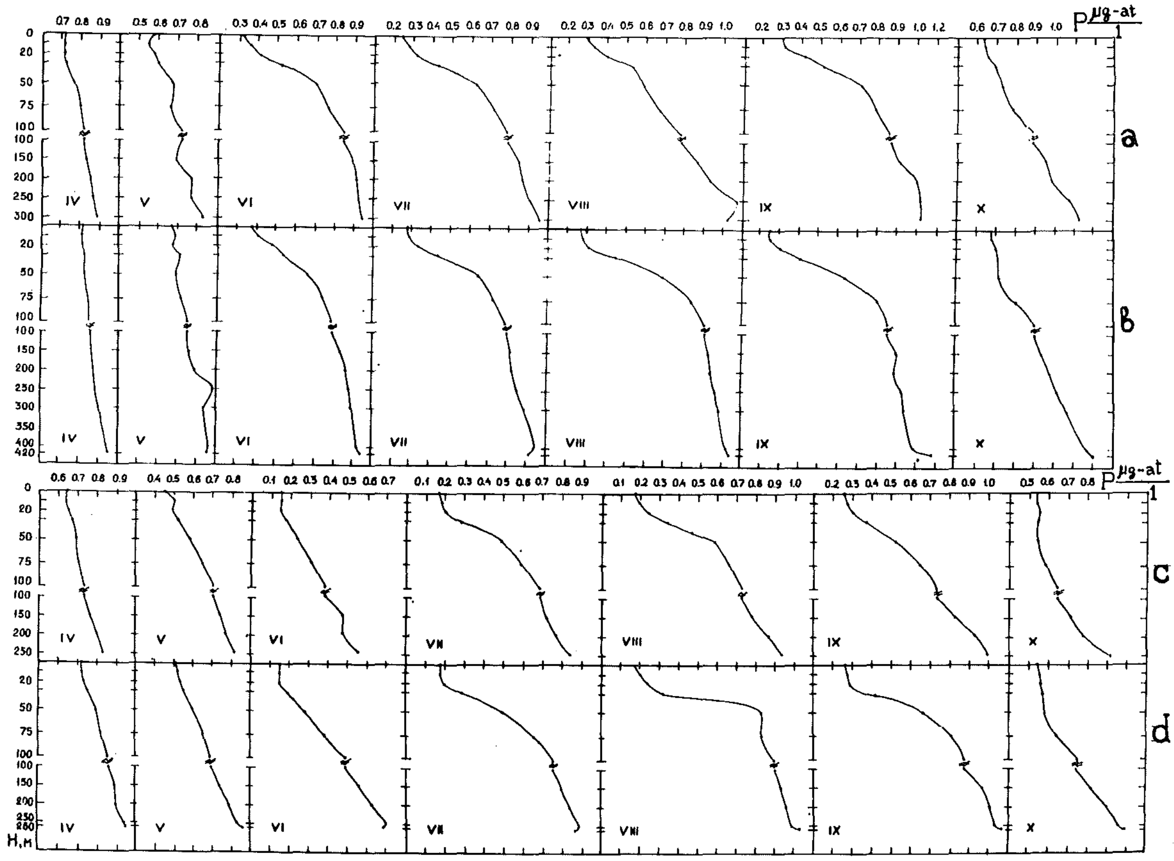

Fig. 3. Long-term mean vertical distribution of phosphates in the Barents Sea waters by months:

a) southern (coastal) branch of the North Cape Current,
b) North Cape Current,
c) coastal branch of the Murman Current,
d) Murman Current.

biological and biochemical processes. It may be concluded from the analysis of the figures that variations of oxygen concentrations in sea waters had a pronounced seasonal character with one maximum during June and one minimum during September/October. Seasonal variations for 0-50 m were rather great and amplitudes decreased with increasing depth. Within a yearly cycle, the near-bottom waters became much less oxygenated than the surface ones. The minimum oxygen content was a result of the highest intensity of biochemical decomposition which was recorded for the near-bottom waters during September/October. It should be noted that a higher summer maximum occurred with a swifter minimum. The deep "diffuse" minimum did not agree, as a rule, with a feebly marked maxima. These peculiarities characterized a different level and rate of primary production. For lack of experimental data to determine the rate of vernal development of photosynthetic organisms, the slope of the curve (which characterized the rate of oxygenation) to abscissa axis was used. Phytoplankton production is an important factor which influences the rate of zooplankton development and the formation of the food supply for commercial fish stocks. The analysis of this parameter with respect to the survival of the Arcto-Norwegian cod larvae in spawning areas demonstrated a positive correlation (r=0.88, n=12) for the rate of vernal production (slope of the curve of oxygenation) and cod survival rate. The linear dependence of these indices was based on good feeding conditions and fast growth of crustaceans on the intensively developing phytoplankton (DEGTEREVA 1979).

The long-term mean vertical distribution of oxygen in the Barents Sea waters is given in Fig. 6. The April curves characterized an initial stage of

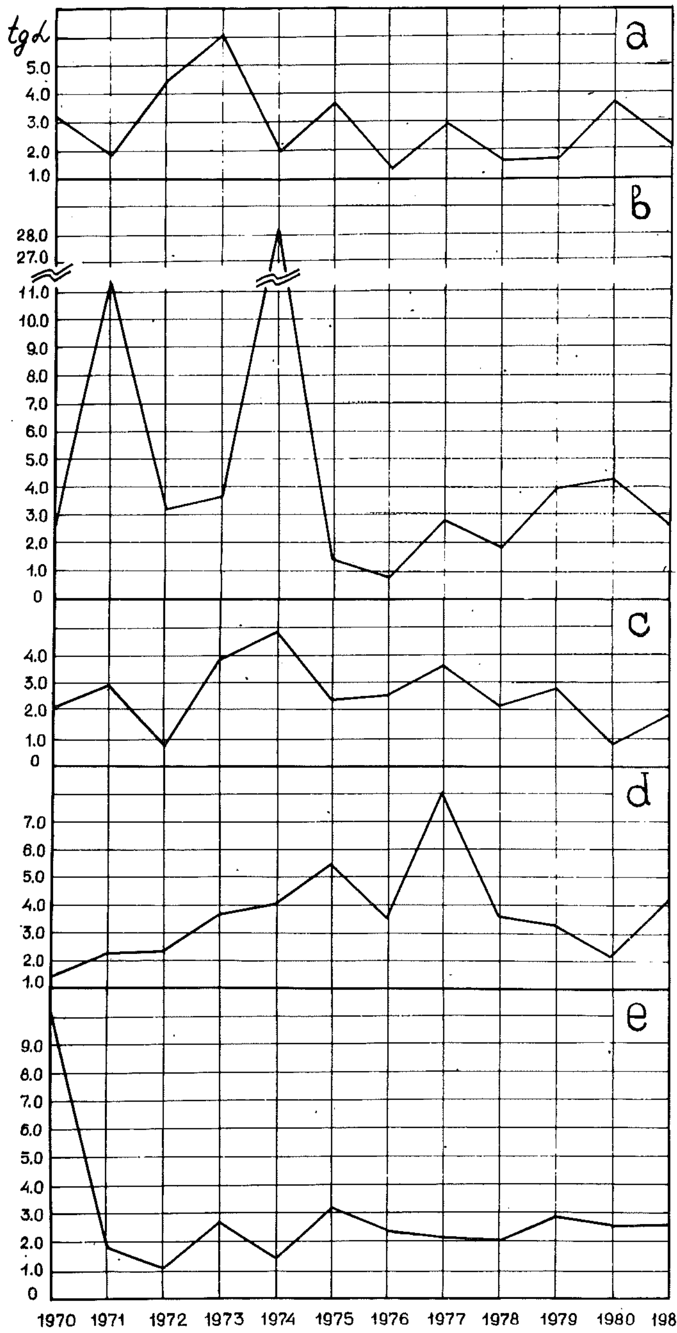

Fig. 4. Year-to-year dynamics of the phosphate consumption rate in the 0-50 m layer in spring:
a) southern (coastal) branch of the North Cape Current,
b) North Cape Current,
c) central branch of the North Cape Current,
d) Murman Current,
e) transformed Atlantic waters of eastern areas.
α) slope of the curve of yearly phosphate variations to abscissa axis.

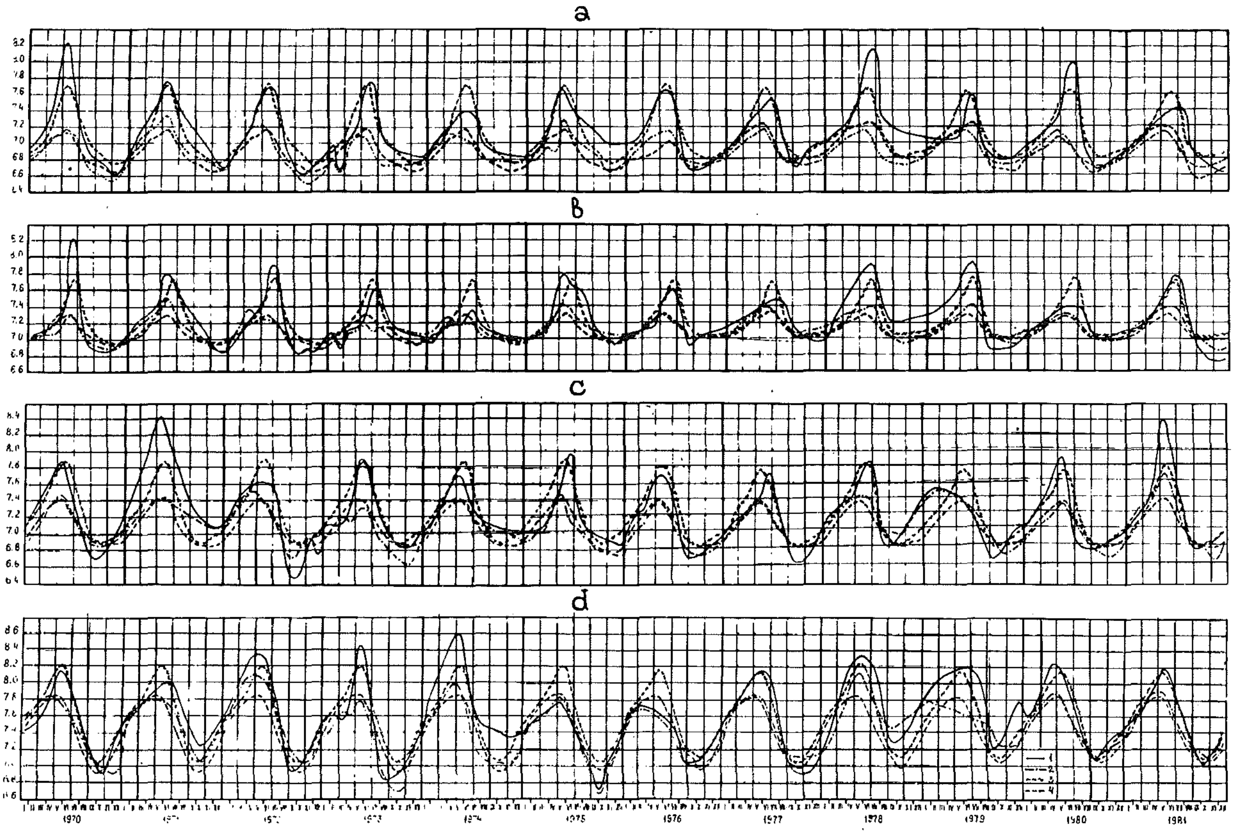

Fig. 5. Year-to-year and seasonal variations of oxygenation:

a) southern (coastal branch of the North Cape Current,
b) North Cape Current,
c) Murman Current,
d) transformed Atlantic waters of eastern areas.

1) 0-50 m layer,
2) 50 m bottom layer,
3) long-term means for the 0-50 m layer,
4) long-term means for the 50 m bottom layer.

biological spring, that is, the superoxygenation of the surface waters hardly reached 101% except for the Murman Current waters where a relative oxygen content made up about 104% (Fig. 6 c). During May, the value of superoxygenation increased to 107-110% in the pronounced pycnocline layer of the surface in western, coastal and central Barents Sea areas. The pycnocline layer (Fig. 6 b) was "vague" for the North Cape Current, and oxygenation was far less (103-104%). During June/July the relative oxygen content reached maximum values in the surface waters (to 115%). By August/September, the intensity of primary production began to decrease which accounted for a lower oxygen concentration during October (<100%).

The present characteristics of habitat are closely connected with the functioning of the first trophic level, but they do not reflect the structure of phytoplankton development, its seasonal succession and physiological state of microalgae. Therefore, it is extremely important to compare indirect characteristics of biological production with pure biological data.

According to the mathematical model of STEELE (1959) one of the factors which influences the level of phytoplankton development is the degree of

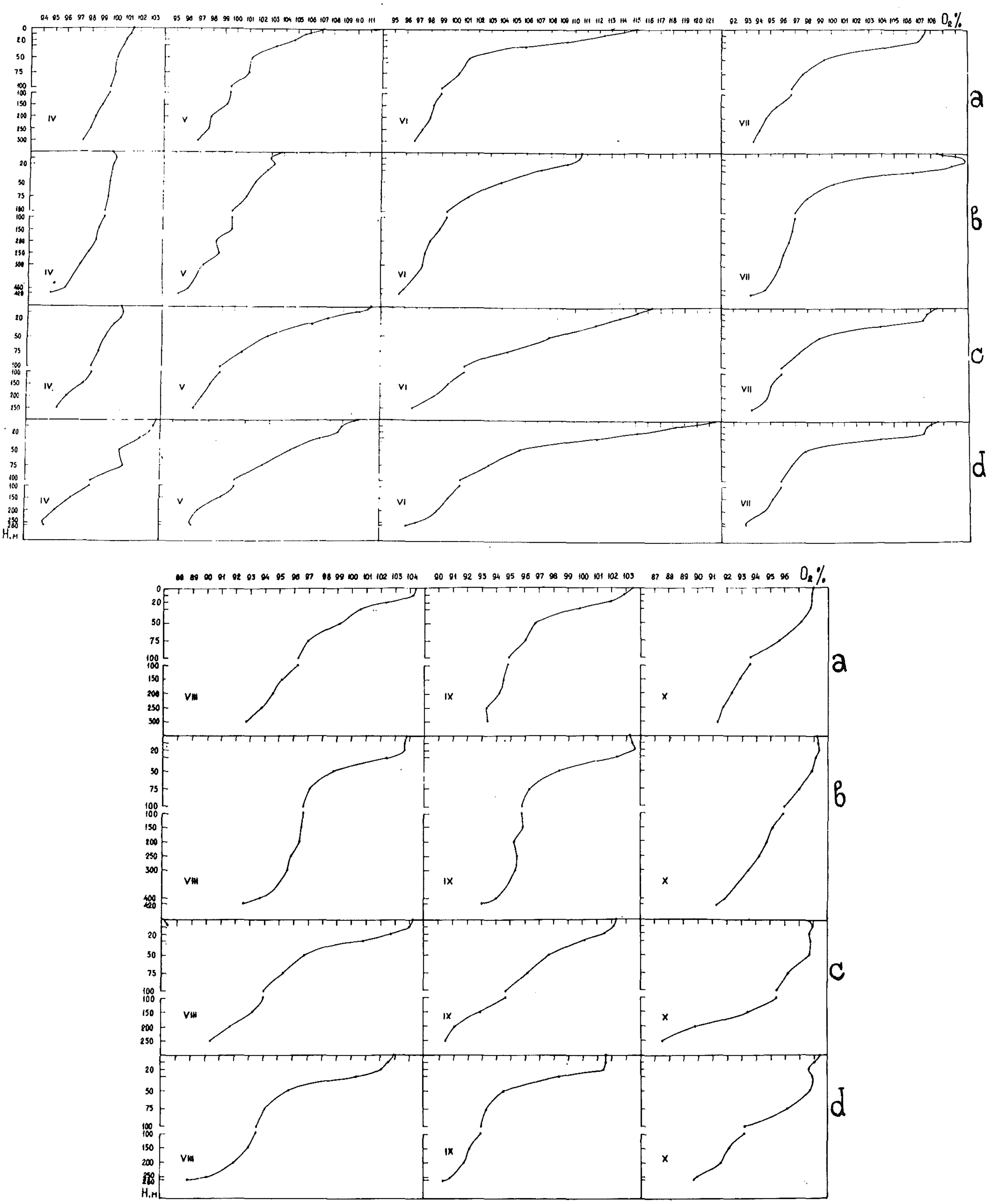

Fig. 6. Long-term vertical distribution of oxygen (%) in the Barents Sea waters by months:

a) southern (coastal) branch of the North Cape Current,
b) North Cape Current,
c) coastal branch of the Murman Current,
d) Murman Current.

vertical mixing. This characteristic depends on the formation of a seasonal pycnocline, its strength and depth of occurrence. We tried to estimate the correlation between these parameters and quantitative indices of phytoplankton development (absolute abundance of cells in the volume unit, amount of oxygen produced, and dynamic distribution of biogenous elements).

This analysis showed that the significance of these parameters in the formation of phytoplankton development changed by the seasons.

Thus for spring, the depth where the pycnocline occurred determined phytoplankton biomass for Atlantic waters. A reliable correlation was obtained for the total number of diatoms and dinoflagellates in the layer above pycnocline (r=0.75-0.80, n=20-25). This was indicative of an even vertical distribution of spring phytoplankton. At the same time the correlation between the water oxygen content in the layer above the pycnocline and level of its stratification (r=0.68, n=22) clearly demonstrated the coherence of primary production and water stratification. In Atlantic waters dinoflagellates alone depended on the vertical extent of biotope in the spring period (r=0.60, n=25). A negative correlation between the value for water superoxygenation and depth of pycnocline occurrence (r=-0.71, n=88) confirmed that a biotope of small vertical extent was required in this period for the whole development of phytoplankton.

In the Barents Sea diatoms were of decisive importance in the formation of vernal phytoplankton development of Arctic waters, while dinoflagellates prevailed in Atlantic waters. By the beginning of summer no diatoms were observed in Arctic waters. C.longipes and P.depressum became dominant, with the latter species being evidently transferred since it was inert to parameters of Arctic waters. As regards C.longipes, it was related with all the parameters of biotope stability except for the depth of pycnocline occurrence. In this case the values of correlation coefficient were higher depending rather on the degree of water stratification above pycnocline layer (r=0.66, n=26) than on values of maximum density gradient (r=0.53, n=26).

The formation of a stable biotope in Atlantic waters, following the increase of density gradient in the summer pycnocline layer, influenced favourably the abundance of C.fusus (r=0.46, n=32) and adversely P.depressum (r=-0.49, n=32). The opposite response of these phytoplankton species to a single characteristic of habitat seemed to indicate the tendency to avoid the competition of nutrients. If the development of P.depressum depended mainly on a continued replenishment of nutrients in the euphotic zone to account for its preferance to areas having small vertical density gradients, then the stability of the water column was more essential for C.fusus. This assumption was confirmed by a positive correlation between the abundance of C.fusus and depth of pycnocline occurrence (r=0.42, n=32) and, as a consequence, by the relationship between increases of the concentration of biogenous elements and vertical biotope extent (the relationship between phosphates and depth of pycnocline occurrence was estimated by the correlation coefficient 0.62 at n=53).

A total analysis of chemical and biological data permits the regularities of conversion of the biogenous elements into the live organic substance of primary producers to be studied, while chemical indices are those integral characteristics which demonstrate the result of complex processes that occur in the ecological system of the Barents Sea.

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THE EFFECT OF OCEANOGRAPHIC CONDITIONS ON DISTRIBUTION AND POPULATION
DYNAMICS OF COMMERCIAL FISH STOCKS IN THE BARENTS SEA
Proceedings of the third Soviet-Norwegian Symposium, Murmansk, 26-28 May 1986
Edited by H. Loeng. Institute of Marine Research, Bergen, 1987.

SPRING PHYTOPLANKTON DEVELOPMENT AND ZOOPLANKTON REPRODUCTION IN THE CENTRAL BARENTS SEA IN THE PERIOD 1979-1984

By

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ABSTRACT

Physical and biological conditions have been studied along a fixed transect across the polar front in the central Barents Sea in late spring or early summer in each year from 1979 to 1984. These data are analysed with respect to the spring bloom development and zooplankton reproduction and the influence of climatic conditions on these processes.

Of the six years analysed, 1979 and 1981 were particularly cold years with considerable melting of ice in Atlantic water south of the polar front. High stability due to the meltwater gave rise to spring blooms that culminated as much as 4-6 weeks earlier than in the warmer years when stability in the Atlantic water arose due to the atmospheric warming of the sea surface. Spawning of the dominant herbivore, *Calanus finmarchicus*, evidently occurred in early spring (late April - early May), as evidenced by dominance of copepodites in stages CI to CIV in June. The degree of copepodite development in the different years was related to the time of sampling, water column stability, and temperature. The timing of the copepodite development was less variable than, and showed no clear-cut relationship to, the timing of the spring bloom. This could reflect slower development of *Calanus* in cold years with early spring blooms. Reproduction of krill and *Metridia longa* occurred also in early spring.

Due to the more rapid development and early culmination of blooms in Atlantic water influenced by melting of ice, we expect the conversion efficiency of primary to pelagic secondary production to be generally lower in cold years than in warm years. Such a relationship is not evident, however, in the data for the period 1979-1984. The produced zooplankton biomass and numbers of *Calanus* copepodites were on the contrary extremely low in 1983 and 1984 which were warm years. Grazing by pelagic fish and advective transport of plankton are factors which need to be taken into consideration. The timing of inflow events of Atlantic water to the Barents Sea in relation to the seasonal vertical migration of *Calanus finmarchicus* in the Norwegian Sea could be of particular importance in this respect.

INTRODUCTION

The distribution and growth of capelin in the Barents Sea have been shown to be influenced by climatic changes (GJØSÆTER and LOENG 1984, 1987). The annual individual growth of capelin has shown considerable variation between different years and between different regions of the capelin distribution area (GJØSÆTER 1985). It is possible that this variation partly reflects a direct effect of temperature variation on growth rate (GJØSÆTER and LOENG 1987). It is likely, however, that much of the effect is mediated through the feeding conditions of capelin, i.e. the plankton production.

In order to study the feeding conditions of capelin, the Institute of Marine Research has since 1979 carried out biological oceanographic investigations in the central and northern Barents Sea. These investigations have been conducted mainly during the summer season, with special emphasis on the receding ice edge. A working hypothesis has been that increased light and stability due to ice melt cause a phytoplankton bloom in the marginal ice zone area (LOENG 1987). This bloom, which follows the receding ice edge northwards during summer, provides an important food source for the development and production of zooplankton, which again is grazed upon by capelin on its northwards feeding migration. Data in support of this hypothesis have been presented by REY and LOENG (1985) and HASSEL (1986). The plankton development in the marginal ice zone area has also been subject of mathematical modelling (SLAGSTAD 1985). From 1984 these biological oceanographic investigations have been extended as a cooperation between our institute and the four Norwegian universities within the framework of the Norwegian Research Program for Marine Arctic Ecology (PRO MARE).

A good conceptual understanding and mathematical description of the feeding conditions of capelin requires detailed knowledge of the relationships between the physical conditions and phytoplankton growth on one hand and phytoplankton growth and zooplankton development and production on the other. This knowledge is a necessary requirement in order to provide realistic descriptions and assessments of the feeding conditions of capelin over its whole area of distribution, which is the scale where climatic changes exert their greatest effect (MIDTTUN and LOENG 1987, GJØSÆTER and LOENG 1987).

The Atlantic and Arctic water masses in the Barents Sea (LOENG 1987) are characterized by different plankton organisms. For instance, the copepod Calanus finmarchicus inhabits the Atlantic water whereas the somewhat larger Calanus glacialis is found in Arctic water (TANDE, HASSEL and SLAGSTAD 1985, HASSEL 1986). The polar front which separates these two major water masses, forms therefore a boundary between two different ecological regions. A third region is represented by mixed Atlantic and Arctic water which covers a considerable part of the eastern Barents Sea. The climatic and oceanographic changes are greatest in this area and local formation and exchange of heavy bottom water have been suggested as explanations for the great magnitude and apparent periodicity in these changes (MIDTTUN and LOENG 1987). Cooling of Atlantic water and mixing of Arctic and Atlantic water masses make the Barents Sea in many ways an extreme environment which may be sub-optimal for reproduction and development of zooplankton. Under such conditions it is possible that climatic changes are being magnified when it comes to their effects on zooplankton production and thereby on the feeding conditions of capelin.

The interrelationships between spring phytoplankton development and zooplankton reproduction and development are of central importance for our understanding of the production processes. Results from the North Sea, Kosterfjorden in Sweden, and Balsfjorden in northern Norway have indicated a close correspondence between the timing of the spring phytoplankton bloom and reproduction of *Calanus finmarchicus* (KRAUSE and RADACH 1980, TANDE 1982, HOPKINS, TANDE and GRØNVIK 1984, BÅMSTEDT 1985). Results from the Norwegian Sea on the other hand, suggest that reproduction and early development of *C. finmarchicus* can occur well before the spring diatom bloom (HALLDAL 1953, ØSTVEDT 1955). A similar pattern with spawning prior to the spring bloom has also been found for *Neocalanus* spp. and *C. marshallae* in the Bering Sea (SMITH and VIDAL 1984).

We have examined data on plankton development from a fixed section (Section I, Fig. 1) in the central Barents Sea covered during the late spring or mid-summer period, in each year from 1979 to 1984. In the present paper we have summarized and analysed these observations with emphasis on mechanisms for water column stabilization and the temporal aspects of plankton development. In an accompanying paper (REY, SKJOLDAL and SLAGSTAD 1987) we consider these results further with emphasis on quantitative and vertical aspects of production.

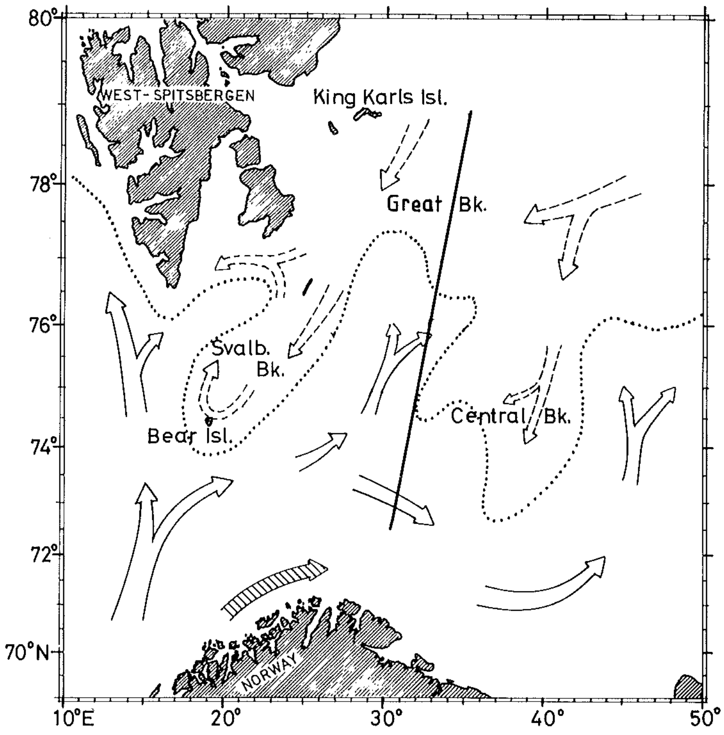

Fig. 1. Schematic picture of the currents in the Barents Sea. Solid line arrows: Atlantic water. Broken line arrows: Arctic water. Hatched arrows: Coastal water. The dotted line shows the position of the polar front. The thick straight line shows the position of the sampled transect, section I (from REY and LOENG 1985).

MATERIAL AND METHODS

An overview of the cruises covering section I (Fig. 1) is given in Table 1. R/V "G.O. Sars" has been used each year to cover the section from the ice edge and southwards. The ice-going vessel M/S "Lance" was used in addition to R/V "G.O. Sars" in 1983 to extend the section about 80 nautical miles into ice-covered waters.

Table 1. Overview of cruises covering section I in the central Barents Sea late spring or summer in the years 1979 to 1984.

Year	Vessel	Section I		
		Date	St. no.	Latitude
1979	R/V G.O.Sars	11-12 July	541-552	$75^{\circ}04'$-$76^{\circ}52'$
1980	R/V G.O.Sars	29-30 June	623-635	$74^{\circ}40'$-$76^{\circ}36'$
1981	R/V G.O.Sars	27-28 June	506-528	$73^{\circ}00'$-$75^{\circ}59'$
1982	R/V G.O.Sars	5-7 June	1145-1167	$73^{\circ}00'$-$76^{\circ}21'$
1983	R/V G.O.Sars	4-8 June	732-748	$73^{\circ}00'$-$78^{\circ}04'$
	M/S Lance		128-145 158-164 173-174	
1984	R/V G.O.Sars	4-6 June	670-702	$74^{\circ}30'$-$77^{\circ}10'$

The time of coverage of the section has varied by approximately 5 weeks, from early June in 1982, 1983 and 1984, to late June in 1980 and 1981, and 11-12 July in 1979 (Table 1).

The part of the section covered has also varied due to the differences in time of coverage and ice conditions between the years. The part of the section between 75° and 76°N has been covered every year, whereas the northernmost station has varied from about 76°N in 1981 to 78°04'N in 1983 when M/S "Lance" was used. The section was covered south to 73°N in 1981 and 1982. In 1983 the section was continued as the Vardø-N section along 31°12'E south of 74°N to the coast of Finmark. We have in this paper included data from 73°N and northwards only.

The data used for the present analysis of the time series have been described previously in the following reports or publications: 1979 and 1980 (ELLERTSEN, LOENG, REY and TJELMELAND 1981, ELLERTSEN et al. 1982); 1981 (GJØSÆTER, HASSEL, LOENG and REY 1983a, REY and LOENG 1985, HASSEL 1986); 1982 (GJØSÆTER et al. 1983a); 1983 (GJØSÆTER et al. 1983b); 1984 (HASSEL, LOENG, REY and SKJOLDAL 1984a).

The methods of sampling and analyses have been described in the above reports and these should be consulted for details of the procedures. Here we limit ourselves to a brief outline of the methods, with emphasis on any changes in the procedures which need consideration when considering the data as a time series.

Standard hydrographic sampling was done with a Neil Brown Mk III CTD sonde. Water samples were collected with Niskin or Nansen bottles. Nutrients were determined with an autoanalyzer based on standard methods (FØYN, MAGNUSSEN and SEGLEM 1981). The samples in 1979 and 1980 were stored frozen and analysed at our institute after the cruises. In the subsequent years the samples were kept cold (+1°C) and in darkness for a maximum of about 12 h prior to analysis on board. Samples for phytoplankton pigments were filtered onto 0.45 µm membrane filters, and stored frozen before extraction with 90% acetone and fluorometric determination of chlorophyll a and phaeopigments (STRICKLAND and PARSONS 1972).

Zooplankton samples were taken by vertical hauls with a 36 cm diameter Juday net. The mesh size of the net and the depth strata sampled have varied somewhat between the years (Table 2). A coarser mesh net, 375 µm, was used in 1981 and 1983 than in the remaining years when either 180 µm (1979, 1980, 1982) or 250 µm nets (1984) were used. The effect of this difference in mesh size is considered later in connection with data interpretation.

The sampling in 1979 was done from ca. 10 m above the bottom to the surface. In the subsequent years, sampling was done from the water column above 200 m depth. The uppermost 50 m was sampled with a separate haul to the surface. The deeper part of the water column was sampled either as a haul from 200 to 50 m or from 200 m to the surface (Table 2).

The zooplankton biomass was determined as displacement volume on formaldehyde-fixed samples (HASSEL 1986) and converted to wet weight assuming a density of 1 g per ml (see WIEBE, BOYD and COX 1975). This procedure was used for all samples from 1979 to 1982 and for the 200-0 m samples from 1983 and 1984. For the 50-0 m samples from these two years, biomass was determined as dry weight (Table 2). The wet weight biomass values have been converted to dry weight biomass, assuming a dry weight content of 19% of the wet weight (OMORI 1969; see also WIEBE _et al_. 1975, OMORI 1978, and BÅMSTEDT 1981).

Table 2. Overview of procedures for zooplankton sampling with 36-cm Juday net and biomass determination.

Year	Mesh size (µm)	Depth stratum (m)	Biomass
1979	180	Bottom[1] - 0	Displacement volume
		40 - 0	" "
1980	180	200 -50	Displacement volume
		50 - 0	" "
1981	375 (180[2])	299 -50	Displacement volume
		50 - 0	" "
1982	180	200 - 0	Displacement volume
		50 - 0	" "
1983[3]	375[4]	200 - 0	Displacement volume
		50 - 0	Dry weight
1984	250	200 - 0	Displacement volume
		50 - 0	Dry weight

[1] From ca. 10 m above bottom.

[2] 180 µm used for the northernmost stations (st. no. 525 - 528).

[3] Juday 80-cm used for the northernmost stations (st. no. 128 - 174)

[4] 180 µm used for the southernmost stations (st. no. 732 - 737).

CLIMATE AND OCEANOGRAPHIC CONDITIONS

Position of the polar front

The variation in the ocean climate is closely related to variations in the ice distribution in the Barents Sea (LOENG 1987, MIDTTUN and LOENG 1987). The position of the polar front in the area of section I is also apparently related to the climatic conditions. Fig. 2 shows a fairly strict relationship between the average temperature at 50-200 m in the Atlantic water mass at the Vardø-N section and the position of the polar front at section I. The position

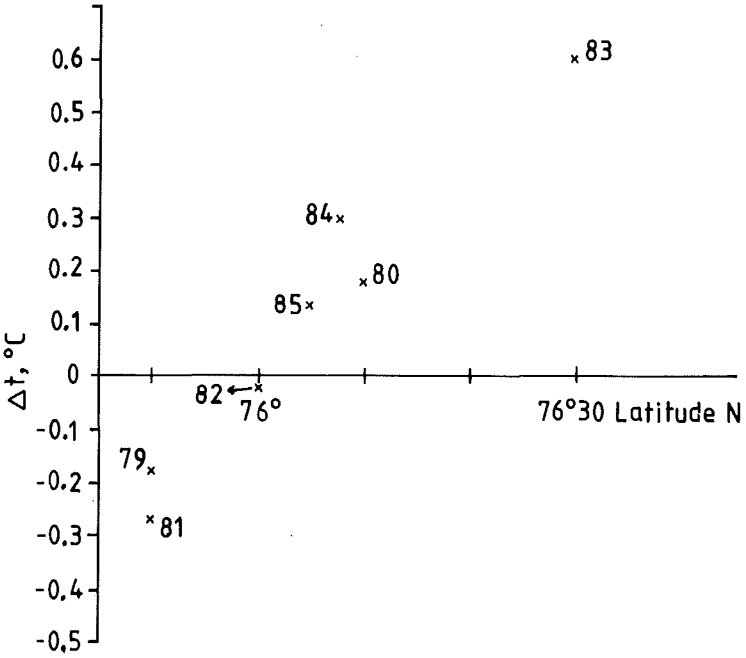

Fig. 2. Relationship between temperature anomaly for the Atlantic water of the Vardø-N section and position of the polar front in the late spring/ early summer for the years 1979-1985.

of the polar front has been determined as the area of sharpest temperature gradient where the subsurface tongue of cold water meets the warmer Atlantic water (Figs 4-9).

The position of the polar front has varied by 40 nautical miles between the cold years of 1979 and 1981 and the warm year of 1983 (Fig. 2). This shift in position may reflect differences in the magnitude and strength of the inflow of Atlantic water to the Barents Sea, as suggested by the relationship with the temperature in the Vardø-N section (Fig. 2). It may also reflect differences in the ice conditions as the position of the polar front may be modified by ice melt or freezing during winter and spring.

Ice and hydrography

MIDTTUN and LOENG (1987) have described the ice and oceanographic conditions in the Barents Sea for the recent years. The ice conditions in the central Barents Sea from 1979 to 1985 have been summarized in Fig. 3, which shows the monthly mean positions for the southern ice border between 30 and 35°E. 1979 and 1981 distinguish themselves from the remaining years. In these two cold years the ice extended south of 75°N in April and May (Fig. 3).

The hydrographical results for section I for the years 1979-1984 are presented as isopleth diagrams in Figs 4-9, along with isopleth diagrams of the concentrations of nitrate and chlorophyll a. Reflecting the southerly distribution of ice, the upper layer of meltwater with reduced salinity extended far to the south in the cold years 1979 and 1981 (Figs 4 and 6). In the remaining years meltwater was not found south of approximately 76°N (Figs 5 and 7-9). A vertical temperature gradient existed in the water masses not influenced by ice, reflecting warming of the surface layer. This gradient was weakest in 1982 (Fig. 7) and strongest in 1980 (Fig. 5).

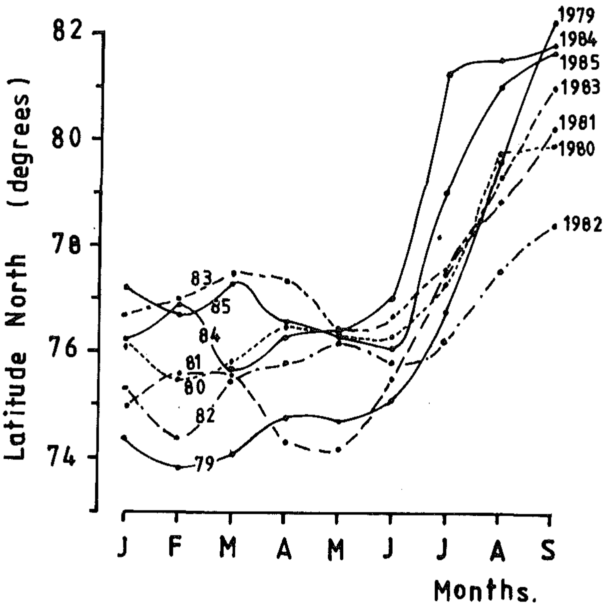

Fig. 3. Monthly mean position of the southern ice border between 30 and 35°E from January to September in the years 1979-1985.

STABILITY AND PHYTOPLANKTON SPRING BLOOM

Mechanisms for water column stabilization

Spring phytoplankton blooms are the result of increased incident light during the spring period and they are therefore, almost by definition, light limited. The average light intensity a phytoplankton cell experiences depends on the rate of vertical mixing. Although not absolutely mandatory (EVANS and PARSLOW 1985), water column stabilization exerts a very strong influence on the development of spring blooms (SVERDRUP 1953, REY 1981, SAMBROTTO, NIEBAUER, GOERING and IVERSON 1986).

Stability formation in the central and northern Barents Sea is caused by two major mechanisms: ice melt and warming. Melting of ice can again be separated into two categories depending on the source of energy: "warm" water or solar insolation. In cold years with heavy ice formation, ice can drift south of the polar front and start to melt due to the heat of the Atlantic water. This melting, which initially is more or less independent of atmospheric conditions, produces an upper layer with reduced salinity which is progressively being cooled by the melting process. Under cold atmospheric conditions, melting will therefore cease and new ice formation starts.

Melting of ice in Atlantic water south of the polar front evidently took place in 1979 and 1981. The section was not covered south of 75°N in 1979, but in 1981 meltwater was found south to about 73°45'N (Fig. 6).

In the absence of meltwater south of approximately 76°N in 1980 and 1982-1984, warming was here the principal cause of stability formation. The stability was low in 1982 (difference in σ_t in the upper 100 m: 0.01-0.08), somewhat higher in 1983 ($\Delta\sigma_t$: 0.05-0.10) and 1984 ($\Delta\sigma_t$: 0.10-0.15), and highest in 1980 ($\Delta\sigma_t$: ca 0.3). It should be noted, however, that the coverage in 1980 was about 3 weeks later than in 1982-1984 (Table 1).

Spring bloom development in 1979-1984

During the relatively late coverage in 1979 (11-12 July), the bloom was over

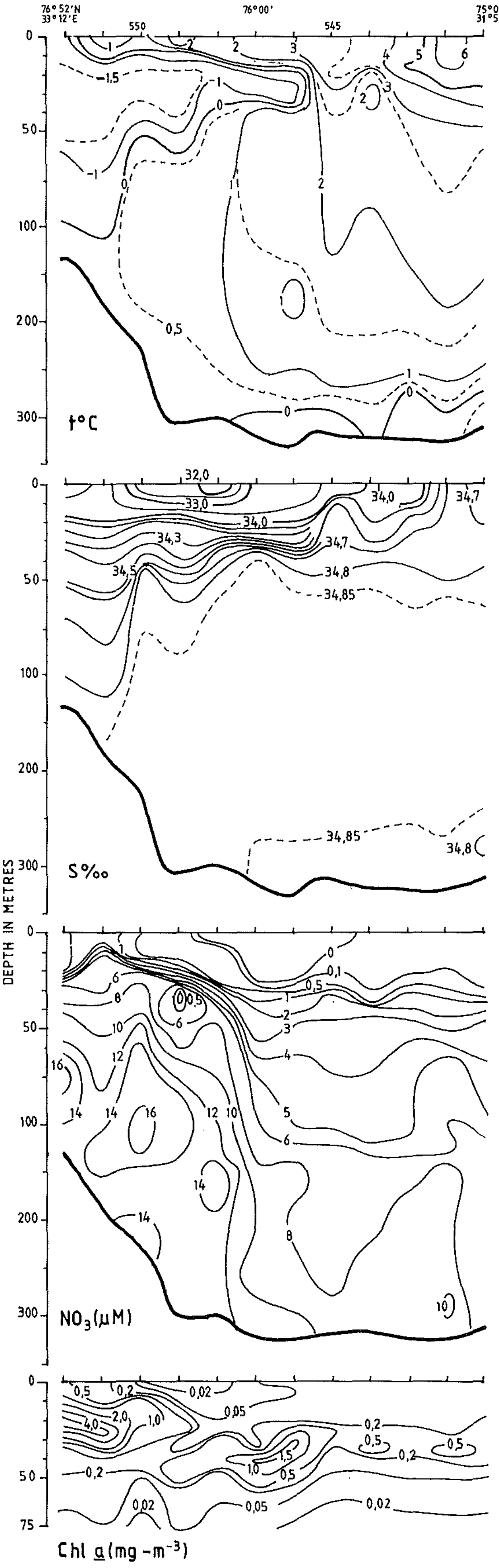

Fig. 4. Temperature, salinity, nitrate (μM) and chlorophyll a (μg·l^{-1}) along section I, 11-12 July 1979.

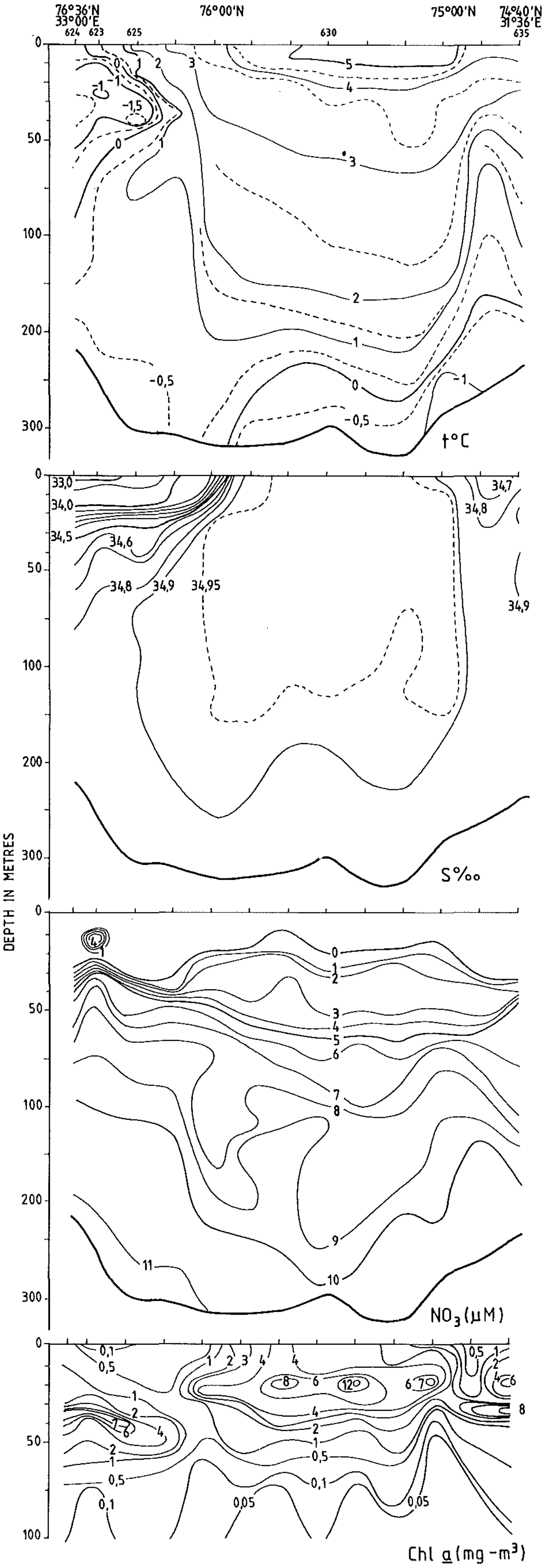

Fig. 5. Temperature, salinity, nitrate (μM) and chlorophyll a (μg•l^{-1}) along section I, 29-30 June 1980.

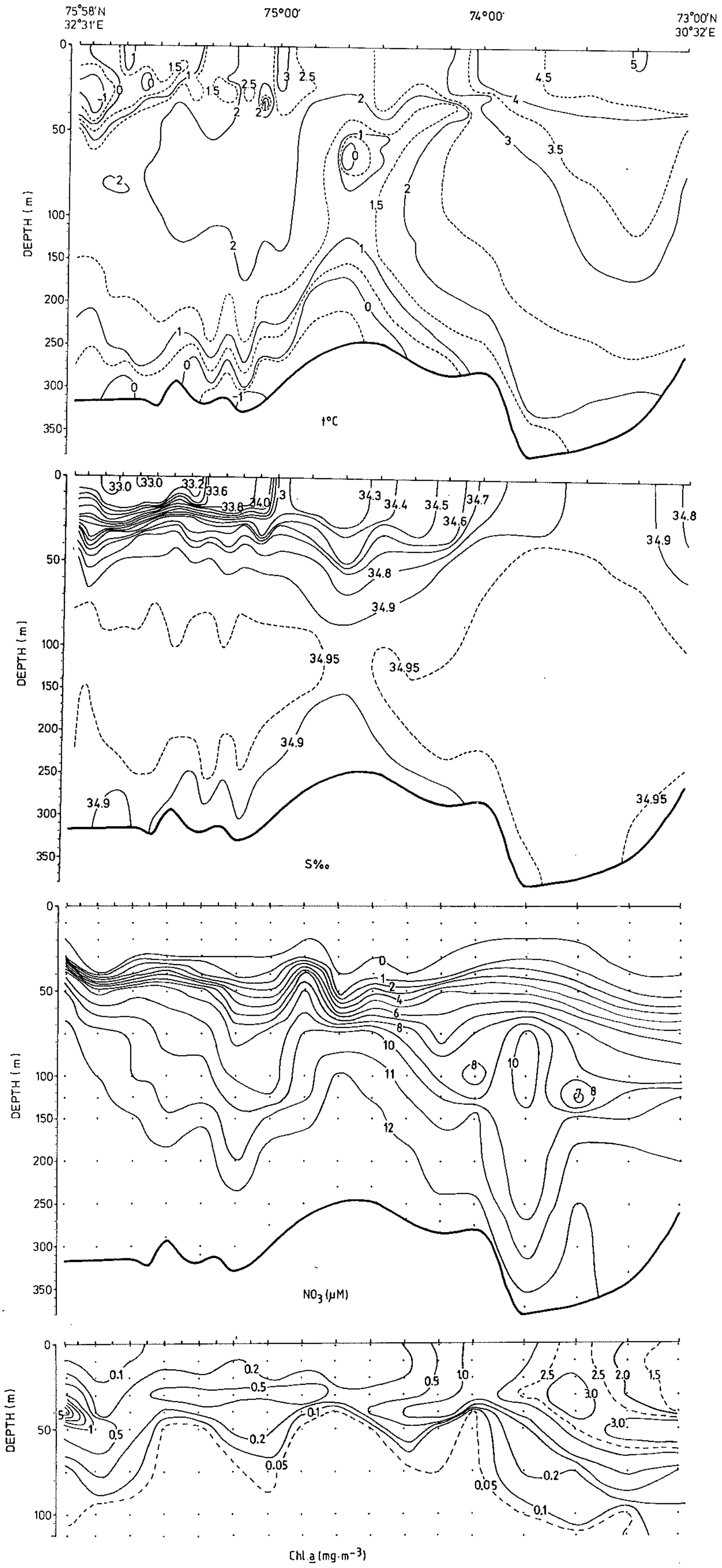

Fig. 6. Temperature, salinity, nitrate (μM) and chlorophyll a ($\mu g \cdot l^{-1}$) along section I, 27-28 June 1981.

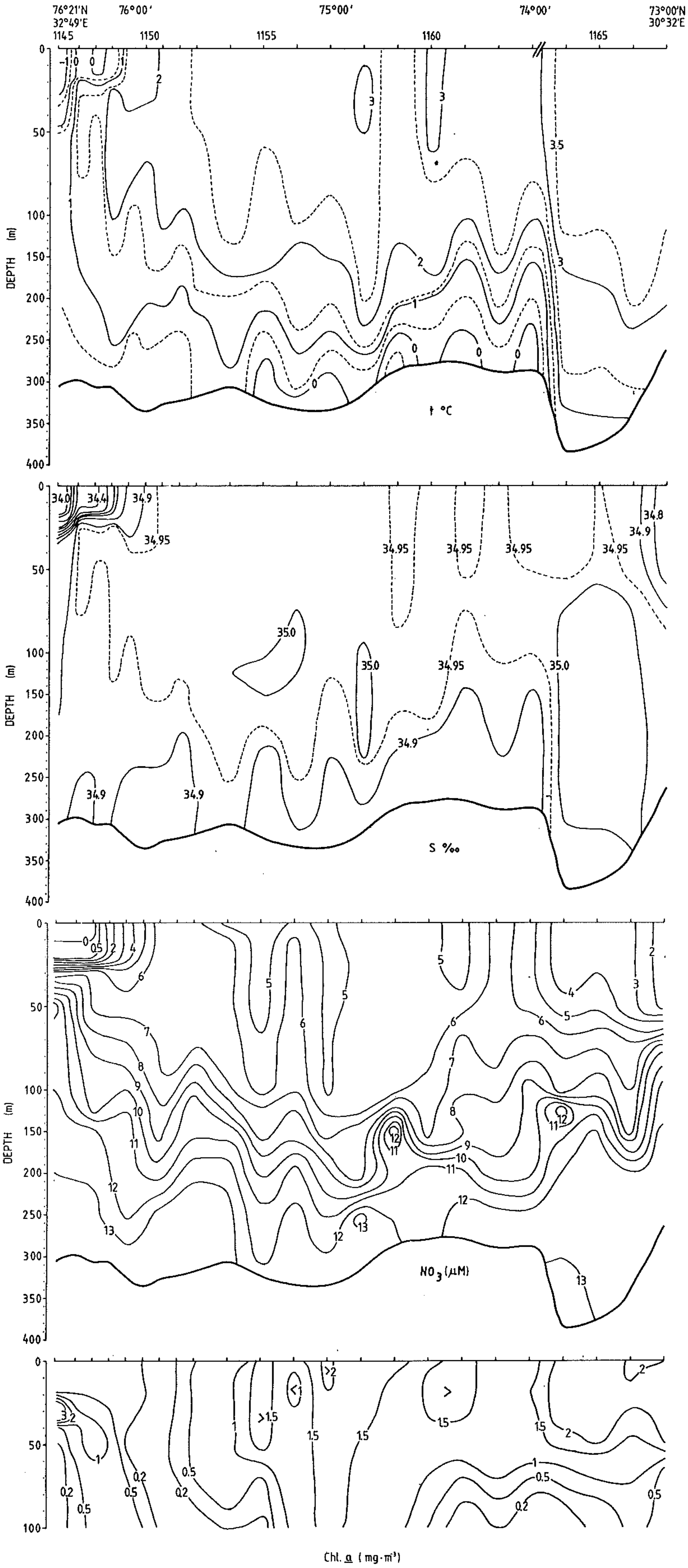

Fig. 7. Temperature, salinity, nitrate (µM) and chlorophyll a (µg·l^{-1}) along section I, 5-7 June 1982.

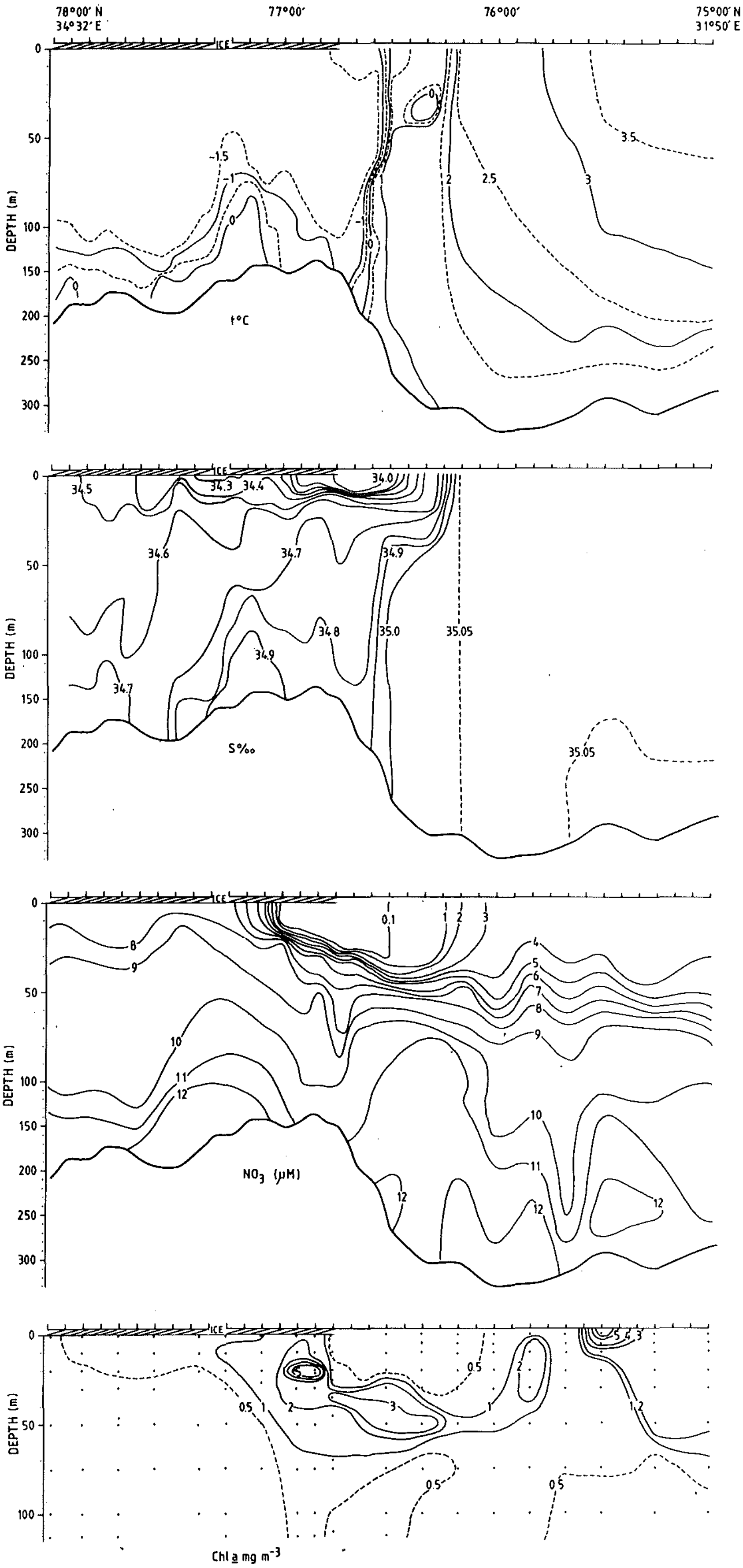

Fig. 8. Temperature, salinity, nitrate (μM) and chlorophyll a (μg•l^{-1}) along section I, 4-8 June 1983.

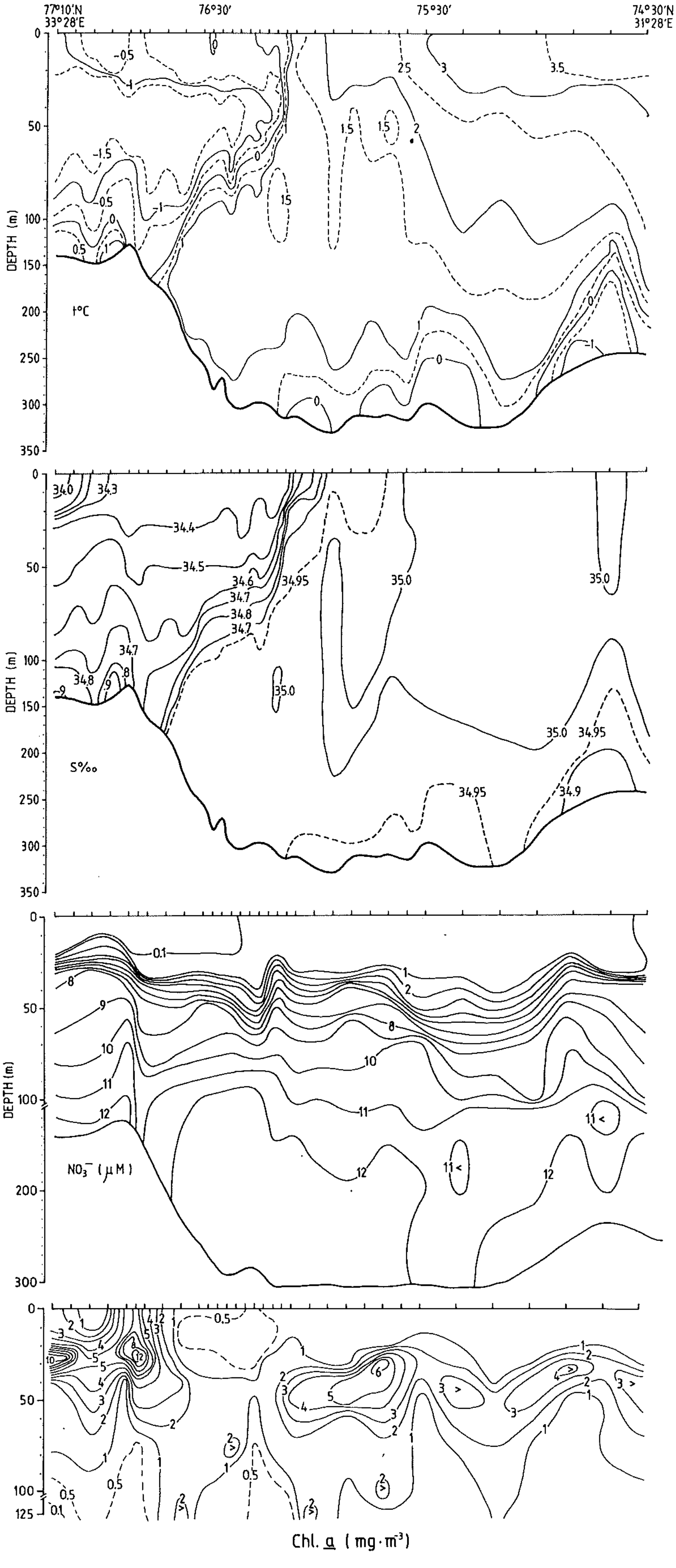

Fig. 9. Temperature, salinity, nitrate (µM) and chlorophyll a (µg·l^{-1}) along section I, 4-6 June 1984.

except for the two northernmost stations close to the ice edge. The post-bloom situation at the stations south of 76°30'N is seen from the low nitrate and chlorophyll a levels in the surface layer and the relatively low chlorophyll a level in the subsurface maximum located at the nitracline around 40 m depth (Fig. 4).

The situation in the second cold year with southerly ice, 1981, was fairly similar to that in 1979. North of 74°N, the spring bloom was over and a moderate subsurface chlorophyll maximum was developed (Fig. 6). The nitracline was very pronounced and located around 40 m. In contrast, the spring bloom was still found south of 74°N in the Atlantic water not influenced by ice melting (Fig. 6). The section was covered during another cruise about 1½ month earlier in 1981 (11-12 May). At this time the spring bloom at about its peak development was observed from about 74°N and north to the ice edge at 74°35'N, whereas the bloom was just starting to develop in the homogenous Atlantic water at about 73°30'N (REY and LOENG 1985).

In contrast to the cold years 1979 and 1981 with southerly ice (Fig. 3), bloom development south of 76°N during the remaining years was influenced by thermal stabilization of the water column. By the end of June in 1980 (29-30 June), a bloom at about its peak development was found, as evidenced by fairly high concentrations of chlorophyll a in the nutrient depleted surface layer (Fig. 5). The nitrate gradient was less sharp under the thermally stratified conditions in 1980 than under the conditions influenced by meltwater in 1981 (Figs 5 and 6). The nitrate distribution in 1980 is indicative of low stability and deep mixing during the early part of the bloom development. Thus, the nitrate isolines dip further down into the deep water in the Atlantic water mass with homogenous salinity than they do in the meltwater region (Fig. 5). This situation can also be seen in the nitrate distributions in other years, e.g. 1982 (Fig. 7). The vertical distribution of nitrate in 1980 showed two steps in the gradient, one around 60 to 70 m depth and the other around 20 to 30 m depth (Fig. 5). The deeper step in the gradient probably reflected the early development of the bloom under conditions of low stability, whereas the shallower step probably reflected a recently formed temperature gradient in the upper layer (Fig. 5).

The section was covered about 3 weeks earlier in 1982, 1983 and 1984 than in 1980 (Table 1). In 1982 the temperature gradient was slight and stability was low. The spring bloom was this year in its early development. The nitrate levels were still fairly high (5-6 μM) and chlorophyll a levels were moderate (0.5-2μg $\cdot$ l^{-1}) (Fig. 7). Both nitrate and chlorophyll a were fairly evenly distributed in the upper 100 m, and the sharpest nitrate gradient was located between 100 and 200 m. This shows that vertical mixing was fairly strong and extended deep in the water column during this early bloom period. At 73°N the bloom development had progressed somewhat further due to the stability at the outer extension of the Norwegian coastal water (Fig. 7).

The spring bloom in the Atlantic water in 1983 had reached a similar or slightly more advanced development compared to 1982. Nitrate levels were 3-4 μM in the upper 30-40 m (Fig. 8). In contrast to the deep nitrate gradient in 1982, the gradient was located much higher in the water column (around 50 m) in 1983 (Figs 7 and 8). The bloom in Atlantic water in 1984 was in a more progressed stage of development than the blooms in 1982 and 1983. Nitrate was depleted from the upper 30 m and fairly high chlorophyll a levels were found in the lower part of the euphotic zone (Fig. 9). The nitrate gradient was found around 40-50 m.

In 1983 the coverage of the section extended about 80 nautical miles into the ice and this allowed a fairly complete description of the ice edge bloom. The peak of this bloom occurred 15-20 nautical miles into the drift ice from its edge. North of this bloom region, a prebloom situation was found with nitrate levels of 7-8 μM and chlorophyll *a* levels around 0.5 $\mu g \cdot l^{-1}$ (Fig. 8). The transition from the prebloom to the bloom situation occurred fairly rapidly, as seen from the strong horizontal gradient in nitrate. In the meltwater region south of the ice edge a late stage of the bloom occurred, with a deep chlorophyll maximum at 40-50 m (Fig. 8).

Similar late stages of ice edge blooms were also found in the meltwater region north of 76°N in 1980, 1982 and 1984 (Figs 5, 7 and 9). The ice receded somewhat earlier in 1984 than in the other years (Fig. 3), and the section could therefore be covered further north (Table 1). Slightly earlier stages of bloom development was found at these northernmost stations in 1984, although the bloom had also here passed its peak (Fig. 9).

Generalizations and ranking of the investigated years

From the above descriptions of bloom development in the years 1979-1984 a few generalizations can be made. Stability formation due to melting of ice is generally more pronounced than that due to surface warming. Ice edge or meltwater blooms will therefore in general proceed more rapidly and last for a shorter while than do blooms in Atlantic water. They will also tend to start at an earlier date than the latter (REY and LOENG 1985).

Of the years considered here, 1979 and 1981 were different from the rest in that considerable ice melting took place in Atlantic water south of the polar front in these cold years. In the remaining years, ice did not extend much south of the polar front at about 76°N (Figs 2 and 3). Ice melting occurred therefore mainly due to solar and atmospheric heating in these years.

For comparison with the reproduction and development of zooplankton, it is of interest to compare the different years in terms of the timing of the spring bloom. Since bloom development needs to be considered as a temporal process with a variable and continually changing vertical structure, it is not a simple and straightforward task to fix dates of given stages of bloom development. We have attempted to do this, however, in a rather coarse and semiquantitative manner. In doing so, we use the following definitions for the start and peak of a bloom. The start of the bloom is defined as the time when 1 $\mu mol \cdot l^{-1}$ of nitrate (about 10% of the winter level) has been utilized in the upper mixed layer. This corresponds to a production of about 0.5-1 μg chlorophyll *a* $\cdot\, l^{-1}$ (REY *et al.* 1987). The peak of the bloom is defined as the situation when the upper layer is nutrient depleted while the chlorophyll *a* level is still high and rather uniformly distributed. This situation corresponds usually to the maximum content of chlorophyll *a* per m^2.

In attempting to date these two bloom events (to the nearest week) for the different years, we have had to extrapolate from the observations made during the few days coverage of the section each year (Table 1). In this, we have been guided by repeated coverages of the section in 1980 (ELLERTSEN *et al.* 1981, 1982) and 1981 (REY and LOENG 1985), as well as in April 1986 (SKJOLDAL 1986, REY and SKJOLDAL unpubl. results). Our estimates of the timing of the bloom events, which are to be regarded as educated guesses, are presented in Table 3.

During the coverage 11-12 May in 1981 the bloom was nearing its peak at

Table 3. Estimated times (week number) for the start and peak of the spring phytoplankton bloom, mean Calanus copepodite stage composition (stage index) by the time of coverage (see Table 2), and estimated dominant copepodite stage by mid-June at different latitudes along section I in each of the years 1979-1984. See the text for further details.

Year	Latitude (°N)	Estimated time of spring bloom (week no.)			
		Start	Peak	Stage index	Dominant stage per 15 June
1979	75	17	21	3.82	I
	76	19	22	3.37	I
1980	75	17	25	3.14	II
	76	18	24	2.64	I
1981	73	18	24	3.08	I
	74	16	20	3.39	I-II
	75	17	21	3.57	II
	76	19	22	2.91	I
1982	74	17	25	1.82	II
	75	18	26	1.58	II
	76	18	24	1.82	II
1983	74	17	24	3.27	IV
	75	17	24	2.90	IV
	76	18	25	2.64	IV
1984	75	15	22	2.06	II
	76	15	22	2.44	III

74°N (REY and LOENG 1985). We expect that the peak was reached about one week later (week 20). We have assumed a delay of one week for the peak bloom at 75°N (week 21) and two weeks at 76°N (week 22). As judged from the observations at 73°N in late June (Fig. 6) we expect that the peak bloom occurred two weeks earlier (week 24) (Table 3). Due to the fairly similar physical conditions, we have assumed similar timing of the bloom in 1979 as that in 1981.

During the coverage in late June 1980 the chlorophyll a distribution suggested that the bloom was just beyond its peak. We estimate that the peak occurred one week earlier at 75°N (week 25) and two weeks earlier at 76°N (week 24) where there was some influence of meltwater (Fig. 5). A bloom beyond its peak was also found during the coverage in early June 1984 (Fig. 9). We have assumed that the bloom at 75 and 76°N peaked about one week earlier (week 22).

During the early June coverages in 1982 and 1983 the blooms in the Atlantic water had still not reached their peaks (Figs 7 and 8). We judge the bloom in 1983 to be more developed than in 1982, peaking one to two weeks after the coverage (week 24 at 74 and 75°N and week 25 at 76°N). Due to the lower stability and deeper mixed layer in 1982 (Fig. 7), we have assumed that the bloom this year needed an additional 1-2 weeks period to reach its peak (week 25 at 74°N and week 26 at 75°N). At 76°N the bloom seemed to be somewhat more progressed than further south due to the influence of meltwater (Fig. 7), and we estimate that the peak here occurred one week later (week 24).

The above analysis of the timing of the peak bloom indicates a variation of 3-4 weeks among the different years when considering only Atlantic water not influenced by meltwater (Table 3). Ice melting can lead to an earlier peak bloom, as examplified by 1981, thus further extending the range of variation among years (Table 3).

Our estimates of the timing of the start of the blooms are generally more uncertain as they have required extensive extrapolations of our data. In 1986, when there was melting of ice in Atlantic water south to about 75°N, the bloom in this area apparently started in early April (SKJOLDAL 1986, REY and SKJOLDAL unpubl. results). Due to the more extensive ice coverages in 1979 and 1981, we have assumed that the blooms in these years started 1-2 weeks later than in 1986 (Table 3).

The part of the section around 73°30'N in 1981 was covered by Atlantic water not influenced by meltwater or coastal water. The bloom in this area seemed to have started just prior to the coverage 11-12 May and to have reached its peak just prior to the coverage 27-28 June (REY and LOENG 1985; Fig. 6). This gives an estimated duration of 7-8 weeks from start to peak bloom in Atlantic water in 1981. We have assumed this duration when estimating the timing of the start of the blooms in 1983 and 1984 and one week longer duration for the blooms in 1980 and 1982 (Table 3).

ZOOPLANKTON REPRODUCTION AND DEVELOPMENT

Calanus finmarchicus and Calanus glacialis

The two Calanus species, C. finmarchicus and C. glacialis, are inhabitants of the Atlantic and Arctic water masses south and north of the polar front, respectively (TANDE et al. 1985, HASSEL 1986). The two species are separated in routine analysis of samples according to differences in size. Where both species co-occur in mixed water masses, size spectra generally show two distinct peaks, the larger one corresponding to C. glacialis (RUNGE et al. 1985, HASSEL unpubl. results). There is some overlap of the peaks, however, which gives some uncertainty to this method of separating the species, especially where one of the species occurs in low abundance relative to the other. Using this method, the two species from copepodite stage II or III and upwards were separated in samples from 1979, 1980, 1982 and 1984 (Fig. 11).

The abundance of copepodites of C. finmarchicus and C. glacialis (not shown separately) showed dramatic variation among the years (Fig. 10). From a moderate abundance in 1979, the numbers of copepodites increased until 1982 when there was 1/4 - 1/2 million individuals m^{-2}. Between 1982 and 1983 there was an almost 100-fold reduction in abundance to 6-9000 copepodites m^{-2}. Low abundance was also found in 1984. The biomass of total zooplankton

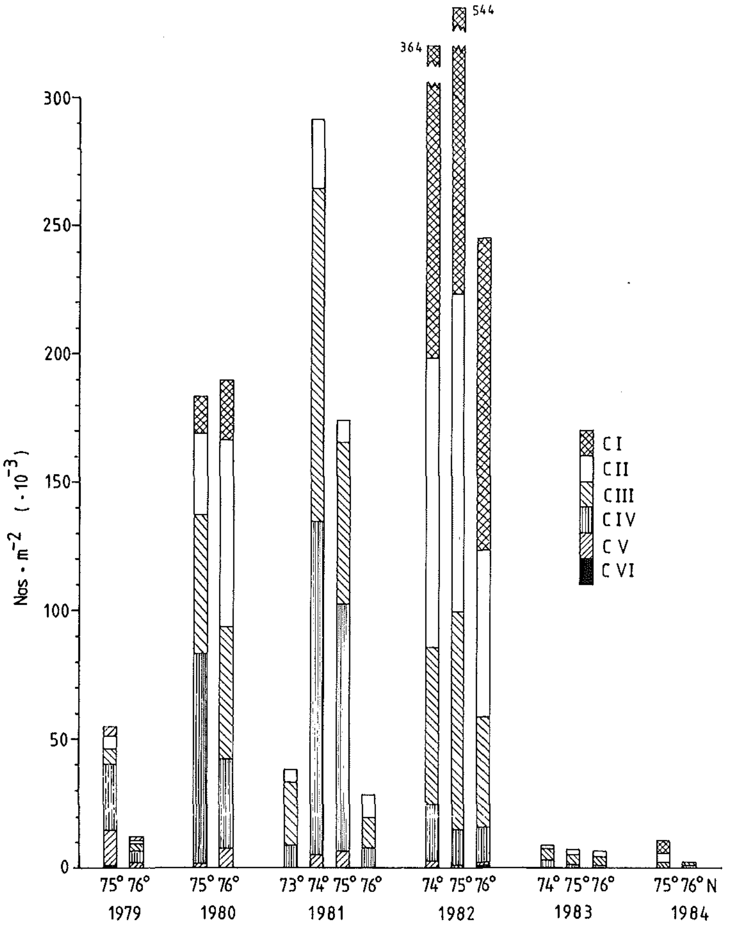

Fig. 10. Abundance (no. of individuals•m^{-2}) of copepodites of *Calanus finmarchicus* plus *C. glacialis* (see Fig. 11) along section I in 1979-1984. The samples in 1980 were from 50-0 m; in the other years from bottom-0 m or 200-0µm. 375 µm net was used in 1981 (except at 76°N) and 1983; 180 or 250 µm net was used the other years (Table 2).

also decreased, although more gradually, from about 20 g dry weight m^{-2} in 1980 to about 2 g dry weight m^{-2} in 1984 (REY *et al*. 1987).

The relative composition of the copepodite stages of *C. finmarchicus* and *C. glacialis* in the different years is shown in Fig. 11. This (as well as Fig. 10) is based on samples from the upper 200 m or the whole water column (Table 2), except for 1980 where samples from the upper 50 m were used. The biomass distribution in 1980 revealed, however, that most of the zooplankton occurred in the upper 50 m (REY *et al*. 1987).

Before we discuss the results in Fig. 11, the effects of variable mesh size and the uncertainty in species separation should be considered. The coarse mesh size of the net used in 1981 and 1983 (375 µm, Table 2) may have resulted in incomplete sampling of the youngest copepodite stages. MATTHEWS, HESTAD and BAKKE (1978) considered a net with 500 µm mesh unsuitable for catching stages I and II of *C. finmarchicus*, with considerable undersampling also of stages III and IV. According to WIBORG (1954), copepodite stages I-III of *C. finmarchicus* would all be retained by 366 µm mesh net (silk no. 2). Using preserved samples collected with 180 µm net, we tested the retention of *C. finmarchicus* copepodites on a 375 µm mesh screen.

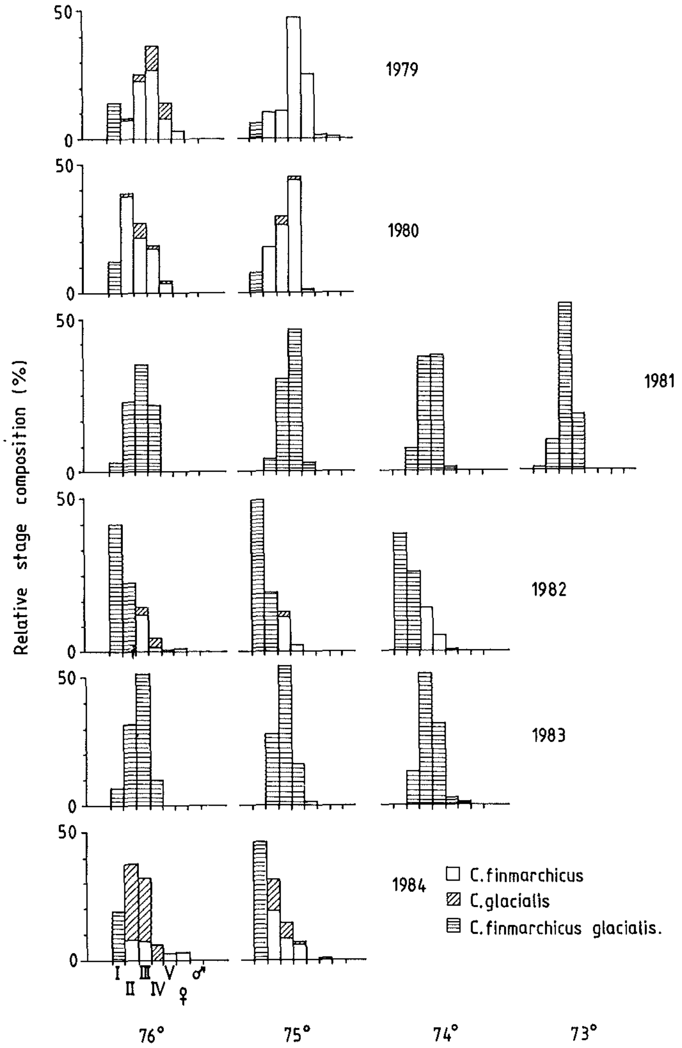

Fig. 11. Relative (%) copepodite stage composition for Calanus finmarchicus and C. glacialis at section I in 1979-1984. The two species were not separated in 1981 and 1983 as were neither stage CI in the remaining years and stage CII in 1982. See legend to Fig. 10 for details concerning sampling.

Almost half the number of stage I was found to wash through the screen (44%). Almost all stage II individuals, however, were retained on the screen (98%). It is therefore probable that stage I copepodites were undersampled in 1981 and 1983, whereas stages II and older apparently were not. In calculating values for the average stage composition (see below), we have multiplied the observed numbers of stage I obtained with the 375 μm net by a factor 2.

Stage compositions of C. glacialis observed in the northern Barents Sea and in the Canadian Arctic have suggested a two years life cycle (LONGHURST, SAMEOTO and HERMAN 1984, TANDE et al. 1985). In ice-covered waters north of the polar front there was a clear predominance of stage IV copepodites and adult females in late May - early June 1983 (GJØSÆTER et al. 1983b). In January 1985 there was predominance of stages III and IV and adult females of C. glacialis in samples both from Storfjordrenna and from the Southeastern Basin (HASSEL, LOENG and SKJOLDAL 1986). These results are consistent with a two years life cycle for C. glacialis.

The apparent contribution of *C. glacialis* to the stock of *Calanus* copepodites varied among the years as well as with latitude (Fig. 11). It was in general higher at 76°N close to the polar front than further south, and it was highest in 1984 when the total abundance was low (Fig. 10). This high relative contribution of *C. glacialis* in the Atlantic water in the "warm" year 1984 is surprising and may reflect difficulties in the method used to separate the species. This need not be the case, however, since *C. glacialis* may have been contained in the cold bottom water (Fig. 9) and migrated upwards to co-occur with the low-abundance stock of *C. finmarchicus*.

In the following analysis of copepodite development in each year we have not separated between the species. This is mainly due to the lack of separation of the species in 1981 and 1983 and of stage CI the other years. Apart from the sample from 76°N in 1984, *C. finmarchicus* constituted the majority of the copepodites (Fig. 11). The copepodite stage composition for *C. finmarchicus* is not drastically altered by including *C. glacialis* for the samples where the two species were separated (Fig. 11). We therefore assume that the stage composition for both species combined is largely representative for the development of *C. finmarchicus*.

The *Calanus* stage composition was generally dominated by the younger copepodite stages (Fig. 11). Adult males were rarely found, as were adult females except in 1979 and 1982 when they occurred with about 500 individuals per m^2 (Figs 10 and 11). These results show that spawning had occurred fairly early in the spring, and that the new generation of *C. finmarchicus* had already gone through a considerable part of its development.

As an index of the *Calanus* stage development we have calculated the mean stage for each of the distributions in Fig. 11 (Table 3). The highest index values were observed during the relatively late coverages in the cold years 1979 and 1981. CIV was the dominant stage 11-12 July 1979, as it also was at 74° and 75°N in late June 1981 (Fig. 11). The copepodite stage composition indicated a somewhat delayed development at 76°N than further south in both years. Also at the southern end of the section (73°N) in 1981, at the outer extension of coastal water (Fig. 6), the development was apparently somewhat retarded in 1981. The sample from 76°N in 1981 was taken with a 180 μm net, and the low proportion of stage CI here indicates that the lack of CI further south was real and not a sampling artefact, due to the coarser mesh net used there (Table 2).

Compared to 1981 the samples from the same time (late June) in 1980 showed a less advanced development, with stage CII as the dominant one at 76°N (Fig. 11). More advanced development in the meltwater front at 76°N than in the Atlantic water at 75°N was found in 1982 and 1984, but not in 1980. In 1983 the meltwater front was located north of 76°N (Fig. 8). The copepodite stage composition indicated a slightly more advanced development at 74°N than at 75°N both in 1982 and 1983 (Fig. 11).

The general pattern which emerges from the results in Fig. 11 is that the copepodite development started first in the southern part of the meltwater region. In the Atlantic water south of the meltwater region, copepodite development was progressively delayed with increasing latitude, as it also was in the meltwater region in the cold years 1979 and 1981.

The copepodite development was least advanced in early June 1982 when CI was the predominant stage (Fig. 11). The total number of copepodites per m^2 was highest this year and even though the relative stage composition was dominated by CI and CII, the absolute numbers of stages CIII and CIV were also generally high (Fig. 10). Compared to 1982 the copepodite development in early June in the two following years were more advanced, especially in 1983 when stage CIII predominated (Fig. 11).

The stage compositions in Fig. 11 and the calculated stage index values (Table 3) are from a time span of 5 weeks, from early June in 1982-1984 to 11-12 July in 1979 (Table 1). Although there is a general correspondence between stage distribution and time of coverage, the results from the last 3 years show that some variation from year to year occurs. We have attempted to normalize the results by extrapolating them to a common date, mid-June, each year. This gives only an approximate description of the real situation since recruitment to CI from nauplii is ignored. However, except for 1982, the relative stage distributions indicates that the peak in recruitment to CI was over. This suggests that any distortions of the data by extrapolation would be small.

Extrapolation requires knowledge of the rate of development of the copepodites. This can be strongly dependent on temperature (RUNGE *et al.* 1985). Some estimates of stage durations of *C. finmarchicus* from field observations or laboratory experiments are summarized in Table 4. These suggest durations of about 1 week for the youngest copepodite stages, with a general increase in stage duration with increasing stage number and size of the copepodites. We have assumed 1 week stage durations for CI, CII and CIII in our extrapolations.

Table 4. Durations of copepodite development for stages CI, CII and CIII of *Calanus finmarchicus* estimated from the development of field populations or, in the case of RUNGE *et al.* (1985), from laboratory rearing or molting rate determination.

Area				
Norwegian Sea	<1wk	1wk	2wk	ØSTVEDT 1955
North Sea	5d	5d	10d	KRAUSE and RADACH 1980
Korsfjorden, W.Norway	-	-	6d	MATTHEWS *et al.* 1978
NW Atlantic (off Nova Scotia)	-	-	3-5d	RUNGE *et al.* 1985

The estimated dominant stage by mid-June varied from stage CI in 1979 to stage CIV in 1983 (Table 3). This represents a variation of about 3-4 weeks in the time of maximum copepodite recruitment.

Calanus hyperboreus

The largest of the *Calanus* species, *C. hyperboreus*, occurred in fairly low numbers (1000 copepodites m^{-2} or less; Table 5). The abundance was usually higher at 76°N than further south. Adults were never found, and the dominant stages were usually CIII and CIV (Table 5). *C. hyperboreus* was not separated from *C. finmarchicus* and *C. glacialis* in stage CI.

C. hyperboreus has an annual life cycle and reproduces in late winter or early spring (ØSTVEDT 1955, MATTHEWS *et al.* 1978, RUDYAKOV 1983). There is some uncertainty as to whether it reaches maturity after 1 or 2

Table 5. Calanus hyperboreus. Abundance (individuals•m^{-2}) of copepodites in samples from section I in 1979-1984. The samples in 1980 were from the upper 50 m; in all other years from bottom-0 m or 200-0 m.

Stage	1979		1980		1981				1982			1983			1984	
	75°	76°	75°	76°	73°	74°	75°	76°	74°	75°	76°	74°	75°	76°	75°	76°
CII	0	20	0	80	0	0	0	0	0	0	0	0	0	0	0	0
CIII	0	40	0	0	0	0	0	0	160	40	160	0	0	20	0	768
CIV	80	800	0	0	0	0	0	820	240	0	240	0	80	20	24	16
CV	0	140	0	0	0	0	0		0	0	0	0	0	0	0	8

years and whether it reproduces successfully in Arctic regions (RUDYAKOV 1983). In Korsfjorden, western Norway, C. hyperboreus was found to develop rapidly after spawning in late winter to reach stage CIV in May (MATTHEWS et al. 1978). The stage compositions in Table 5 are consistent with such an early development. Although based on fairly low numbers, the copepodite development seemed to be somewhat more progressed in the cold years 1979 and 1981 than in 1982 and 1984 (Table 5). This trend is similar to that found for C. finmarchicus (Fig. 11).

Pseudocalanus sp. and Metridia longa

Pseudocalanus sp. and Metridia longa were the most abundant herbivorous copepods in the samples from the Barents Sea after the Calanus spp. Their numerical abundances varied considerably among the years, being generally low in 1983 and 1984 (Fig. 12), as was the case also for C. finmarchicus (Fig. 10).

During sample analysis, stages were grouped as CI to CIII and CIV to CV and not further discriminated. This makes a detailed analysis of the development in the separate years more difficult than for C. finmarchicus. The use of 375 µm net in 1981 and 1983 (Table 2) also complicates the interpretation, especially for the smaller Pseudocalanus sp. A considerable proportion of stages CI-III could have passed through this net. The similarity between the sample from 76°N in 1981 taken with 180 µm net and the samples from 74° and 75°N taken with 375 µm net, may indicate, however, that the majority of copepodites had by then developed into larger stages that were more representatively sampled. A screening test with Metridia longa gave as result that 25% of stage CI passed 375 µm mesh. In contrast to the case for Pseudocalanus sp., the use of 375 µm net should therefore not have caused any substantial influence on the results for this species.

The dominant stages of Pseudocalanus were CIV-V except in 1980 when stages I-III were equally or slightly more abundant. At Weathership M in the Norwegian Sea ØSTVEDT (1955) found P. minutus to develop through to stage IV by early June. The stage distributions in Fig. 12a could therefore reflect that the development through stages CI-III was in general completed by the time the cruises were conducted. However, results from a later cruise in 1981 (8-19 August) showed a pronounced increase in stages CI-III as well as in CIV-V (HASSEL 1986). A similar pronounced increase in the younger copepodite stages was also observed in August 1984 (HASSEL, LOENG, REY and SOLBERG 1984b). This late summer increase in the number of copepodites

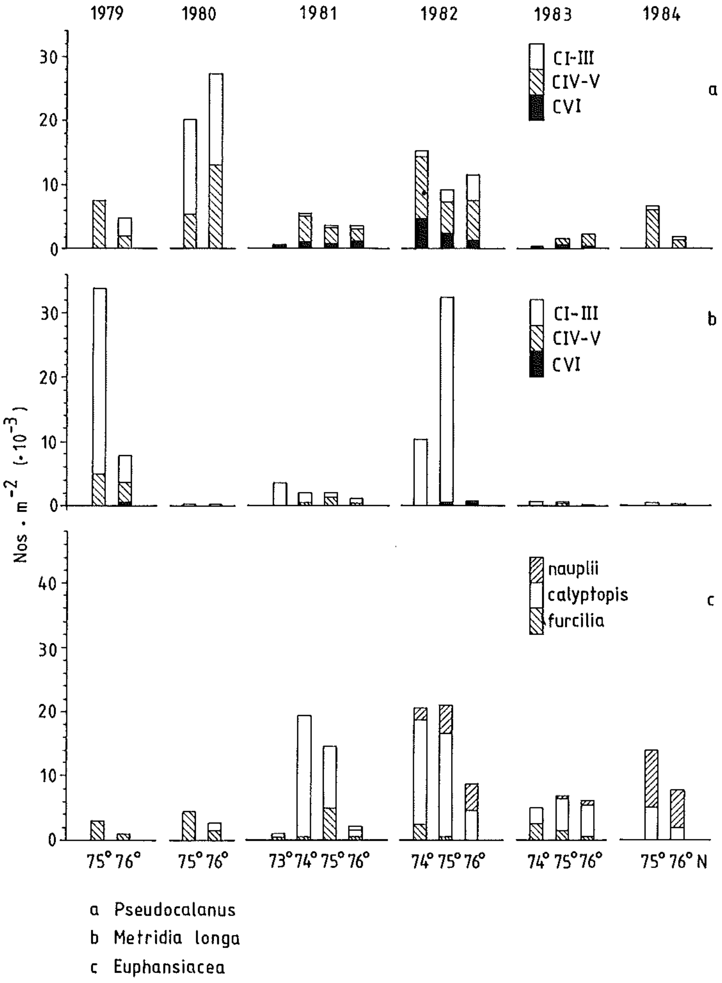

Fig. 12. Abundance (no. of individuals•m^{-2}) of copepodites of Pseudocalanus sp. (a) and Metridia longa (b) and larval stages of krill (c). See legend to Fig. 10 for details concerning sampling.

may represent a second generation of Pseudocalanus sp. However, ØSTVEDT (1955) observed only a single spawning period for P. minutus in the Norwegian Sea. If this is also the case in the Barents Sea, the stage compositions in Fig. 12a are indicative of a fairly late spawning and development for Pseudocalanus.

Assuming a single generation per year, we interpret the large proportion of adults in 1982 as indicative of late spawning this year (Fig. 12a), which also was the year with the least developed Calanus population (Fig. 11). 1980 seemed to be the year with the earliest development of Pseudocalanus sp. (Fig. 12a).

Metridia longa occurred in very low numbers in 1980, 1983 and 1984 (Fig. 12b). The development was apparently more progressed in 1979 than in 1982, which were the only years when the species occurred in moderately high abundance. Metridia longa was found to spawn and develop somewhat later than Calanus finmarchicus in Balsfjorden in northern Norway (HOPKINS et al. 1984). This seems also to be the case in the Barents Sea (Figs 11 og 12b).

Krill

Only the juvenile stages of krill are sampled properly with the Juday net.

Thysanoessa inermis was usually the dominant krill species, but T. raschii also occurred.

During the coverage 11-12 May 1981 krill eggs and nauplii were predominant and few calyptopis or furcilia stages were observed (HASSEL 1986). By the end of June 1981, nauplii were no longer found except for low numbers at 76°N. Calyptopis and, to a lesser degree, furcilia were the dominant stages (Fig. 12c). Reproduction of Thysanoessa spp. in the Barents Sea therefore occurs in early spring as it does also in Balsfjorden (HOPKINS et al. 1984).

The abundance of juvenile krill showed a 10-fold range of variation, from a low in 1979 to highest values in 1981 and 1982 (Fig. 12c). The recruitment of krill was least developed in early June 1984 as indicated by the high proportion of nauplii and absence of the furcilia stage (Fig. 12c). The development seemed to be progressively more advanced in early June 1982 and 1983, late June 1981 and 1980, and early July 1979 (Fig. 12c).

ZOOPLANKTON REPRODUCTION IN RELATION TO SPRING BLOOM DEVELOPMENT

The foregoing analysis of spring bloom and zooplankton developments in the years 1979-1984 have revealed a variation of about one month in both these processes among the different years (Table 3). We now address the questions of how the variation in zooplankton development relates to the differences in spring bloom development, and how these variations relate to the differences in ocean climate.

Besides the differences in estimated times for the blooms to peak (Table 3), there were other qualitative differences in the bloom developments with regard to water column stabilization and pycnocline strength and depth. The degree of stability, expressed as the difference in σt between 100 m and the surface, explained much of the variability in bloom development among the years (REY et al. 1987). Stability also explained part of the variation in copepodite development of Calanus (Fig. 13). Thus the greatest proportion of older stages was generally found when stability was high due to meltwater. Exceptions to this pattern occurred. The stage index values were higher in 1983 than in 1984 (Fig. 13), despite the greater stability and further developed bloom in the latter year (Figs 8 and 9).

The nitrate utilization in the upper 100 m can be used as a measure of bloom development, integrating both the temporal and vertical aspects (REY et al. 1987). A plot of Calanus stage index values versus amount of nitrate utilized shows, however, only a weak relationship (Fig. 14). If one removes the high values for 1979 and 1981 there is no relationship for the remaining data points. Also there seems to be no clearcut relationship between the normalized Calanus stage composition, expressed as the dominant copepodite stage in mid-June, and the estimated time for peak bloom (Table 3). Thus, the stage development was further advanced during the rather late bloom in 1983 than during the earlier bloom in 1984.

Any strict relationship between Calanus development and the spring bloom remains elusive and is not easily demonstrated by any single measure of bloom development. A relationship could nevertheless exist, being dependent on a more complex representation of the blooms. To examine this any further would require more extensive extrapolation and reconstruction of the various phases of bloom development.

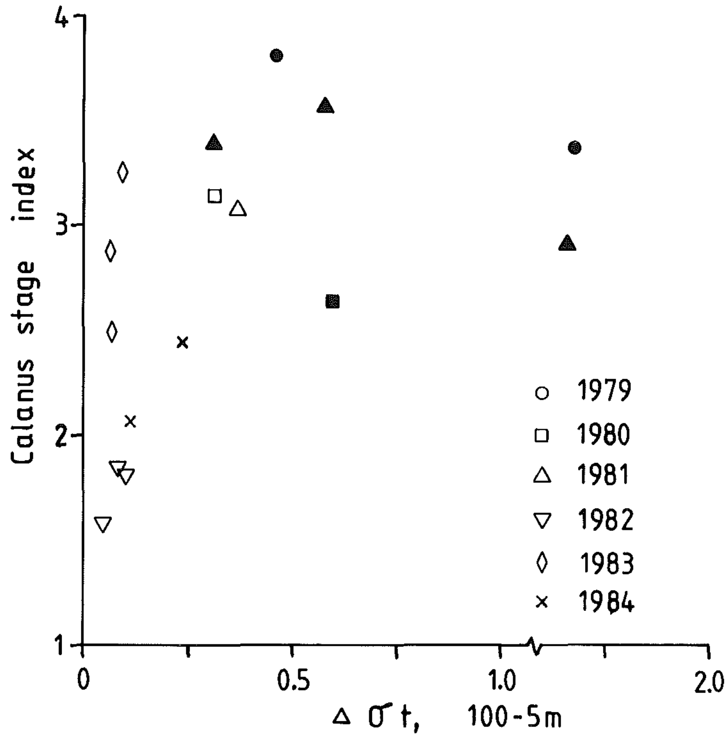

Fig. 13. Relationship between average copepodite stage index) of Calanus finmarchicus plus C. glacialis and water column stability expressed as difference in temperature between 100 m and the surface for stations along section I in 1979-1984. Filled symbols: meltwater. Open symbols: thermal stability. Half-filled symbol: outer extension of coastal water.

What remains clear is that the reproduction of the dominant herbivores occurs early in the spring, in general well in advance of the spring bloom. This is similar to the pattern described for C. finmarchicus from the Norwegian Sea (ØSTVEDT 1955, HALLDAL 1953). It is possible that spawning is influenced by phytoplankton growth in an early phase of the bloom development and that this to a certain degree fixes the further timing of copepodite development. There is no clear relationship between the copepodite stage development and our estimates of time for the start of the blooms (Table 3). This could, however, reflect the uncertain nature of these estimates.

Another source of variation is the temperature dependency of the rates of development of nauplii and copepodite stages (RUNGE et al. 1985). According to an equation for this dependency based on laboratory rearings of C. finmarchicus (RUNGE et al. 1985), the time from hatching to stage CIII would be 78 days at 0°C, 55 days at 2°C, and 35 days at 5°C. Field observations have indicated times for this development to CIII as approximately one month in the North Sea (KRAUSE and RADACH 1980) and in Korsfjorden (MATTHEWS et al. 1978) at temperatures of 5-10°C, and 1½ to 2 months in Balsfjorden at about 3°C (TANDE 1982, HOPKINS et al. 1984). It has been suggested that the success of development is reduced at temperatures below 2°C due to high mortality rate (TANDE pers. comm.).

Temperature explained part of the variation in Calanus stage development in our data (Fig. 15). The temperature values used were those of the upper mixed layer at the time of the cruises. This gives only a very approximate representation of the temperature conditions during the early development. A

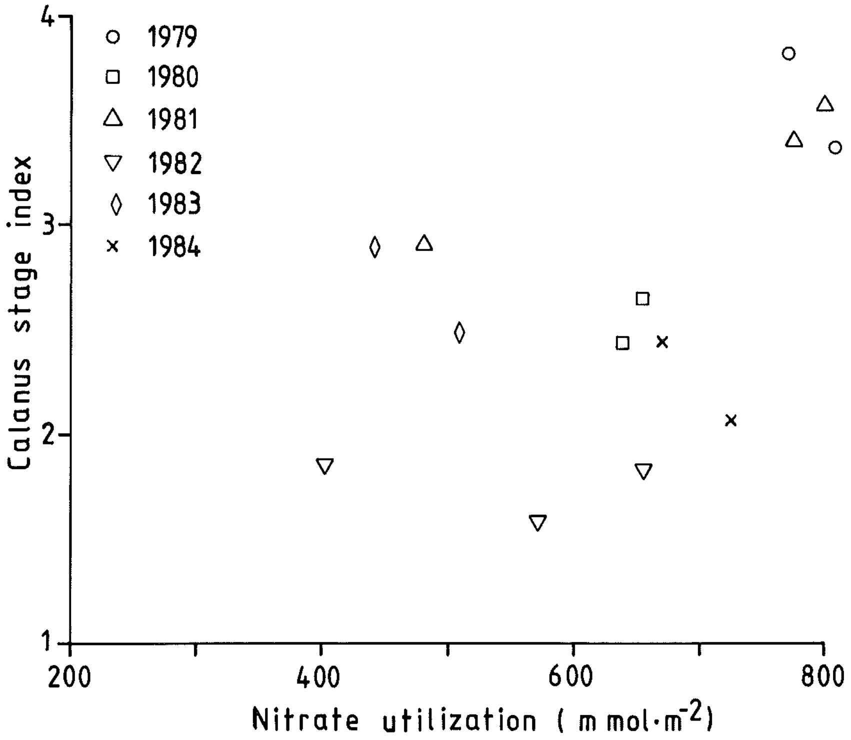

Fig. 14. Average copepodite stage number (stage index) of Calanus finmarchicus plus C. glacialis plotted against nitrate utilization (0-100 m) by the spring phytoplankton bloom in 1979-1984.

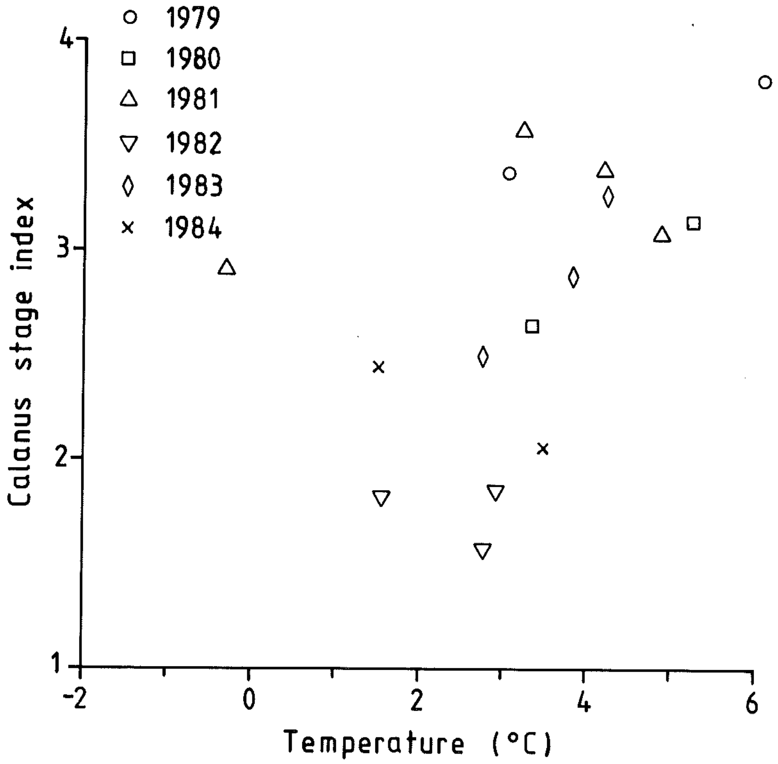

Fig. 15. Relationship between average copepodite stage number (stage index) of Calanus finmarchicus plus C. glacialis and temperature of the upper mixed layer at the time of coverage of section I (Table 1) in 1979-1984.

further difficulty in interpreting the relationship in Fig. 15 lies in the interdependency between temperature on one hand and time, stability formation and bloom development on the other. The data point for 76°N in 1981 is exceptional and noteworthy. The copepodite development here was fairly advanced with CIII as the predominant stage (Fig. 11), despite temperature below 0°C (Fig. 6). This suggests that development of *C. finmarchicus* can take place at very low temperatures, although the abundance of copepodites was considerably lower here than at higher temperatures further south (Fig. 10). *C. finmarchicus* was not separated from *C. glacialis*, however, and it is therefore possible that the latter species contributed to the high stage index value found at 76°N.

The temperature isopleth diagrams (Figs 4-9) suggest that the early development of *Calanus* in Atlantic water not influenced by meltwater has mainly occurred at temperatures of 2-4°C. With the influence of ice melting, such as in 1979 and 1981, the temperature conditions were assumedly more variable, being very low in the early phase of development. Such low temperatures could retard the hatching and development of nauplii, thus countering the possible effect of earlier spring bloom development under such conditions. This could be one reason for the fairly similar level of development reached in mid-June in each year. Except for 1983, the dominant stage by that time was estimated to be stage CI or CII (Table 3). There was in fact a weak tendency of slightly less advanced development in the cold years 1979 and 1981 than in the warmer years (1980, 1982-1984).

The phytoplankton spring bloom is to a great extent influenced by the physical oceanographic conditions and thereby also by the climatic conditions. In cold years with extensive ice melting in Atlantic water south of the polar front, stability formation is mainly due to meltwater. This is examplified by the years 1979 and 1981. Such stability formation is usually more pronounced and occurs earlier than stability formation due to warming of the upper layer. The spring bloom is therefore expected to start earlier in the cold years and to culminate a month or more prior to the culmination of the blooms in Atlantic water in warmer years (Table 3). One might ask which of these conditions are more favourable for the development and production of herbivores such as *Calanus finmarchicus*. The early blooms in cold years might be advantageous for maturation and spawning and possibly also for the development of the nauplii. However, the copepodites may not reach a size which allows them to fully utilize the bloom prior to its culmination. In contrast, the slower bloom development in warmer years may be more favourable for copepodite development. Assuming that the Norwegian Sea is the true home area of *Calanus finmarchicus* where its ecological properties have been molded through evolution, one would intuitively believe the development in warmer years to be the more favourable for this species.

One can envisage an alteration from a closely coupled and efficient pelagic system in warm years to a system where a greater fraction of the spring bloom is left ungrazed to sediment out to the deeper water or benthos in cold years. This generalization applies mainly to the area immediately south of the polar front where the variable influence of ice melt is taking place. If we turn to our data for *Calanus* abundance (Fig. 10), they provide no clear-cut support for this hypothesis. Thus the recruitment of *Calanus* seemed to be successful in the cold year 1981, although the highest zooplankton biomass (REY *et al.* 1987) and copepodite numbers occurred in the warmer years 1980 and 1982, respectively. The copepodite numbers were, on the other hand, very low in the warm years 1983 and 1984.

Zooplankton abundance and biomass depend perhaps as much on predation as on growth and production. Grazing by capelin and other predators is no doubt a factor to be reckoned with in order to fully explain variations in zooplankton as influenced by climatic conditions.

Advective transport of plankton is another process which is potentially very important. The inflow of Atlantic water from the Norwegian Sea is possibly related to climatic phenomena within the Barents Sea and may occur in pulses rather than as a steady flow (MIDTTUN and LOENG 1987). The population of C. finmarchicus in the Norwegian Sea overwinters mainly below 600 m (ØSTVEDT 1955, HASSEL et al. 1986). Its ascent to the surface layer takes place in February-March (ØSTVEDT 1955). Inflow to the Barents Sea prior to this ascent could introduce water practically devoid of C. finmarchicus. Computer simulations have shown the number of overwintering females to be important for the total production (SLAGSTAD 1981, REY et al. 1987). The timing of major inflow events in relation to the seasonal vertical distribution of C. finmarchicus could therefore be of great ecological significance for the Barents Sea.

ACKNOWLEDGEMENT

This work has been partly supported by the Norwegian Fisheries Research Council (NFFR).

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THE EFFECT OF OCEANOGRAPHIC CONDITIONS ON DISTRIBUTION AND POPULATION
DYNAMICS OF COMMERCIAL FISH STOCKS IN THE BARENTS SEA
Proceedings of the third Soviet-Norwegian Symposium, Murmansk, 26-28 May 1986
Edited by H. Loeng. Institute of Marine Research, Bergen, 1987.

EFFECT OF HYDROMETEOROLOGICAL FACTORS ON THE REGULARITY OF THE LONG-TERM VARIATIONS IN EUPHAUSIID (CRUSTACEA, EUPHAUSIACEA) ABUNDANCE IN THE SOUTHERN BARENTS SEA

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ABSTRACT

To elucidate the origin of Thysanoessa inermis and Thysanoessa raschii year class strength fluctuations in the Barents Sea, the frequency of the long-term variations in abundance of these macroplankton species at age 0+ were studied together with the main environmental factors (water temperature, hydrographic spring period, indices of atmospheric circulation) influencing the formation of forthcoming euphausiid year classes in their early stages of development. Three components of variations: trend, periodic (about 14 years), and shortperiodic (2-3 years), prevailed both for the abundance of T.inermis and T.raschii at age 0+ and for the mean water temperature in the Kola Meridian section from July to September 1953-1981. A close correlation between periodic variations in euphausiid recruitment and water temperature allowed prediction of the year class strength of these macroplankton species by means of a component-based calculation.

INTRODUCTION

The pelagic crustaceans - euphausiacea - are in certain periods the main food objects for commercial fishes (cod, haddock, capelin, herring, redfish) of the Barents Sea (BOLDOVSKY 1944, GRINKEVICH 1957, DROBYSHEVA 1957, BARANENKOVA, DROBYSHEVA and PONOMARENKO 1964, SONINA 1976, and others). The dynamics of both the abundance and quantitative distribution of this macroplankton group influence the behaviour of fish during the feeding (SONINA 1969, PANASENKO 1978) as well as their year class strength (SYSOEVA 1973, PONOMARENKO 1973).

The arctic boreal species of shelf waters, Thysanoessa inermis (Kröyer) and T.raschii (M.Sars), represent the bulk of euphausiids in the southern Barents Sea. The former species occurred in all areas, but the highest numbers of these crustaceans were found in waters of Atlantic origin in western and southern regions. In the Barents Sea concentrations of T.inermis were formed due both to local spawning and to the transfer of euphausiids from spawning grounds off the northwestern Scandinavia into the Barents Sea. Representatives of typically neretic and more coldwater species, T.raschii, were predominant in the shallow southeastern part of the sea, where their abundance was established due to local recruitment (DROBYSHEVA 1982). Therefore, the presence of T.inermis in the Barents

Sea were connected to a set of environmental conditions both in the Barents Sea and Norwegian Sea, while T.raschii were only found under certain conditions in the southern Barents Sea.

The pattern of reproduction, growth rate, succession of development and life cycle for the above species were very similar. However, due to different ecological conditions, the reproduction of T.inermis lasted 1.5 months (April-May) in the southwestern Barents Sea, and 3.5 months (May-July) for T.raschii. Since survival of larvae was a condition determined by different time periods, the survival of either species depended on the peculiarities of hydrometeorological processes during their respective times of maturation.

To learn the effect of abiotic factors upon the long-term variations in the Barents Sea euphausiid abundance, we gave much attention to the most numerous group of specimens at age 0+, since the 1-year-olds (1+) and 2-year-olds (2+) made up a small part of the population and were eaten to a greater extent by fish.

MATERIAL AND METHODS

The yearly observations of biological factors and quantitative distribution of euphausiids in the Barents Sea have been carried out by the Polar Research Institute since 1952. The data for assessing euphausiid abundance were collected by research vessels from October to January. During this period, the size groups 0+ and 1+ dwelt together, and by keeping to the near-bottom layer (no vertical migration), were little preyed on by fishes. As a result of the treatment of biological samples, the relative indices of abundance for all age groups of the main euphausiid species were obtained, that is, the mean catch per trawling hour with a trawl-attached net (diameter 50 cm, gauze No. 140) which equaled the number of specimens in 10^3 m^3 of water (DROBYSHEVA 1979).

A check on the frequency series for T.inermis and T.raschii at age 0+ (1953-1981) showed that the euphausiid stock followed a logarithmic rather than a normal distribution. Hence, the time series using decimal logs were subject later on to a statistical analysis.

The historic investigations of ecology for neritic arctic boreal species of the Barents Sea euphausiids permitted the main abiotic factors influencing the formation of year classes to be determined: water temperature and atmospheric circulation. The beginning and duration of hydrographical spring regulates the intensity of the spring and summer vegetation of phytoplankton - the food object of euphausiids (PONOMARENKO 1973, ZELIKMAN 1964, DROBYSHEVA and DEGTYAREVA 1974, EINARSSON 1945). The direction of atmospheric circulation near the sea surface greatly influenced the seasonal dynamics of the upper water layer which, in its turn, regulated the distribution of macroplankton juveniles in the Barents Sea areas (DROBYSHEVA 1979).

In this paper the mean water temperature in the 0-50 m layer in the Kola Meridian section (stations 3-7) from July through September was used as an index of heat content of the water mass in the southern Barents Sea. The period of averaging included the start and duration of spawning, and also the development of pelagic juveniles of the examined euphausiid species. The choice of this section, to obtain characteristic for the heat content of the water mass within the distribution area of euphausiids, was based on a close correlation between the long-term variations in summer water temperature in the Kola Meridian section and other oceanographic sections located at different parts of the Barents Sea. According to our calculations, the correlation coefficients between the variations of mean water temperature in the 0-50 m layer in the Kola Meridian section during July-September and on sections 3, 29, 8 and 10 (1953-1980) were equal to 0.77, 0.84, 0.84 and 0.69, respectively (positions of sections is given in Fig. 1).

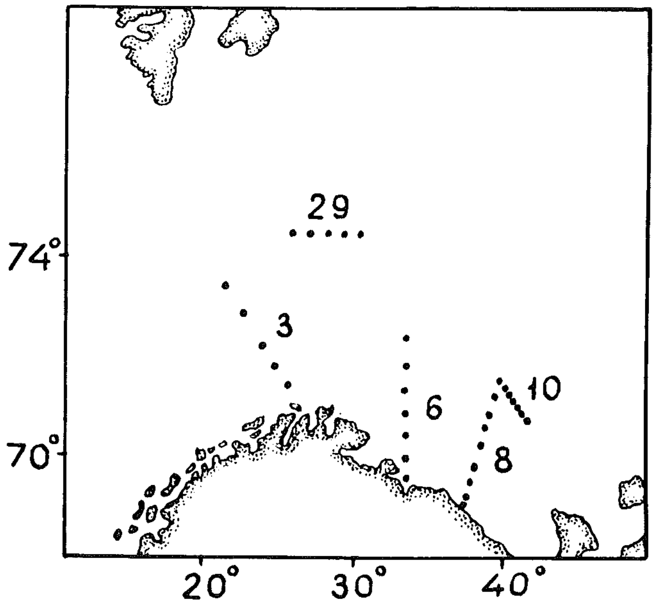

Fig. 1. Position of stations at standard sections in the Barents Sea.

The beginning and duration of hydrographical spring was determined by temperature variations in vertical water masses in the Kola Meridian section (No. 6) and these terms were believed to characterize the development of vernal processes in the whole southern Barents Sea (BOYTSOV 1980). The mean difference between water temperatures in the 0-50 m layer in June and April for sections 6, 8 and 10 was also used as an indirect characteristic of phytoplankton growth rate. The indices proposed by KATS (1960) may serve as the quantitative characteristic of intensity of meridional transport of air across 70°N between 30° and 50°E, and zonal circulation from 70° to 80°N between 20° and 40°E. These indices were averaged for the period of May through August, and were used as the indirect characteristic of the dynamics of the upper water layer. The latitude/longitude draw the limits where the drift of euphausiid eggs and juveniles took place in the southern Barents Sea.

To study the internal structure of year-to-year fluctuations in the abundance of T.inermis and T.raschii at age 0+, as well as abiotic factors, a variational series of these parameters were processed using periodogramanalysis, least squares technique and moving linear and non-linear averaging method (VARSAR 1934, VAINU 1977, POLLARD 1982). The agreement between the year class strength of dominating euphausiid species and different hydrometeorological indices were checked through a correlation analysis. The relations revealed were approximated by regression analysis.

RESULTS AND DISCUSSION

The analysis of abundance dynamics of T.raschii and T.inermis at age 0+ indicated that a complex structure of year-to-year variations was formed as a result of superposition of non-periodic trends and various periodic components. The period for observations of long-term variations in young euphausiid abundance (n=29) did not allow the use of the modern theory of random functions (e.g. autocorrelational and spectrum analysis). Therefore we used a combined statistical technique for sampling the components from the complex process.

The non-periodic trend components were first sampled by a method of least squares (POLLARD 1982) from initial variational series of relative abundance of T.raschii and T.inermis year classes. Hydrometeorological parameters and their analytical equations approximating tendencies were also found. Fig. 2 demonstrates a trend components of the parameters in the long-term variations to which they contribute. The variational series of abundance of the year class at age 0+ had a linear increasing trend, which contribute about 54% in total variation of the process (Fig. 2A). The existence of such a trend component for variations of recruitment for this euphausiid species may be explained by the following phenomena:

- A tendency towards cooling of the southern Barents Sea water masses (Fig. 2C) favoured the western expansion of the optimum zone for the distribution of these species without changing the eastern boundary. In this case the density of euphausiid distribution decreased, and the number of young specimens having food, increased.

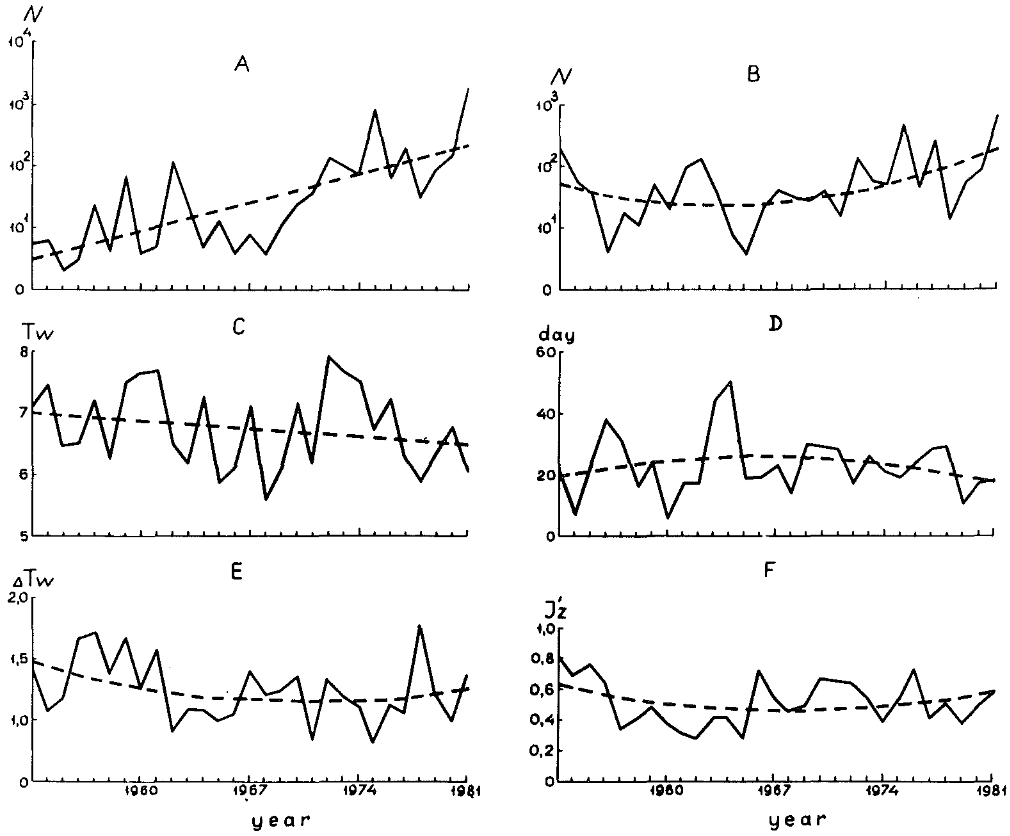

Fig. 2. Year-to-year variations (solid line) in abundance of T. raschii (A), T. inermis (B) at the age of 0+ (on a logarithmic scale), mean water temperature in the 0-50 m layer of the Kola Meridian section from July to September (C), hydrological spring period (D), mean difference of water temperature in the 0-50 m layer (from June to April) on sections 6, 8 and 10 (E), indices of zonal circulation from 70° to 80°N between 20° and 40°E (F) and their trend components (broken line).

- During the 1970s, the feeding area of cod and capelin was displaced slightly westward in the Barents Sea (SONINA 1976, PANASENKO 1978). This is the reason why the eastern concentrations of euphausiids were not subject to intensive eating. Furthermore, the abundance of many fish species, feeding on macroplankton, tended to decrease.

The trend of variations in abundance for T.inermis at age 0+ had a quadratic polynomial approximation and accounted for about 24% of total variation of this index. From mid 1950s to mid 1960s a decrease in abundance of this species took place, followed by a stable tendency toward its increase. Such a characteristic of total variation for T.inermis recruitment for 1953-1981 might have been caused by:

- the formation of abundance of this Barents Sea euphausiid species may be greatly influenced in certain periods by young T.inermis being transferred from the Norwegian Sea (DROBYSHEVA 1979). This is confirmed by the existence of variational series for zonal circulation (70-80^{o}N, 20-40^{o}E, May-August) with the same trend as for the long-term variations of T.inermis recruitment (Fig. 2F);

- survival of young T.inermis to a large extent depends on the pattern of the spring and summer development of phytoplankton. An early and quick bloom was favourable for this species of euphausiids (DROBYSHEVA and DEGTYAREVA 1974). Shorter periods in development of the hydrographical spring during the 1950s occurred, compared to the following decade. This was also correlated to variations of the water temperature for the 0-50 m layer from April to June, which promoted a more frequent occurrence of abundant T.inermis year classes during this period (Fig. 2D, E);

- the total increase in abundance of T.inermis as well as T.raschii at age 0+ was probably due to a decrease in the abundance of the main fish species feeding on euphausiids during the 1970s.

Thus, the long-periodic variations in recruitment of euphausiids in the southern Barents Sea were formed through the influence of a whole set of biotic and abiotic factors. Some of these may have favoured the appearance of abundant year classes during certain periods, while others adversely affected the early ontology development of organisms.

At the next step, after-trend sampling, all the series were subject to periodogramanalysis (VARSAR 1934) to obtain informations about the available periodic components. The results of the calculations showed that the long-term changes of some parameters involved quasi-periodic variations in the duration of:

- abundance of T.raschii of 11-14 years, and T.inermis of 10-13 years;
- mean water temperature in the 0-50 m layer in Kola Meridian section from July to September of 11-14 years;
- a period of hydrographical spring of 6-8 years;
- indices of zonal transport (70-80^{o}N 20-40^{o}E, May-August) of about 20 years.

However, the amplitude of these periodic components was not constant with time. Therefore, the application of Fourier analysis for their approximation was unreasonable. In order to sample and estimate the quasi-periodic components, the time series (with trends excluded) were subject to smoothing by a running mean method in which the five- and three-membered linear equilibrium sequence was used as a function for filtering.

Fig. 3 presents the graphs of the sampled periodic components which equaled 13-14 years. Naturally, it is difficult to estimate the stability of given variations with a limited sample size. Yet, their reliability for this analysis was confirmed by similar variations, which were revealed earlier for a longer series of water temperature for the southern Barents Sea (POTAICHUK 1972, BOCHKOV 1977). So long as an identical pattern of calculating the variational series of euphausiid recruitment with respect to water temperature was used in the present paper, the quasi-14-year variations can be considered reliable for estimates of abundance of macroplankton at age 0+.

The 13-14 year periodic fluctuations in young euphausiid abundance which were revealed, made a relatively small contribution to total variability of these indices. These constituted about 16% for T.raschii and 20% for T.inermis. But

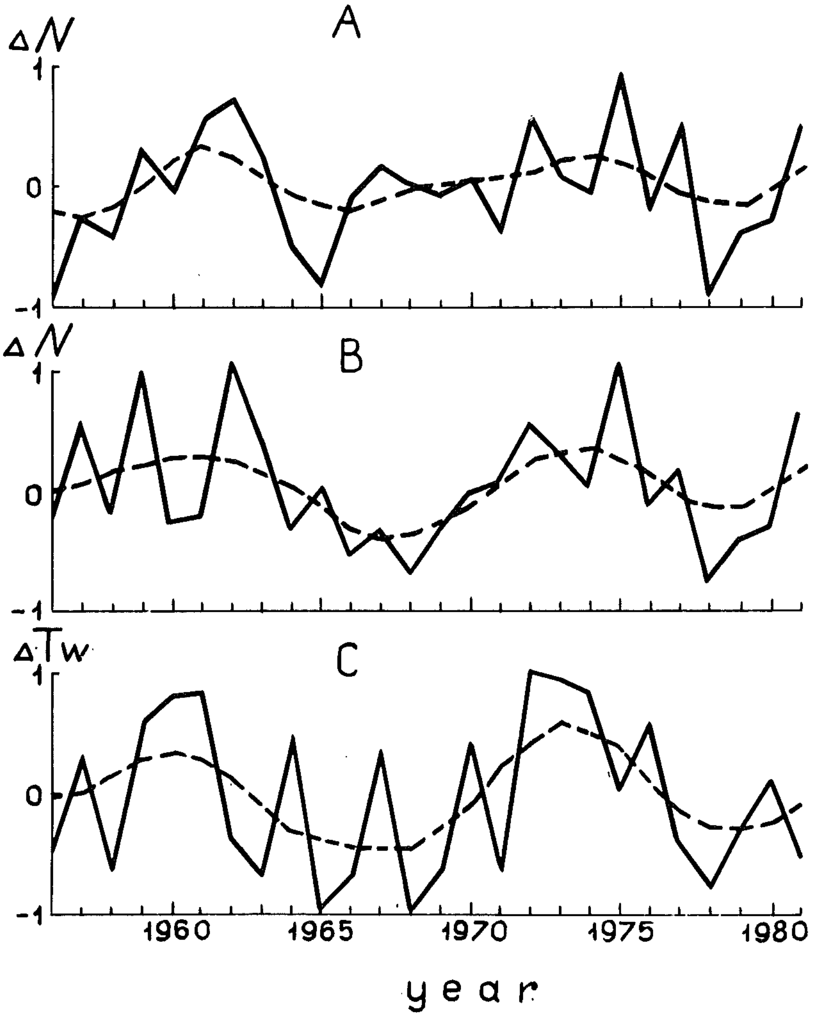

Fig. 3. Dynamics of abundance of T. inermis (A), T. raschii (B) at the age of 0+ and mean water temperature in the 0-50 m layer on Kola Meridian section in July to September (C) with the trend excluded (solid line) and periodic components (broken line).

during years, when this quasi-periodic component reached maximum, its significance increased considerably.

It was established through intercorrelation analysis that the maximum correlation between the fluctuations in abundance for two species of young euphausiid and mean water temperature for the 0-50 m layer in Kola Meridian section, with a frequency of quasi 14-year variations, was observed when the hydrographic parameter was shifted by a year backward relative to indices of macroplankton abundance (for T.raschii r=0.915; for T.inermis r=0.855). A time lag existed which permitted periodic component variations in the young euphausiid abundance to be found by the change of behaviour and amplitude of this water temperature frequency component.

The sampling and successive elimination of relative indices for euphausiid recruitment and from water temperature of trend and periodic components from initial variational series, allowed estimates of short-periodic fluctuations of these parameters to be obtained. The comparative analysis of fluctuations for a different period indicated that high-frequency variations prevailed in the total abundance variability for T.inermis at age 0+ (56%) and for summer water temperature (67%). The trend component accounted for about 54% of the total variance which dominated the year-to-year variations of T.raschii year classes, and short-periodic fluctuations did not contribute more than 30% to the total.

A graphic comparison of high-frequency (2-3 year) variations for recruitment of two species of euphausiids with water temperature permitted us to suggest a hypothesis about the existence of a variable correlation between the dynamics of macroplankton abundance and a physical parameter. As a result of the correlation analysis made with a different moving interval, it was established that the sign of this correlation changed in 7 year intervals (Fig. 4). The positive correlation was observed for the ascending part of quasi-periodic 13-14-year components, while the negative correlation occurred during the 7 years going from a maximum to a minimum of this component. The existence of a constant period with the changing sign of correlation for a long period (29 years) allowed the structure of co-fluctuations in euphausiid recruitment and water temperature at a frequency of short-periodic variations to be preserved. This is why that to predict the year class strength at a frequency of 2-3-year variations, the regression equations approximating the positive and negative correlations between euphausiid recruitment and mean water temperature for the 0-50 m layer on Kola Meridian section during July through August may be used.

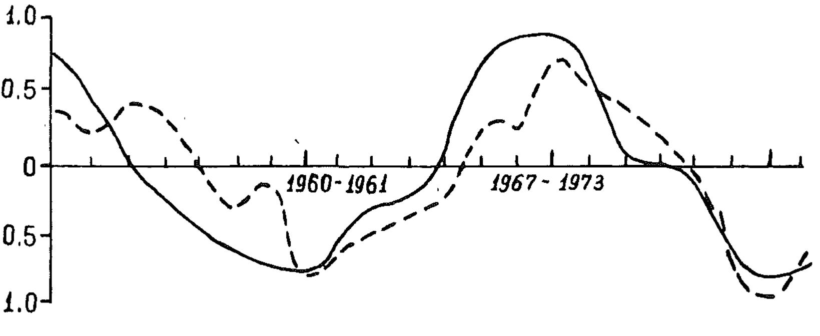

Fig. 4. Variations of moving coefficients of correlation between short-periodic fluctuations of mean water temperature in the 0-50 m layer on Kola section from July to September and abundance of T. raschii (solid line) and T. inermis (broken line) at the age of 0+.

Thus, by using a combined statistical technique, the variational series of abundance for young T.raschii and T.inermis at age 0+ can be presented in the form:

$$y(t) = f(t) + g(t) + n(t)$$

where y(t) is an initial series; f(t) a trend component; g(t) a quasi-periodic component; and n(t) a short-periodic component. The period of the latter coincided with the lifetime of euphausiids and may depend on self-regulation of the abundance for the population.

The identity of frequency structure of year-to-year variations for euphausiid recruitment and mean water temperature of the 0-50 m layer in the Kola Meridian section during July and September, and the existence of the close correlation between periodic fluctuations of these parameters, permitted us to work out a model of the various components for T.raschii and T.inermis year class strength (Fig. 5). The accuracy of statistical estimates for young euphausiid abundance obtained with the help of the model allowed it to be used in practice.

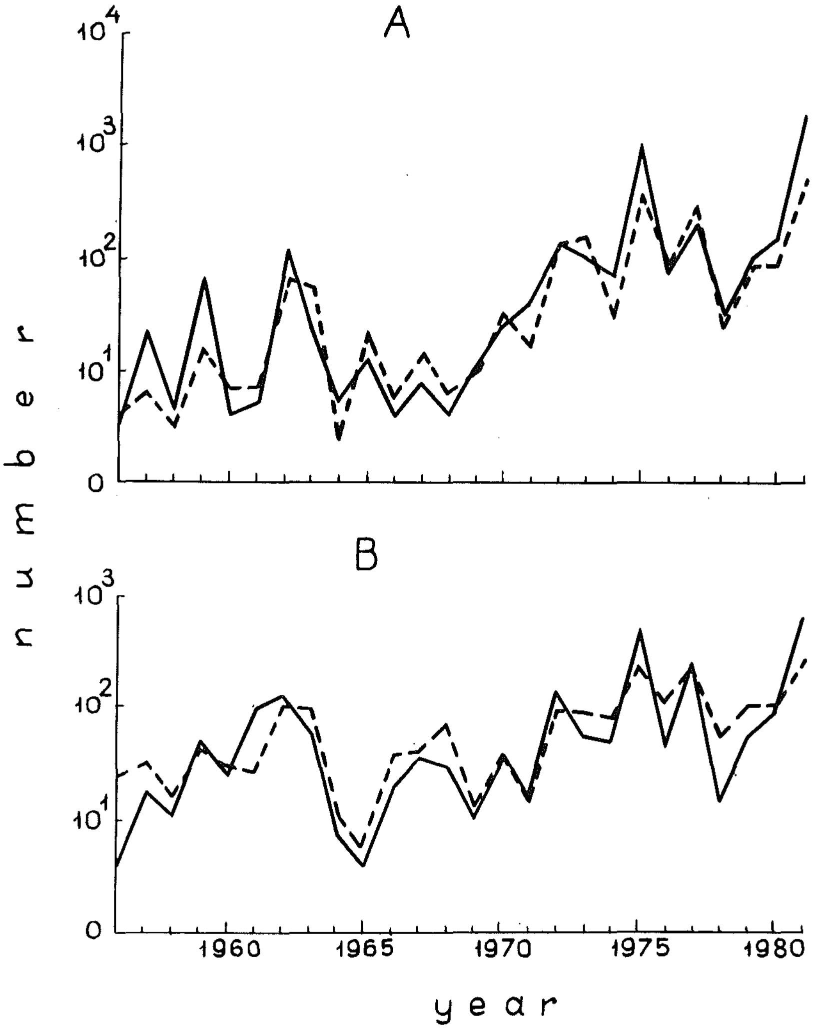

Fig. 5. Actual (solid line) and calculated (broken line) abundance of T. raschii (A) and T. inermis (B) at the age of 0+ in 1956 to 1981 (on a logarithmic scale).

A complex internal structure of fluctuations for the considered parameters suggests that a continuous observation over the pattern of the time variation for each component of the frequency structure of processes and checking the extent of influence of abiotic factors on their variability.

CONCLUSIONS

Through the use of a combined statistical technique, depending on a set of abiotic factors and periodic (14 years) and short-periodic (2-3 years) variations, trend indices were calculated from a long series of data on the abundance of young T.raschii and T.inermis at age 0+.

The identity of a frequency structure for year-to-year variations in euphausiid recruitment and mean water temperature for the 0-50 m layer in Kola Meridian section during the period July - September were established. The maximum correlation between fluctuations of young macroplankton abundance and mean water temperatures was observed to occur with a frequency of quasi-14-year variations, with the hydrographic parameter being shifted backward by a year. The sign of the correlation between the abundance of young T.raschii and T.inermis and water temperature changed every 7th year, in high-frequency variations with a period of about 2-3 years. The positive correlation was observed during the ascending part of the periodic 13-14-year component, the negative correlation occurred during the descending part.

The existence of a close correlation between the periodic variations in euphausiid recruitment and mean water temperature for the 0-50 m layer in the Kola Meridian section during the period July - September, permitted the model of the component-based prediction for T.raschii and T.inermis year class strength to be worked out.

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THE EFFECT OF OCEANOGRAPHIC CONDITIONS ON DISTRIBUTION AND POPULATION
DYNAMICS OF COMMERCIAL FISH STOCKS IN THE BARENTS SEA
Proceedings of the third Soviet-Norwegian Symposium, Murmansk, 26-28 May 1986
Edited by H. Loeng. Institute of Marine Research, Bergen, 1987.

THE EFFECT OF BIOLOGICAL AND PHYSICAL FACTORS ON THE SURVIVAL OF ARCTO-NORWEGIAN COD AND THE INFLUENCE ON RECRUITMENT VARIABILITY

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ABSTRACT

Data from egg and larval field investigations in the Lofoten area are used together with long time series of data on temperature and zooplankton in Lofoten and abundance indices of Arcto-Norwegian cod. The importance of environmental factors at the spawning grounds on the year class strength is discussed.

High temperature is a necessary, but not sufficient condition for the production of strong year classes. Spawning of Calanus finmarchicus in Lofoten is strongly influenced by the temperature in the upper layer, causing large variations in the time of nauplii production.

The peak spawning of the Arcto-Norwegian cod is fixed within a period of one week in late March/early April and is very stable between years. The incubation period is influenced by the temperature of the coastal watermasses which vary between 0.5 and 4.5°C, causing a maximum difference in peak hatching of more than two weeks.

Young larvae are found to have the center of their distribution close to the spawning ground, where the best feeding conditions for the larvae also are found. However, the distribution of subsequent stages of eggs shows both spreading and transport. Only the most advanced larvae seem to be able to survive the drift through "poorer" feeding areas on their way from the "retention" area to the Barents Sea.

Gut analyses of larvae subjected to different prey densities indicate that the critical prey density for successful feeding must be on the order of 5-10 plankters per liter.

Length/dry weight plot of larvae from 1982-1985 indicate the best growth conditions in 1983 followed by -84, -82, and -85. In 1983, 1984 and 1985 outstanding year classes of Arcto-Norwegian cod were produced, while the year class was of medium size in 1982.

INTRODUCTION

The Arcto-Norwegian cod, (Gadus morhua L.) is a boreal species, migrating between its feeding area in the Barents Sea and its spawning grounds in Norwegian coastal waters, mainly the Lofoten area. The Arcto-Norwegian cod stock is situated close to the limits of its environmental range (GARROD and COLEBROOK 1978). Annual temperature variations, as shown by SÆTERSDAL and LOENG (1984), influence the distribution area of cod significantly. These authors put forward the following hypothesis: "....through evolutionary processes the reproduction of the Arctic cod is adjusted to the variations in the feeding area caused by climatic fluctuations". The coastal current in Lofoten and adjacent waters, where eggs and larvae are found, also shows annual variation in temperature. The temperatures in the Barents Sea and along the coast of northern Norway are to a certain degree correlated because most of the variations are large scaled (BLINDHEIM, LOENG and SÆTRE 1981).

The year class strength is mainly determined during the first year (HJORT 1914). Recent results indicate that there is good correlation between the number of postlarvae present in the sea in June-July and the year class strength at age 0.5 year (BJØRKE and SUNDBY 1986). Thus there is reason to believe that the year class strength is established during the early stages. Many attempts have been made to identify the factors responsible for yearly variations in year class strength. The starvation hypothesis first put forward by HJORT (1914) as "the critical period concept", was further analysed by WIBORG (1957), KISLYAKOV (1961), SYSOEVA and DEGTEREVA (1964), BARANENKOVA (1965), ELLERTSEN et al. (1976, 1977, 1979, 1980, 1981). The role of predation upon fish eggs and larvae has been investigated by MURPHY (1961), HUNTER (1984), and MELLE and ELLERTSEN (1984). Physical factors acting directly on the egg and larval populations are shown to influence the mortality significantly (GARROD and COLEBROOK 1978, KOSLOW 1984, SINCLAIR, TREMBLAY and BERNAL 1985). An effect of the age distribution on year class strength is suggested by PONOMARENKO (1973).

In the present paper the year class variations will be related to biological and physical factors, with special reference to the effects of temperature.

MATERIAL AND METHODS

Time series of temperature in the upper 30 m in March-April at a fixed hydrographical station Skrova in Vestfjorden, Fig. 1, were analysed for the period 1947-1985. The data were compared to the year class strength of three year old cod based on Virtual Population Analysis (ANON 1985).

The occurrence of C. finmarchicus from the Skrova fixed station in Lofoten, was analysed for the period 1960-84. Zooplankton was sampled weekly by a 36 cm Juday net with 180 µm mesh size from 300-0 meters. The frequencies of the different developmental stages were determined by identifying to stage the first 100 C. finmarchicus observed in a counting chamber.

The vertical distribution of microzooplankton was investigated in connection with the cod larval surveys. Samples were usually taken using small submersible electric pumps (200 l/min) from the following depths: 0, 2.5, 5, 7.5, 10, 15, 20, 25, 30 and 40 m. The samples were collected in calibrated

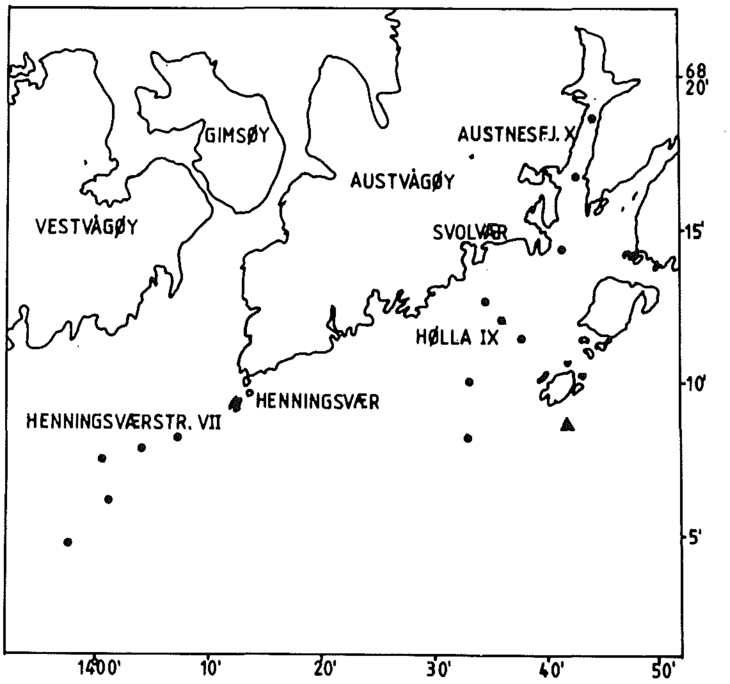

Fig. 1. The main traditional spawning area of Arcto-Norwegian cod in Lofoten. Sampling stations for vertical net hauls are shown (●) and the fixed station Skrova (▲).

tanks (23.7 l), filtered through 90 µm mesh size nylon gauze and the zooplankton preserved in 4% formaldehyde. The entire sample was counted and identified under a binocular microscope.

The zooplankton data were compared with sea temperature and time of appearance of the different developmental stages of *C. finmarchicus*.

Cod eggs were sampled from 13 localities on the spawning grounds in the Lofoten area in March-May (Fig. 1) with vertical net hauls (diameter 80 cm, mesh size 375 µm) from 100-0 meters, to calculate the spawning intensity curves. These curves were based on abundance estimates of eggs from fertilization to 2 days of development.

Cod egg surveys were performed in the northern Norway in March-April 1983-85 (SUNDBY and SOLEMDAL 1984, SUNDBY and BRATLAND 1987). The eggs were sampled with vertical net hauls (diameter 56 or 80 cm, mesh size 375 µm) from 50-0 meters to calculate the egg production of the different spawning areas of the Arcto-Norwegian cod. The egg production was calculated from abundance estimates of eggs from fertilization to 7 days of development.

Cod larvae were sampled during the first fifteen days of May with vertical net hauls (diameter 80 cm, mesh size 375 µm) from 50-0 meters and with large submersible electrical pumps (SOLEMDAL and ELLERTSEN 1984). The larvae were preserved in 4% formaldehyde in 10^{o}/oo sea water.

One of the main objectives of our investigations was to show the possible correlation between the number of food organisms in the larval gut and the prey density in the sea. The larvae most suitable for such studies are the larvae that have just resorbed their yolksac, stage 7 larvae (see FOSSUM 1986, for a description of the different stages). These larvae are fully developed and able to fill their gut at optimum feeding conditions (TILSETH and ELLERTSEN 1984a), and would therefore better reflect the feeding conditions for first feeding larvae in the sea than older or younger larvae.

Survival of eggs and larvae was calculated in 1983 and 1984. The number of 7-15 and 15-20 day old eggs and cod larvae in age groups 1-4, 4-8, 8-16 and 16-24 days post hatching was calculated from the horizontal distribution found at different surveys. The calculation was made according to the method described in SUNDBY and SOLEMDAL (1984). The number of eggs and larvae in different age groups was compared with the estimated number of eggs spawned 1-5 weeks earlier calculated from the egg surveys described in SUNDBY and BRATLAND (1987). In this way different independent estimates of the survival can be calculated. The total number of larvae found in early May was also calculated according to the method described in SUNDBY and SOLEMDAL (1984), based on the horizontal distribution of the larvae.

RESULTS

Spawning and transport of eggs

The spawning period in Lofoten for the years 1976-1983 is shown in Fig. 2. Data for 50% spawning are given in Table 1, showing a high degree of stability between years, with the mean peak spawning occurring the 31 March.

The distribution of cod eggs, both horizontal and vertical, is described elsewhere (ELLERTSEN *et al.* 1981, SOLEMDAL and SUNDBY 1981, SUNDBY 1983).

The temperature in the coastal water varies considerably from year to year. The mean temperature in the upper 30 meters at Skrova each year for the period 1980-83 is shown in Fig. 3. The relation between temperature and incubation time of cod eggs is shown in Fig. 4.

The years 1981 and 1983 represent extreme cold and warm years. Hatching curves for 1981 and 1983 are calculated on the basis of the spawning curve and temperature. Adding 1 week to the hatching curve, one gets the date of first feeding. The results are shown in Fig. 5.

About 40% of the eggs of the Arcto-Norwegian cod are produced in the Lofoten area. Within the Lofoten spawning area 50-80% of the eggs are spawned in a small area around Henningsværstraumen (SUNDBY and BRATLAND 1987). Fig. 6 shows the characteristic distribution of newly spawned eggs (0-2 days old), which are concentrated along the Lofoten archipelago. Fig. 7 shows the distribution of the same eggs, 5-7 days later. They have been spread out due to the horizontal turbulent diffusion. During the 5 days period the area of their distribution has increased approximately 2.5 times, and the average peak concentration (at Henningsværstraumen) decreased to 1:2.1. The advection of the eggs during the 5 day period has been relatively small in Vestfjorden, but on the west side of Lofoten a tongue of the eggfield has rapidly run out in an offshore direction. Fig. 8 shows the distribution of the same spawning products 30 days later as first feeding larvae. In spite of the transport and diffusion indicated by the younger egg stages, the distribution of first feeding larvae show no large changes from the newly spawned eggs, but as the figure indicate there has been a considerable reduction in abundance.

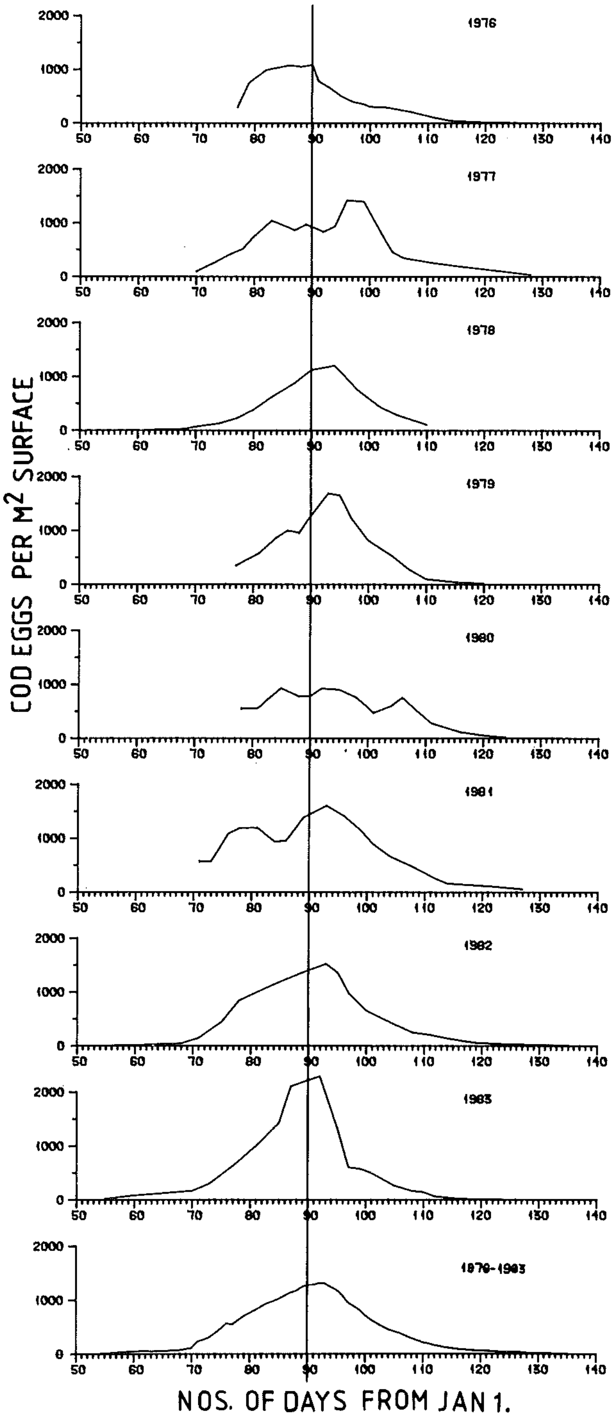

Fig. 2. Spawning intensity curves from Lofoten for the years 1976-83 and the mean spawning curve. Vertical bar represent mean date of 50% spawning for the period 1976-83.

Table 1. Day of 50% spawning in Lofoten during the years 1976-83. Ma=March, Apr=April.

Year	1976	1977	1978	1979	1980	1981	1982	1983	1976/83
Day	28 Ma	2 Apr	31 Ma	2 Apr	3 Apr	31 Ma	30 Ma	29 Ma	31 Ma

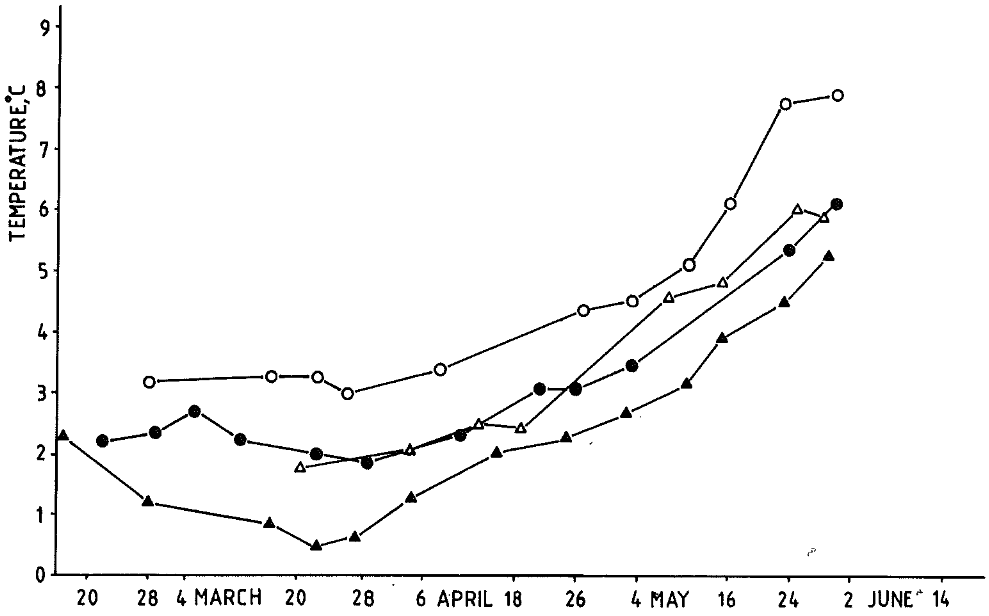

Fig. 3. Mean temperature in the upper 30 meters at the fixed station Skrova (see Fig. 1), (●) 1980, (▲) 1981, (Δ) 1982, (o) 1983.

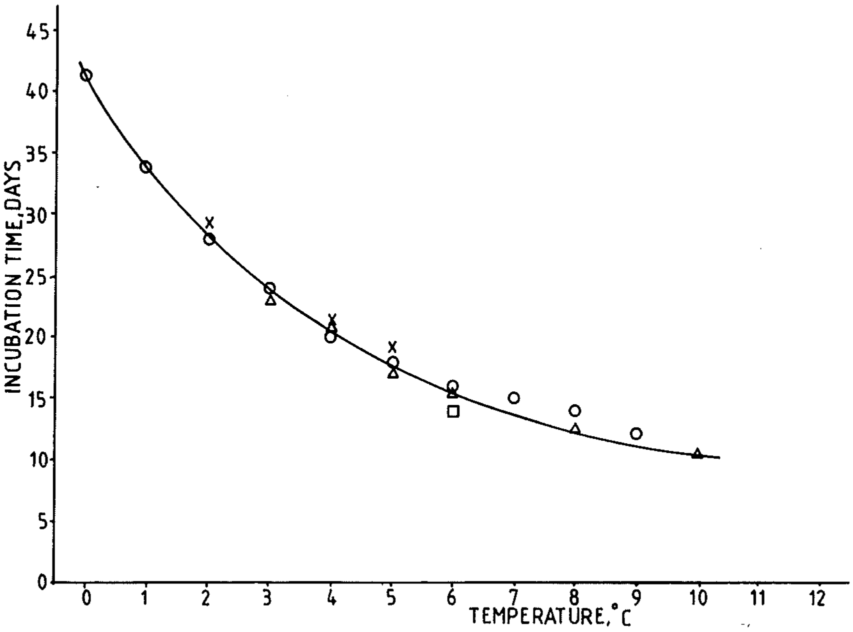

Fig. 4. Incubation period of cod eggs in different temperatures according to APSTEIN (1909) (o), DANIELSSSEN and IVERSEN (1974) (□), DANNEVIG (1895) (Δ) and STRØMME (1977) (x).

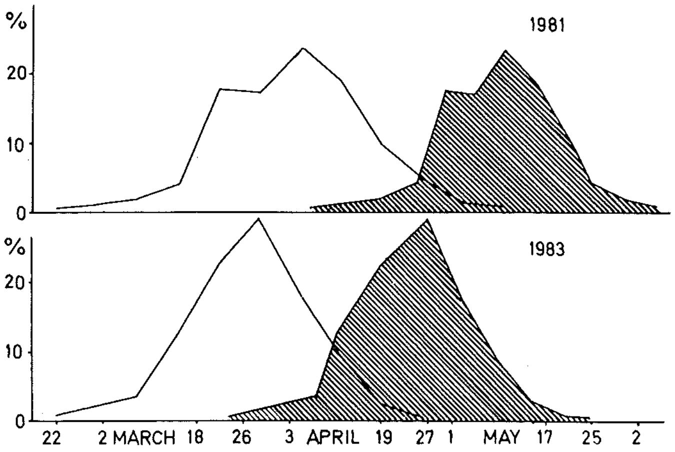

Fig. 5. Spawning curves (open) and first feeding curves (hatched) from the years 1981 and 1983.

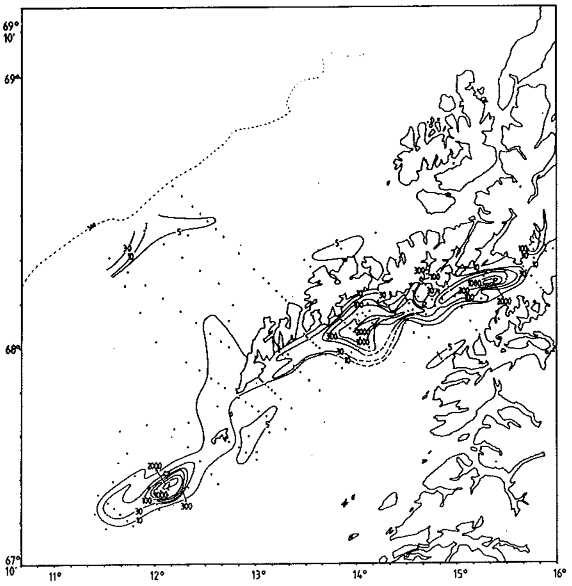

Fig. 6. Distribution and abundance of stage 1 eggs, 0-2 days old, number·m^{-2}.

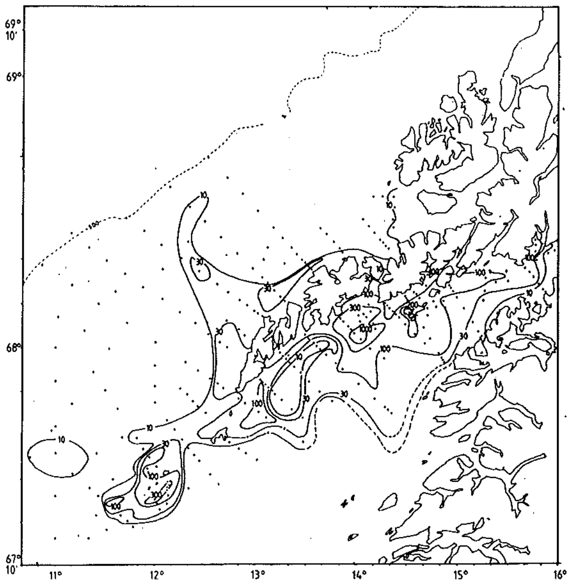

Fig. 7. Distribution and abundance of stage 3 eggs, 5-7 days old, number·m^{-2}.

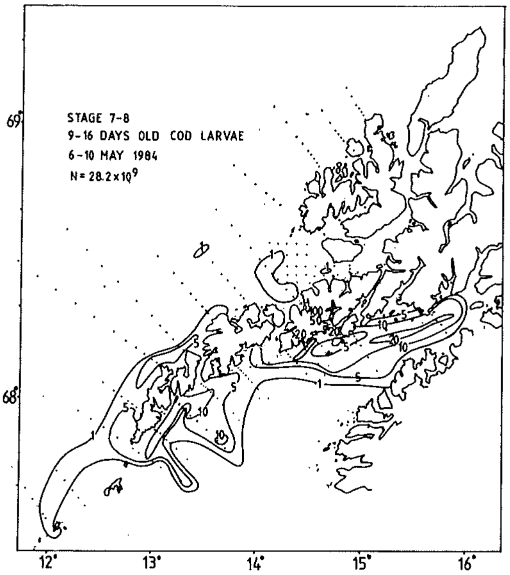

Fig. 8. Distribution and abundance of first feeding larvae, 9-16 days post hatching, number·m^{-2}.

Calanus finmarchicus spawning and naupliar distribution

The time of spawning of Calanus finmarchicus is important for the cod larvae, as they mainly feed upon C. finmarchicus nauplii (Ellertsen et al. 1977).

The C. finmarchicus samples consist 60-90% of adult females at the end of March, but only 4-5% a month later when the copepodit stages I (CI) and II (CII) dominate.

When comparing the dates for maximum occurrence of C. finmarchicus CI with the sea temperatures in April (Fig. 9), a linear regression analysis gives

$$y = 7.62 - 0.037X \qquad (R^2 = 0.85)$$

A more rapid development from eggs to nauplii to CI at higher temperatures contributes slightly to the correlation. However, the temperature difference of about 2.5°C from a "cold" (1981, 1.9°C) to a "warm" (1960, 4.4°C) year would result in only a few days difference in development time, not a month or more as shown in Fig. 9. The figure therefore expresses temperature dependent spawning in C. finmarchicus.

The distribution of nauplii for the years 1980-85 is shown in Fig. 10. These maps, together with a series of previously published (ELLERTSEN et al. 1984, TILSETH and ELLERTSEN 1984b) data give an impression of the Lofoten as a variable area with regard to naupliar distribution.

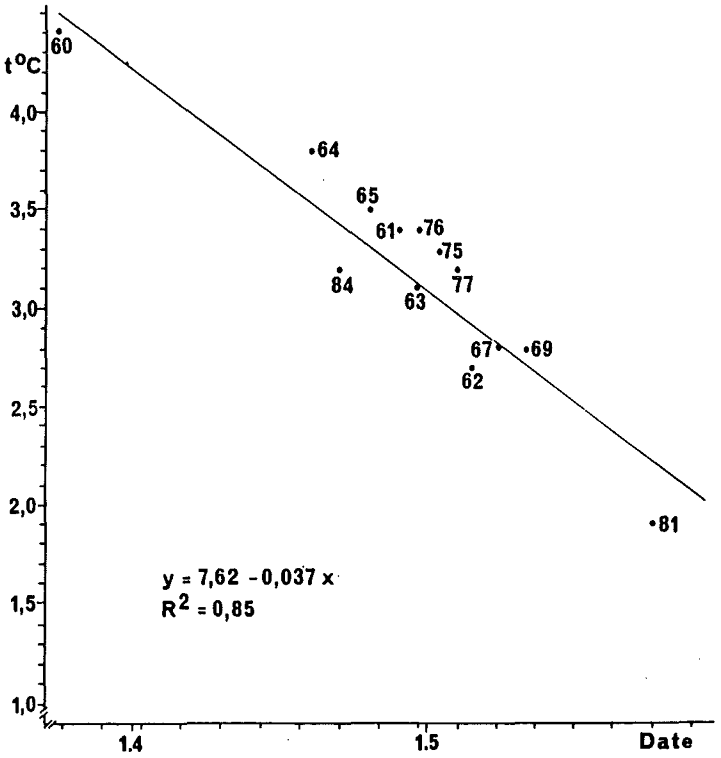

Fig. 9. Time of maximum occurrence of Calanus finmarchicus copepodite stage I versus temperature.

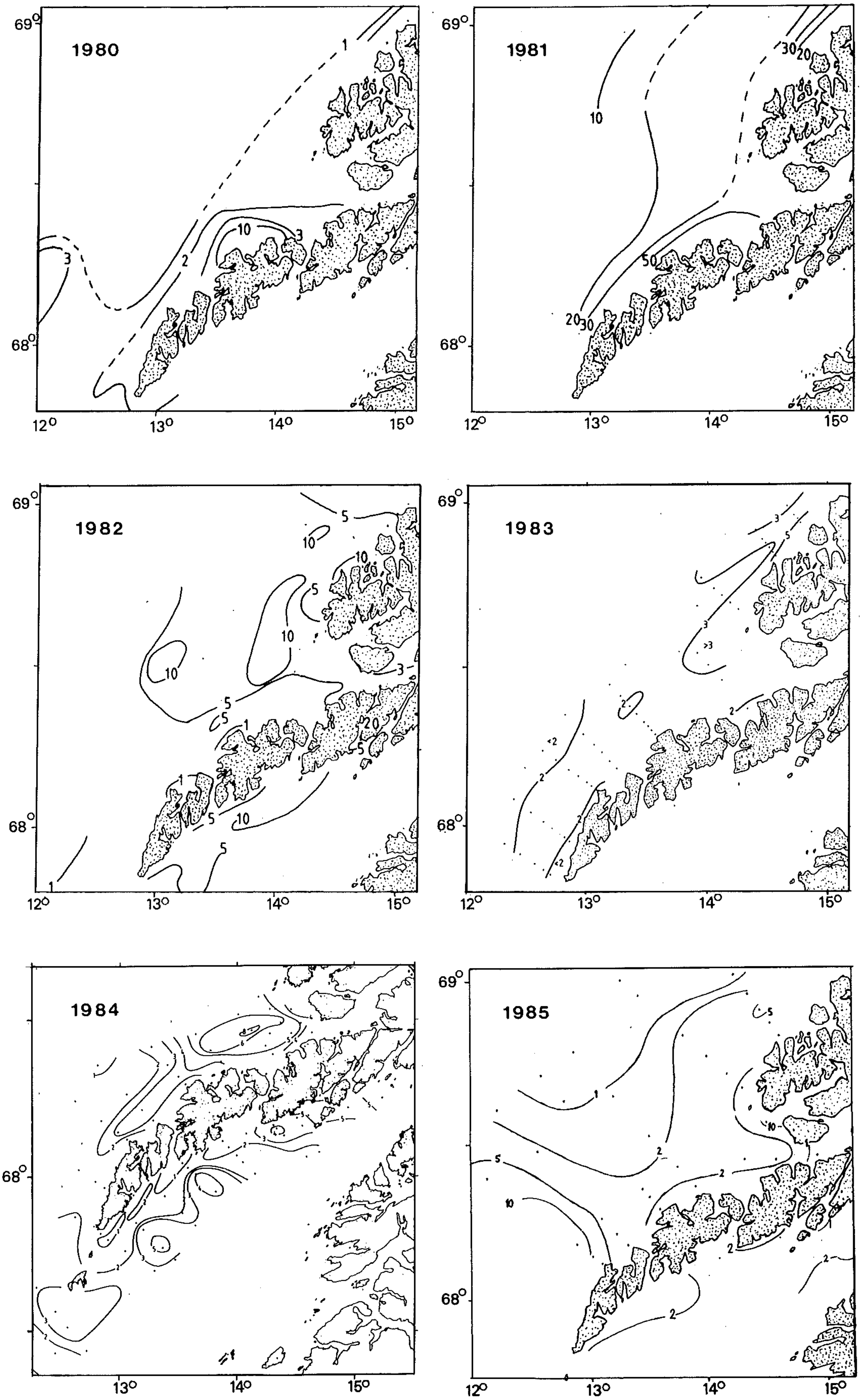

Fig. 10. Distribution and abundance of copepod nauplii 1980-85, number·l^{-1}.

In the years 1980-82 the horizontal distribution of nauplii (Fig. 10) and cod larvae (Fig. 15) was covered at the same time, while there was a time lag of one week between the coverages in 1983 and -84 (the horizontal distribution of cod larvae was found first). In 1985, however, the horizontal distribution of nauplii was covered 3 weeks in advance of the cod larval investigation.

The sheltered Austnesfjord usually has the highest densities, 10-20 up to 600 nauplii per liter, followed by the less sheltered Vesterålsfjord (1-20 n/l), the Lofoten east side (1-10 n/l) and the west side of Lofoten, usually 1-5 n/l. Numbers given in Fig. 10 are based upon integrating all pump samples (10) in the water column at each station. The actual density at a given depth might deviate considerably from the integrated value (TILSETH and ELLERTSEN 1984b).

The relation between yearclass strength and temperature

Fig. 11 shows the relation between the year class strength represented by estimates of 3 year old cod by VPA and the mean temperature in March and April for the upper 30 meters in Lofoten. RANDA (1984) showed that the VPA of the year classes at age 3 is well correlated with the 0-group estimates. The figure shows that in cold years good year classes never occur, while in warm years good year classes may be produced. The four years 1963, 1969, 1973 and 1975 are excluded since they all appear to be inconsistent with the other independant estimates (NAKKEN, pers. comm.).

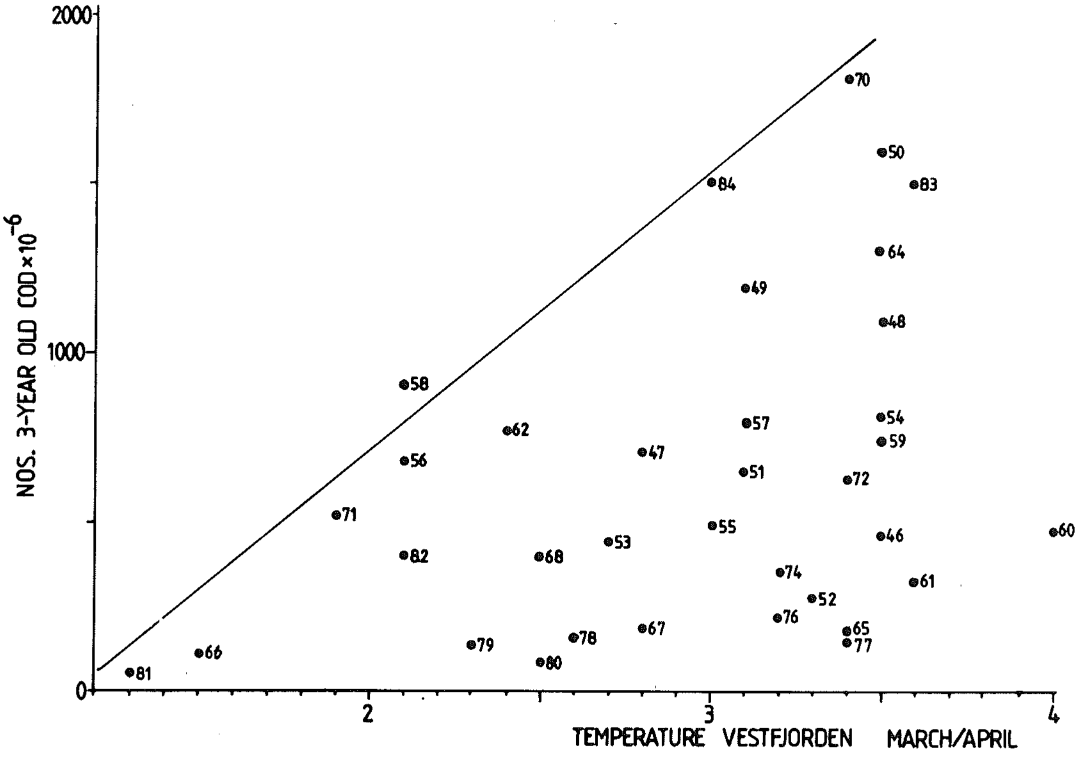

Fig. 11. The relation between the yearclass strength and the mean temperature in March-April in Lofoten.

Density dependent food uptake

Table 2 shows the results of larval cod (stage 7) gut content analyses and the integrated density of nauplii in the water volumn at different stations in the Lofoten area. Only samples made at daytime are included. A plot of larval feeding ratio against integrated naupliar density is given in Fig. 12.

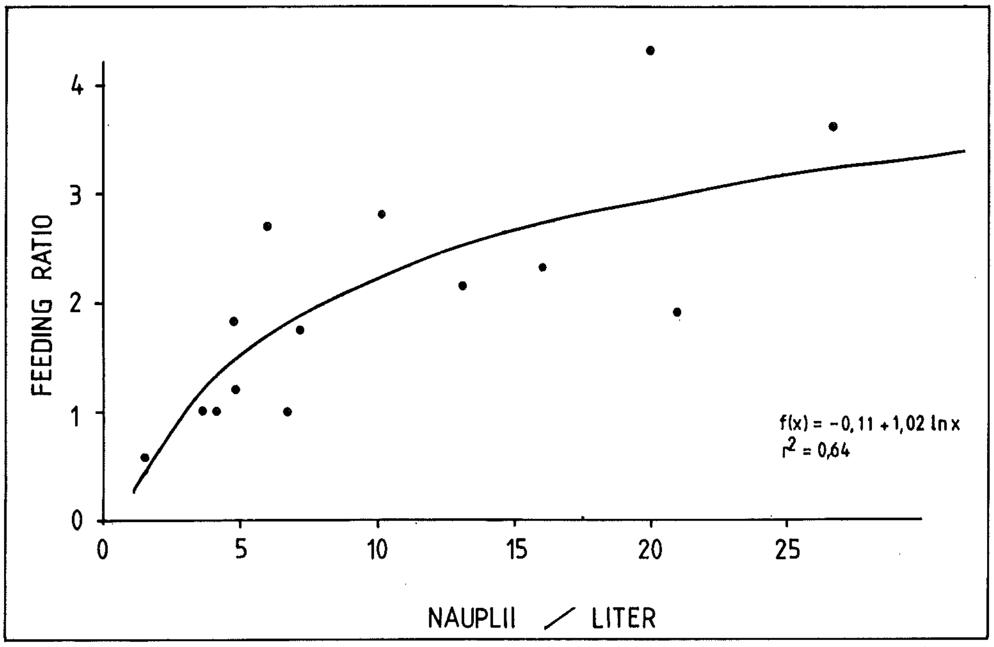

Fig. 12. Feeding ratio in cod larvae in relation to food density.

Table 2. Feeding incidence, % of larvae with gut content, and feeding ratio, number of prey organisms per larval gut, of stage 7 larvae, from surveys and diurnal stations in the period 1976-84. The abundance of copepod nauplii is estimated from plankton pump samples.

Area		Abundance of copepod nauplii, n/L	Number of cod larvae	Feeding ratio	Feeding incidence
Austnesfjorden	(84)	31.5	26	3.5	96
Austnesfjorden	(77)	26.7	67	3.6	94
Austnesfjorden	(82)	21.0	8	1.9	88
Austnesfjorden	(82)	20.0	15	4.3	93
Austnesfjorden	(83)	16.0	26	2.3	81
Vesterålsfjorden	(82)	13.1	24	1.9	79
Austnesfjorden	(84)	10.3	20	2.8	90
Henningsvær	(82)	7.2	12	1.8	75
Vesterålsfjorden	(82)	6.7	91	1.0	55
Vesterålsfjorden	(82)	6.0	8	2.7	88
Ballstad	(82)	4.8	5	1.2	80
Austnesfjorden	(76)	4.7	88	1.8	86
Sørvågen	(82)	4.1	11	1.0	45
Hølla	(82)	3.6	12	1.0	58
Lofotodden	(83)	1.5	9	0.6	44

A statistically significant correlation is found between the gut content of the cod larvae and the density of copepod nauplii ($p<<0.05$, $r^2=0.64$, $N=14$, logaritmic correlation). The figure indicates that the critical density for successful feeding must be in the order of 5-10 nauplii per liter.

The carapace length of the nauplii in the gut of the larvae is shown in Fig. 13. The mean carapace length increases along the drift route of the larvae. The area of investigation is divided into 6 subareas shown in Fig. 14.

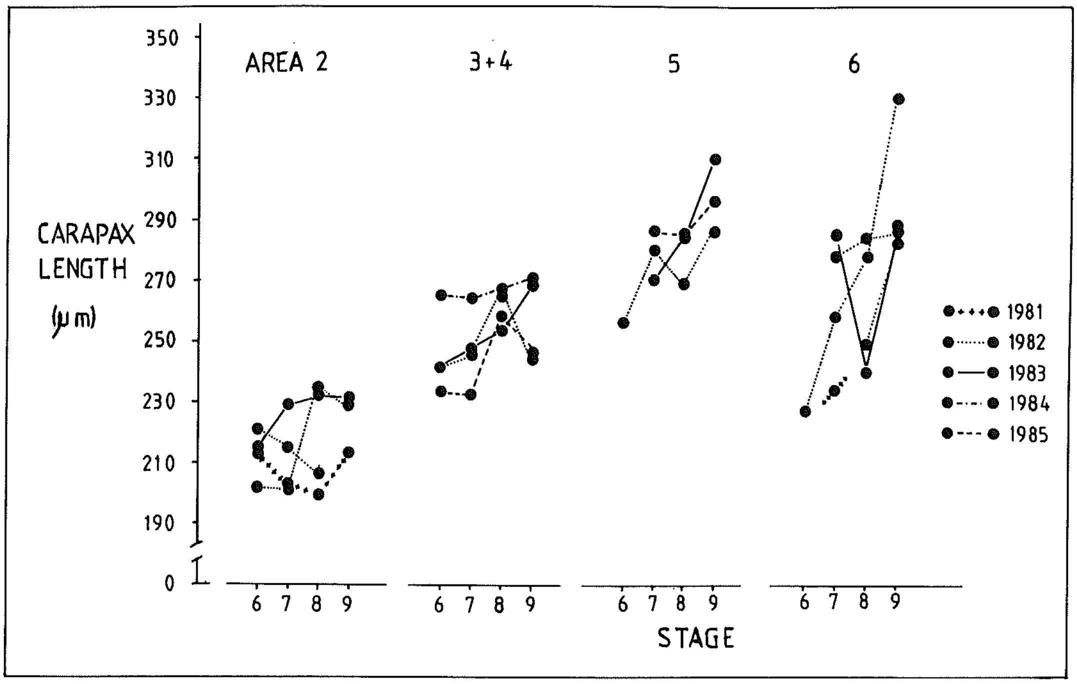

Fig. 13. Naupliar carapax length in stomach content of cod larvae in relation to area and cod larval stage.

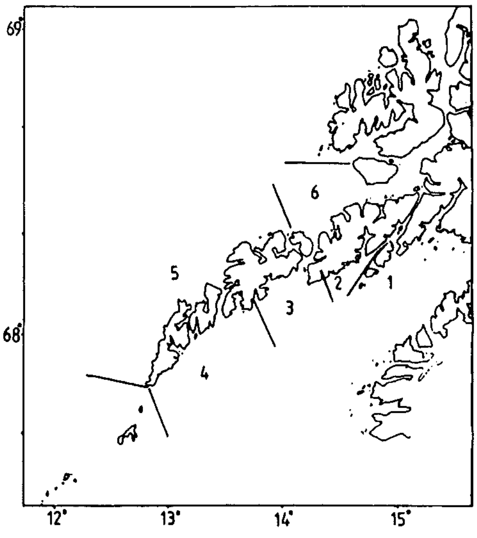

Fig. 14. Lofoten subareas 1-6.

"Good" and "bad" areas

The distribution and abundance of larvae in early May for the period 1979-1985 is shown in Fig. 15. Large numbers of larvae were found in the period 1983-1985, and the center of their distribution was the Vestfjord (for distribution of first feeding larvae see Fig. 8). The number of larvae estimated from the horizontal distribution is shown in Table 3. The number of cod larvae varies by approximately two orders of magnitude from 2 x 10^9 larvae in 1980 to 125 x 10^9 in 1985.

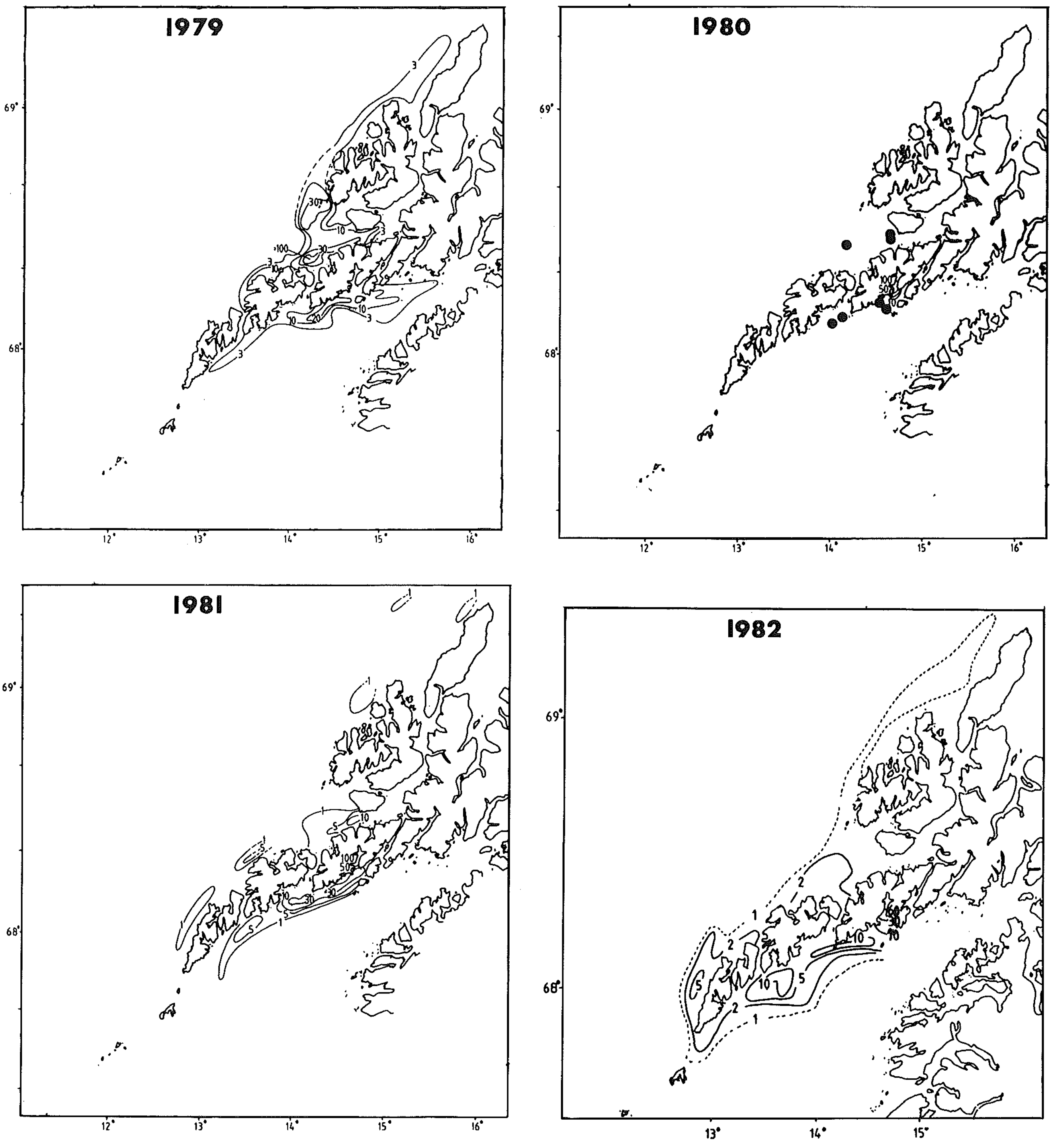

Fig. 15. Distribution and abundance of cod larvae 1979-85, number·m^{-2}.

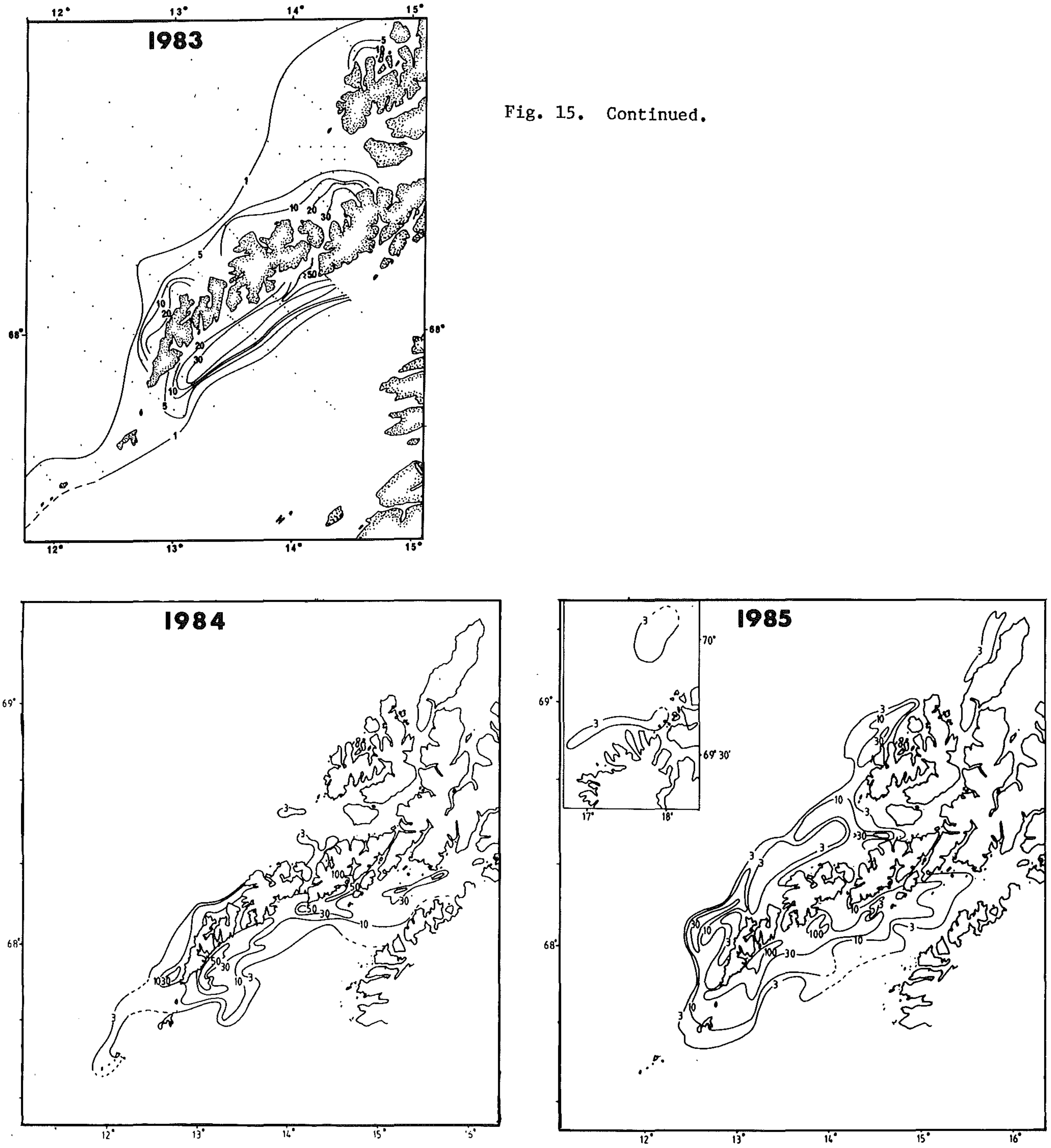

Fig. 15. Continued.

The feeding incidence and feeding ratio of the cod larvae from the different subareas are presented in Tables 4 and 5.

The feeding incidence and ratio are indicators of the food availability in the sea the last hours before the larvae were caught. The feeding ratio and incidence show that the best feeding conditions are found on the inner side of Lofoten, subareas 2-3, and in the Vesterålsfjord, subarea 6, while the conditions on the outer side of Lofoten seems to be more marginal. Subarea 4 in the outermost part of Vestfjord shows larvae in an intermediate feeding condition.

Table 3. Nos. of cod larvae (N) in the Lofoten area for the period 1979-85 (N_1=Nx10^{-9}).

Year	1979	1980	1981	1982	1983	1984	1985
N_1	30	2	15	13	89	89	125

Table 4. Feeding incidence, % of larvae with gut content, in different larval stages from different subareas during the years 1982-85. A.1= Area 1, etc.

Stage	6				7				8				9			
Year	82	83	84	85	82	83	84	85	82	83	84	85	82	83	84	85
A.1	-	-	26	-	-	-	66	-	-	-	91	-	-	-	89	-
A.2	34	70	51	22	75	98	83	82	90	100	96	-	100	100	100	-
A.3	15	28	-	63	67	83	-	92	88	95	-	-	100	100	-	-
A.4	11	35	30	37	99	94	86	81	-	100	90	80	-	-	94	100
A.5	29	13	44	67	69	59	82	87	75	77	-	91	100	91	-	-
A.6	36	25	-	-	88	74	-	-	88	87	-	-	100	94	100	-

Table 5. Feeding ratio, prey organisms per larval gut, in different larval stages, in the different subareas, during the years 1982-85.

Stage	6				7				8				9			
Year	82	83	84	85	82	83	84	85	82	83	84	85	82	83	84	85
A.1	-	-	0.2	-	-	-	1.2	-	-	-	2.4	-	-	-	3.3	-
A.2	0.6	1.7	1.2	0.3	1.4	3.4	2.4	1.8	2.5	5.1	3.0	-	4.5	7.7	4.4	-
A.3	0.2	0.5	-	1.2	1.6	1.5	-	3.3	2.1	2.5	-	-	2.0	4.5	-	-
A.4	0.2	0.5	0.5	0.5	1.2	2.1	2.3	2.0	-	1.7	3.3	2.4	-	-	5.4	5.8
A.5	0.7	0.1	0.6	0.5	0.9	0.8	1.4	1.3	2.3	1.8	-	2.6	2.2	1.8	-	-
A.6	0.7	0.4	-	-	2.4	1.7	-	-	2.2	3.8	-	-	4.3	6.0	7.4	-

The dry weight is a more conservative factor and dependant on the conditions some time in advance of the catch of the larvae. The dry weight of the larvae after fixation and removal of the gut and liver is given in Table 6.

There is larger differences in dry weight between years than areas. 1983 was an outstanding year, and the stage 9 larvae from 1983 were heaviest compared to the other stage 9 larvae in all areas. The results with larvae in stage 7 and 8 are more variable and there are little consistency in these data. Small variations in dry weight may be camouflaged by variable loss of dry weight during fixation as indicated by the results on larvae in stage 5-7 in Table 7.

Survival of the spawning products

Fig. 16 shows the survival of the spawning products in 1983 and 1984. The

Table 6. The dry weight of the different larval stages in the different areas, during the years 1982-85. Mean=weighted mean of all larvae in a certain stage. Mean/area=weighted mean of all larvae (stage 5-9) in a certain area.

Stage	7				8				9				Mean/area			
Year	82	83	84	85	82	83	84	85	82	83	84	85	82	83	84	85
A.1	-	-	54	-	-	-	76	-	-	-	124	-	-	-	66	-
A.2	41	53	51	56	65	78	66	-	115	139	101	-	45	60	52	59
A.3	51	51	54	62	68	66	68	77	91	119	97	-	44	54	56	57
A.4	44	52	50	51	65	71	70	71	102	143	138	113	42	70	58	49
A.5	53	53	48	54	58	71	70	79	133	156	114	-	66	91	53	57
A.6	40	75	40	58	83	94	72	84	196	201	161	147	129	155	195	76
Mean	50	53	52	56	68	75	69	79	146	170	117	131	60	84	59	58

Table 7. Shrinkage due to fixation.

Larval stage	Before fixation	After fixation	Shrinkage,%
5	4.7±0.06mm (N=10)	4.4±0.3 mm (N=35)	6
	60 ± 7 γg "	46 ± 6 γg "	23
6	4.7±0.3 mm (N=24)	4.4±0.3 mm (N=12)	5
	53 ± 10 γg (N=11)	45 ± 11 γg "	15
6	4.7±0.2 mm (N=15)	4.4±0.2 mm (N=53	6
	65 ± 11 γg "	46 ± 6 γg "	29
7	4.9±0.4 mm (N=24)	4.6±0.4 mm (N=9)	6
	69 ± 13 γg "	57 ± 10 γg "	17
7	5.2±0.3 mm (N=12)	4.7±0.3 mm (N=35)	10
	83 ± 14 γg "	59 ± 10 γg "	23

figure shows that there is a heavy egg and larval mortality. Only 10% of the eggs were hatched and produced 2-3% first feeding larvae in these two years which both produced outstanding year classes. Fig. 17 shows larval length/dry weight relationship in the years 1982-85. The best growth was seen in 1983 followed by 1984, 1982 and 1985.

DISCUSSION

SÆTERSDAL and LOENG (1984) found that rich year classes of cod occurred at the beginning of warm periods in the Barents Sea, when the feeding areas were expanding. Their data show that the temperature starts to increase one year ahead of the occurrence of a rich year class. Similar yearly variations in temperature are found in the coastal waters of northern Norway (BLINDHEIM, LOENG and SÆTRE, 1981), indicating that most of these variations are large scaled. It is possible that the improved feeding conditions for the mature population contribute to a better survival through better egg quality. Both timing of spawning, fecundity and egg quality can be related to temperature

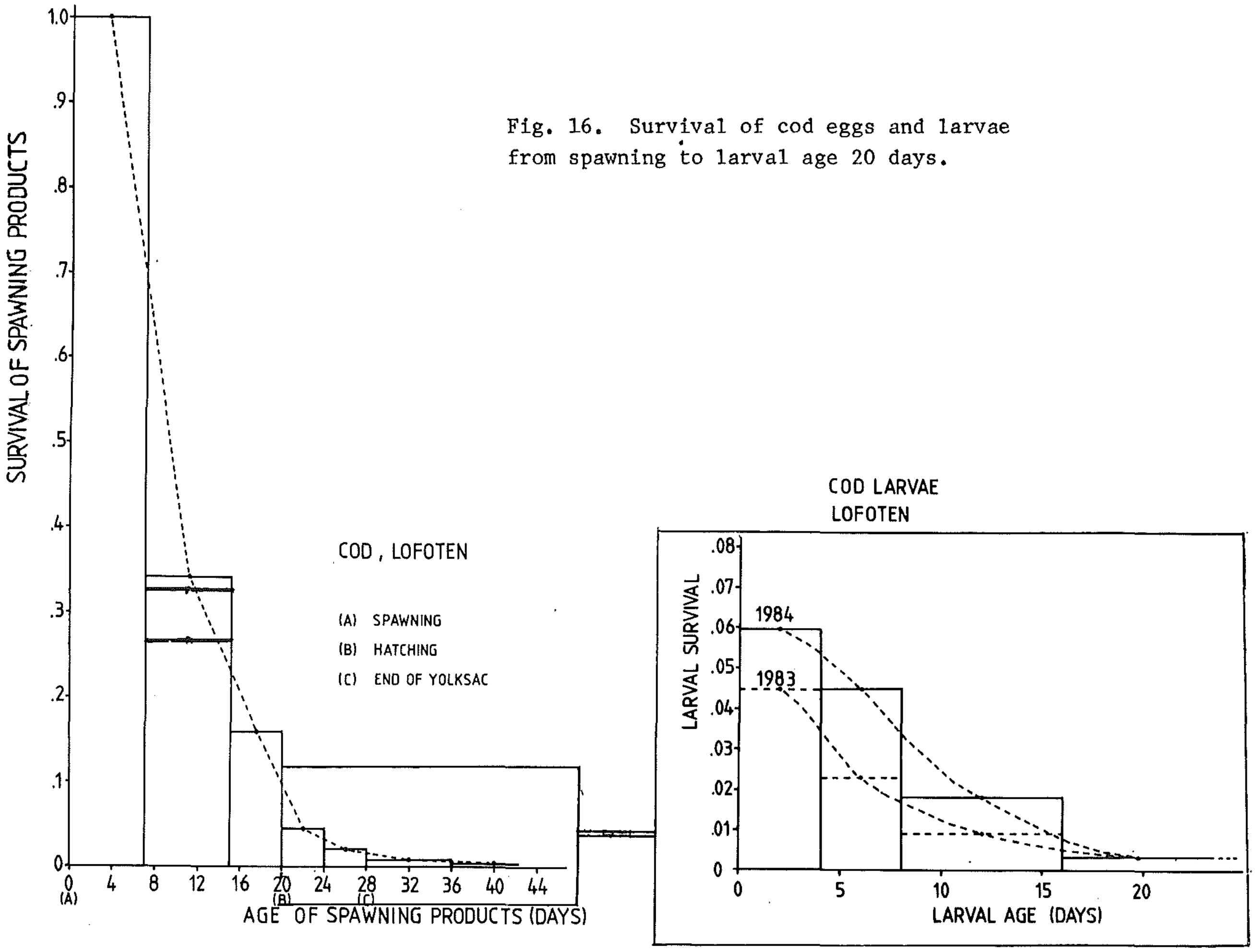

Fig. 16. Survival of cod eggs and larvae from spawning to larval age 20 days.

and feeding conditions (WOODHEAD and WOODHEAD 1965, HISLOP, ROBB and GAULD 1978, DE VEEN 1976). However, these factors have not been proved to influence the year class strength in Arcto-Norwegian cod.

Investigations on the distribution and number of cod age groups I and II show that they are found in the easternmost parts of the distribution areas in the Barents Sea with lowest temperatures (PONOMARENKO 1973). It has been postulated that the adaption force of the year class to the ambient feeding area is mortality on these stages due to temperature/feeding conditions acting at these stages. However, it has recently been shown by BJØRKE and SUNDBY (1986) that there is a good correlation between the indices from the postlarval surveys and the 0-group surveys indicating that the major regulation of the year class strength takes place during the early developmental stages in Norwegian coastal waters.

The "triangle plot" between the temperature at the spawning field and the abundance of the produced year class only appears when using the temperature during the spawning period in March/April. As earlier mentioned the temperature in the Barents Sea is to some extent correlated with the temperature in the coastal waters of Northern Norway. The correlation coefficient between the annual mean temperature of the Kola section in the Barents Sea and the mean temperature at the spawning field is 0.6 (r^2=0.6) (SUNDBY, pers. comm.). Using the Kola section temperature a similar "triangle plot" as that for Vestfjorden is obtained when using the temperature in August and September, (it takes about 6 months for the watermasses of

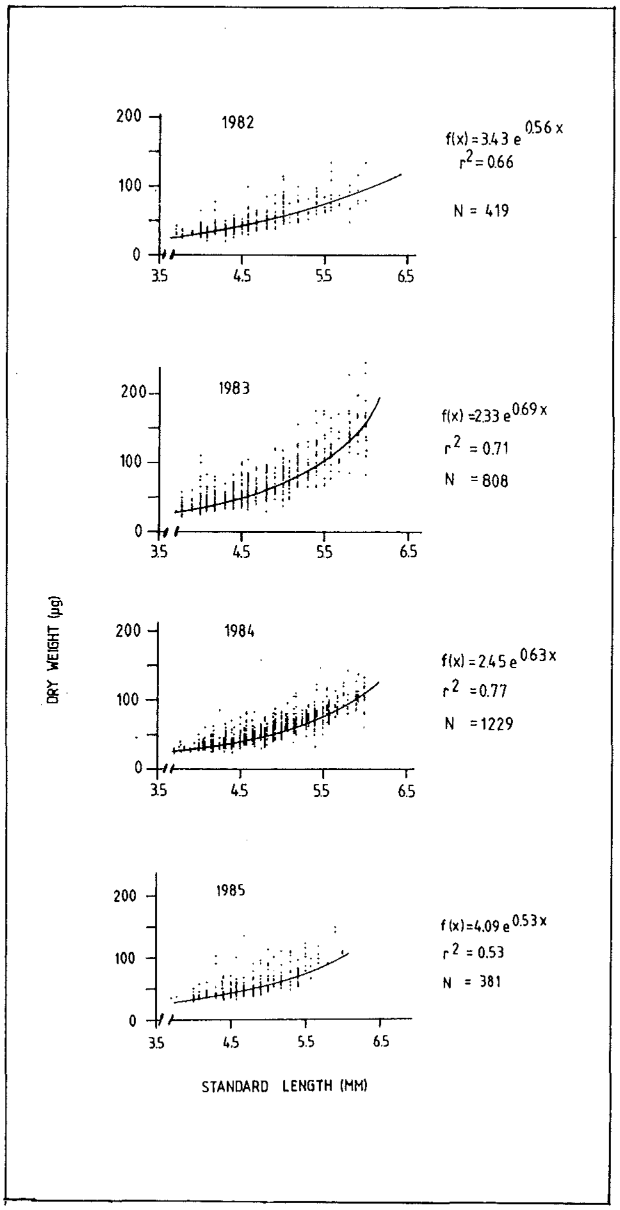

Fig. 17. Cod larval length/dry weight relationship in Lofoten area in 1982-85.

the Norwegian Coastal Current in the Vestfjord to reach the Kola section) which coincides with the time when the produced year class appear as 0-group fish in that area.

A similar relation between temperature and year class strength is found for eggs and larvae from the West-Greenland cod population (HERMAN, HANSEN and HORSTED 1964), but not on the older stages. The same phenomenon is also found in other cod populations living close to the limits of their distribution range (GARROD and COLEBROOK 1978).

The peak of spawning is very stable from year to year as also found by CUSHING (1969). However, he used the mean data of catch in the Lofoten area as an index of peak spawning and arrived at a date 14 days earlier than was found in the present paper. CUSHING (1969) argues that the stability of the peak spawning in fish has indirect adaptation to "the variability of the production cycle and dependence of the fish populations upon it during their larval lives".

We believe that the stability of the peak spawning is the result of the constant temperatures during spawning migration and spawning, since the cod migrates and spawns in the subsurface thermocline between the cold coastal water and the Atlantic water which has a constant temperature that do not vary between years.

PEDERSEN (1984) showed a delay in peak spawning of about 1 week since 1929 which correlates well with the increasing proportion of first-time spawners during the same period. It is well known that larger fish spawn earlier than the first-time spawners (SOROKIN 1957). Contrary to PEDERSEN (1984), CUSHING (1969) found an opposite trend in the peak spawning during the same period, probably as a result of a change in fishing pattern in Lofoten.

SINCLAIR et al. (1985) focus on Hjort's second hypothesis which stress "the differential loss of larvae from their appropriate larval distribution area due to interannual differences in advection".

Such an area is described in the present paper, corresponding to the main spawning area of the Arcto-Norwegian cod. According to the current system in the Vestfjord (FURNES and SUNDBY 1981) the first feeding larvae should be transported 240 kilometers away from the spawning area. The fact that most eggs and larvae are still found over the spawning grounds in April-May implies that the Vestfjord is a "retention area". Similar retention areas, where eggs and larvae are kept within a certain area caused by different physical forces (gyres, transition zones etc.), are described by ILES and SINCLAIR (1982).

The release of larvae from the "good area" is a continuous but highly variabel process. The larvae which happen to stay within the area for the longest time period, will have the best conditions for growth and survival.

Analyses of the naupliar density and stomach contents of cod larvae in Lofoten show that 5-10 nauplii per liter seem to represent a critical level for successful food uptake. This agrees with investigations in other areas (DEKHNIK, DUKA and SINYUKOVA 1970, INCZE et al. 1984). This was also seen in the case studies reported in ELLERTSEN et al. 1984, where the larvae, stage 6-9, exposed to plankton densities in the Austnesfjord, above 20 nauplii per liter, were in a good state of feeding. The larvae caught in the Vesterålsfjord diurnal station, however, exposed to a mean naupliar density of 6.7 per liter, had a much lower feeding ratio.

In the beginning of May the naupliar density is often less than 10 nauplii per liter in most of the investigated area. However, the area of high naupliar densities usually correspond with the area of high abundance of first feeding larvae (area 2-4).

Nauplii of other species (mostly Oithona spp.) are of minor importance since cod larvae feed almost exclusively on C. finmarchicus. Nauplii of O. similis are occassionally found in relatively high numbers in the area (ELLERTSEN, pers. comm.). A comparison between the gut contents of equal staged cod larvae, showed that the size of the copepod nauplii in their guts increased along their drift route. The reason for this may be that the time of spawning of C. finmarchicus is somewhat delayed in the inner part of the Vestfjord compared to the mouth of the fjord and outer side of Lofoten (ELLERTSEN unpublished data, SØMME 1934, WIBORG 1954). Then the mean age of the nauplii, the carapace length and the calory content, will increase along the drift route of the cod larvae as the watermasses containing the cod larvae mixes with watermasses containing some retained nauplii in older stages along the drift route. This will give some compensation for the decreasing prey densities found on the outer side of the Lofoten archipelago (area 5).

The incubation of cod eggs takes place in the upper 50 meters of the water column in the Coastal Current, which shows a relatively large variation in temperature between years. The difference in incubation time between a warm and a cold year is about 14 days. High temperatures therefore increase the changes for a first feeding larvae to stay within the good area.

Another important point is that the size of the cod eggs is reduced significantly during spawning (SIVERTSEN 1935, SOLEMDAL 1970, SOLEMDAL and SUNDBY 1981). This is a general phenomenon (HIEMSTRA 1962), and is the result of portion spawning. The first batches contain the largest eggs (HISLOP 1975, MAYENNE 1940). The positive correlation between egg size and size of larvae was demonstrated by KNUTSEN and TILSETH (1985). This means that if the feeding conditions are favourable early in the season, this will coincide with the occurrence of large larvae better suited for feeding. It is also possible that high temperature will have a positive effect on feeding as demonstrated by PAUL (1983) on pollock larvae.

The development time of copepod eggs and nauplii is directly affected by the temperature. However, the temperature affects the timing of spawning in Calanus finmarchicus to a significant larger degree than the effect upon development rate. Developing time from spawning to copepodid I (CI) at 4.4°C is about 30 days, and at 1.9°C about 40 days (interpreted from TANDE 1981). In the warm year 1960 (mean April temperature 4.4°C, March 3.5°C) the time of maximum occurrence of CI was about April 1. This implies that the spawning was most intense in early March, while a maximum occurrence of CI in 1981 about May 24 (mean April temperature 1.9°C) suggest a peak spawning in the late April. An unusually early spawning of C. finmarchicus in Norwegian waters in 1960 was reported by BARANENKOVA (1965). That year the nauplii production was well over when the first feeding cod larvae occurred in the area, which may explain the resulting poor year class. The match/mismatch in time between nauplii and cod larvae occurrence the other years needs further investigation.

Good year classes produced in warm years might be attributed to a series of temperature related biological phenomena:

1. Good feeding conditions early in the season, favouring the large larvae that are produced in the beginning of the spawning season (KNUTSEN and TILSETH 1985).
2. Short incubation period increasing the changes to stay in the "good area" during first feeding.
3. Facilitated feeding. PAUL (1983) found a better feeding success at higher temperature in Pollock (Theragra chalcogramma).

The year class produced in 1983 was especially strong at the postlarval stage. This may be due to the above mentioned phenomena: Short incubation period of the eggs as seen from Fig. 5, and good feeding conditions as indicated by the fast growth at all larval stages.

The reasons for the relatively high mortality, also found in other species (see DAHLBERG (1979) for a review on the subject), are not fully known. Dispersal of spawning products out of the investigation area may account for a minor part of what is estimated as mortality, since the whole distribution area of eggs and larvae is supposed to be covered by the investigation. Part of the mortality may be due to predation, as herring (Clupea harengus), ctenophors (Bolinopsis infundibulum) and medusae (mainly Aurelia aurita ephyrae) are found to feed on cod eggs and larvae in the area (MELLE and ELLERTSEN 1984, MELLE 1985). An additional effect can be that low success at the onset of feeding of larvae exposed to low prey densities can make them more vulnerable to predation.

There is good agreement between the abundance of larvae in early May and the size of the resulting year class in the period 1979-85. No such agreement was found by WIBORG (1957) on the same stock for the period 1948-56.

The large variability in larval survival reported in the literature reviewed by DAHLBERG (1979), makes it difficult to draw any firm conclusions on yearclass strength from larval abundance estimates.

ACKNOWLEDGEMENT

We are indebted to Dr. K.F. Wiborg who has kindly given to our disposal zooplankton material and data from fixed station in Lofoten 1960-84.

This work is partly supported by the Norwegian Fisheries Research Council (NFFR).

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THE EFFECT OF OCEANOGRAPHIC CONDITIONS ON DISTRIBUTION AND POPULATION
DYNAMICS OF COMMERCIAL FISH STOCKS IN THE BARENTS SEA
Proceedings of the third Soviet-Norwegian Symposium, Murmansk, 26-28 May 1986
Edited by H. Loeng. Institute of Marine Research, Bergen, 1987.

DISTRIBUTION AND ABUNDANCE INDICES OF POSTLARVAL AND 0-GROUP COD

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ABSTRACT

Postlarvae surveys have been carried out in the southwestern part of the Barents Sea and the northeastern part of the Norwegian Sea in June/July since 1977. The aim of the investigations has been to study characteristic distributions of fish larvae and their relation to the distribution of water masses, and to establish abundance indices. It has been shown that mesoscale features of the larval distribution are very pronounced, and that they are connected to the current features. Therefore the survey strategies was changed in 1983, and emphasis was laid on the investigation of cod larvae. Postlarval cod is especially abundant at Tromsøflaket due to the reduced diffusion by the existence of the anti-cyclonic vortex above the bank. It is shown that the cod postlarvae tend to be larger in the western part. The postlarvae and 0-group distribution are discussed and compared, and similar features of the two stages are found. The postlarvae and 0-group indices are discussed and compared, and a correlation coefficient of 0.82 was found.

INTRODUCTION

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

The Institute of Marine Research has been sampling fish eggs and larvae since 1948 at different localities along the Norwegian coast (e.g. WIBORG 1960, HOGNESTAD 1969, DRAGESUND 1970, GJØSÆTER and SÆTRE 1974, ELLERTSEN et al. 1981, BJØRKE 1981, 1984, SUNDBY and SOLEMDAL 1984, SUNDBY and BRATLAND 1987). The sampling has taken place during the spring and summer seasons and has partly been aimed at the study of single species, such as herring and cod.

Offshore sampling of older larvae (postlarvae) started in 1977. The aim was to study the distribution of larvae in June/July and if possible calculate an abundance index of the different species. Results from the period 1977-1983 and a discussion of the sampling strategy are presented by BJØRKE and SUNDBY (1984).

The aim of this paper is to present some of the results of this work with the emphasis on the distribution of cod in the area Lofoten - Bear Island, and to compare the results with the 0-group indices.

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 KOKHLINA (1964), BARANENKOVA, SOROKINA and KOKHLINA (1973), MUKHINA (1980) and MUKHINA and DVININA (1983).

MATERIALS AND METHODS

The geographical distribution of larvae was found by fishing with a midwater trawl. A trawl with an effective opening of 4 x 10 m was used in 1977, and from 1978 until 1985 a trawl with an opening of 18 x 18 m was used. In 1985 a trawl with an opening of 29 x 29 m was introduced. The different types of trawls had diminishing mesh sizes towards the end and a 4 m long net with mesh size 4 mm (stretched) at the inner part of the cod end (wrongly described as 15 mm mesh size in BJØRKE and SUNDBY, 1984). Attempts made in 1985 to compare the fishing efficiency between the latter two kinds of trawls failed unfortunately, and the only way to compare the 1985 data with those of previous years was to regard the opening of the two trawls.

Regarding the reduced avoidance for larger gears we used the ratio 2.8:1 for fishing efficiency between the largest and smallest trawl.

During the period 1978-1981 two hauls were made at 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 of this haul was 30 minutes.

Only one kind of haul was made at each station from 1982 onwards. From 1982 until 1985 the depths and towing time were the same as the previous years, and five big floats were used on the headline during the haul. The same procedure was followed in 1985, but the towing time at each depth interval was halved.

Towing speed during all the years was 2-3 knots. The volume of the filtered water is not known. Therefore the computed index is based on the number of larvae caught per trawl hour. Hydrographic observations were made with a Neil Brown CTD microprofiler down to the bottom or to 500 m depth where bottom depths were more than 500 m.

All the fish larvae were identified, and a subsample of 50 larvae was taken to measure the length.

The results from the six years 1979-1981 and 1983-1985 are plotted on horizontal maps. and the indices were estimated by using a planimeter tracing the isolines. In 1977 a smaller trawl was used, and in 1978 and 1982 the station net was not dense enough to reveal the mesoscale features, and therefore the abundance indices for these years are not calculated. From 1983 the sampling program was stratified to map the mesoscale features more correctly.

The abundance index may be formulated

$$A = \iint_{x,y} N(x,y)\, dxdy$$

where A is the abundance index

N is the concentration of larvae expressed as number caught per trawl hour

x and y are the geographical coordinates.

The abundance index has the unit no.larvae per trawl hour • km^2 • 10^6. The reason for using this index instead of absolute no. of postlarvae is that the exact opening of the trawl and the fishing efficiency is unknown.

When calculating the abundance of cod larvae in different subareas (Table 2) the same procedure was used.

KVENSETH (1983) measured a growth rate from 0.47 to 0.68 mm/day for cod larvae at an age of about 40 days. By assuming a growth rate of 0.5 mm/day for the postlarvae, synoptic maps can be made to show the length distribution of larvae with reference to the same day i.e. half way through the cruises.

RESULTS AND DISCUSSION

Distribution of postlarvae 1983-1985

Figs 1-6 show the distribution of postlarval cod in the six years 1979-81 and 1983-85. The results from the first four years were presented by BJØRKE and SUNDBY (1984). In 1983 the sampling program was revised based on the knowledge obtained during the previous years sampling program. Since then a more stratified sampling program was worked out, and this has lead to a more detailed mapping of the horizontal distribution of cod, and hence more correct abundance indices.

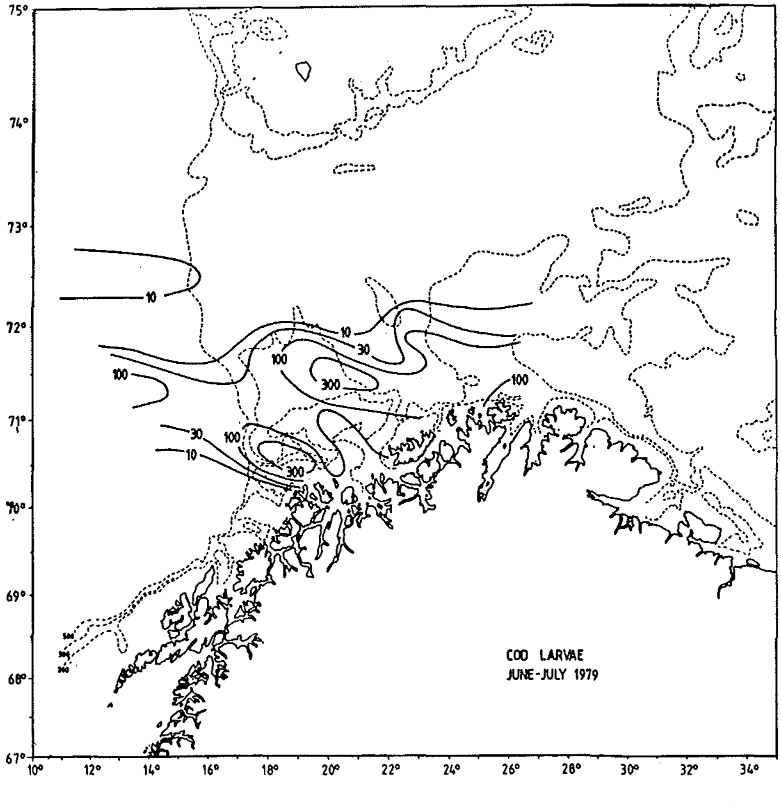

Fig. 1. Distribution of postlarval cod 20 June-10 July 1979. Number per trawl hour.

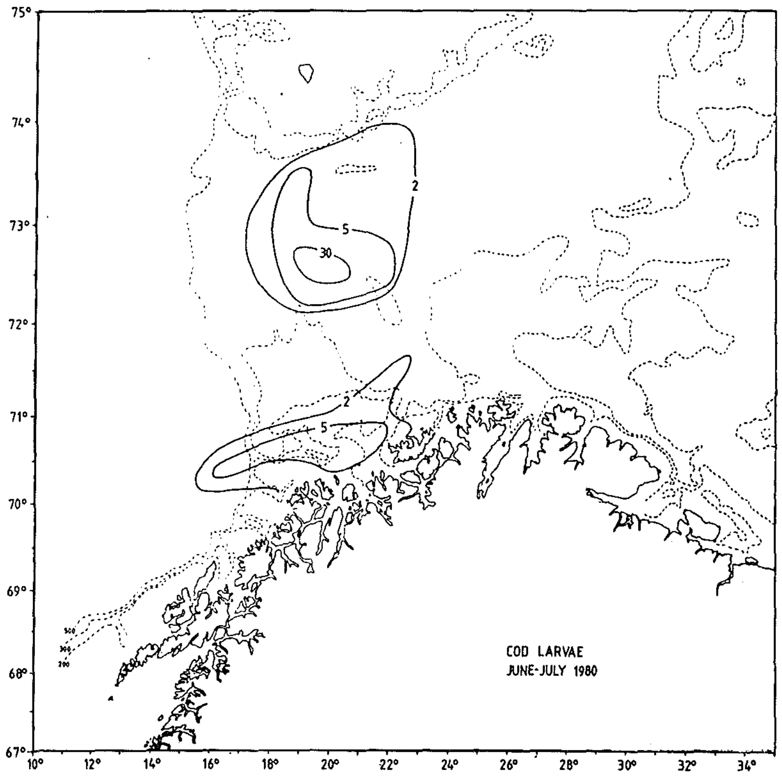

Fig. 2. Distribution of postlarval cod 24 June-10 July 1980. Number per trawl hour.

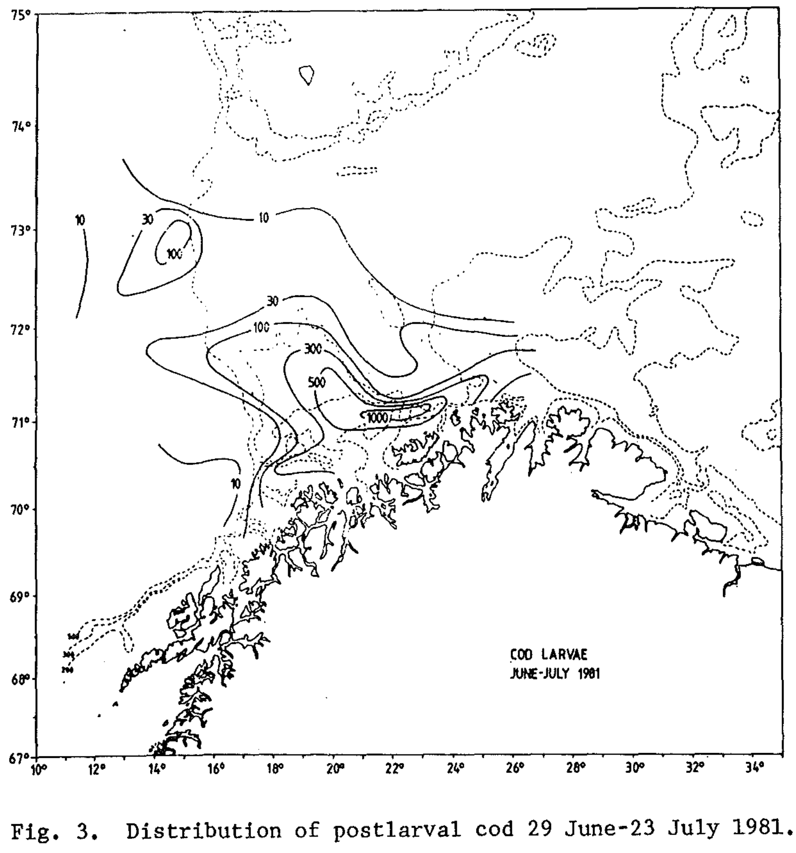

Fig. 3. Distribution of postlarval cod 29 June-23 July 1981. Number per trawl hour.

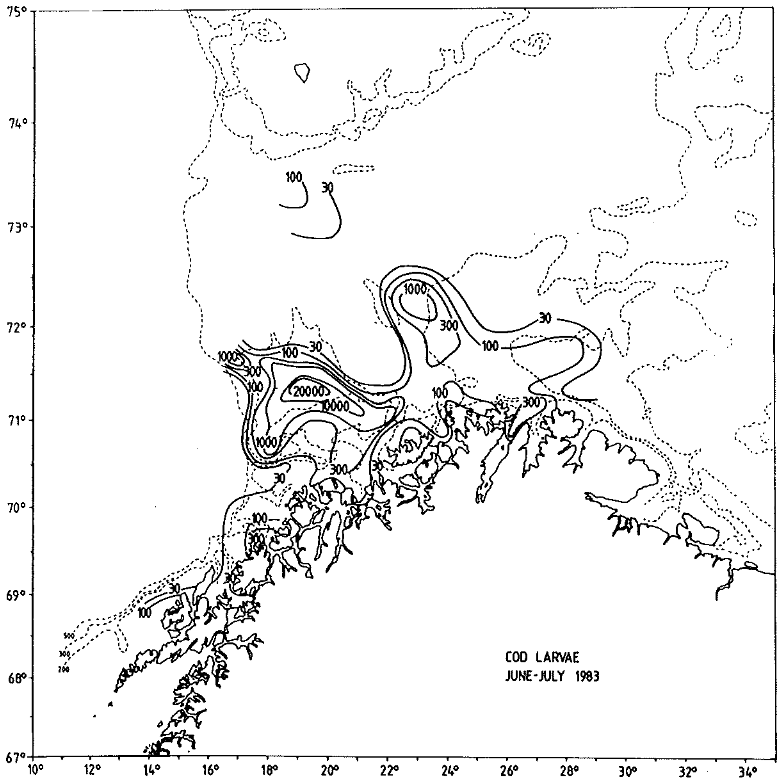

Fig. 4. Distribution of postlarval cod 24 June-17 July 1983. Number per trawl hour.

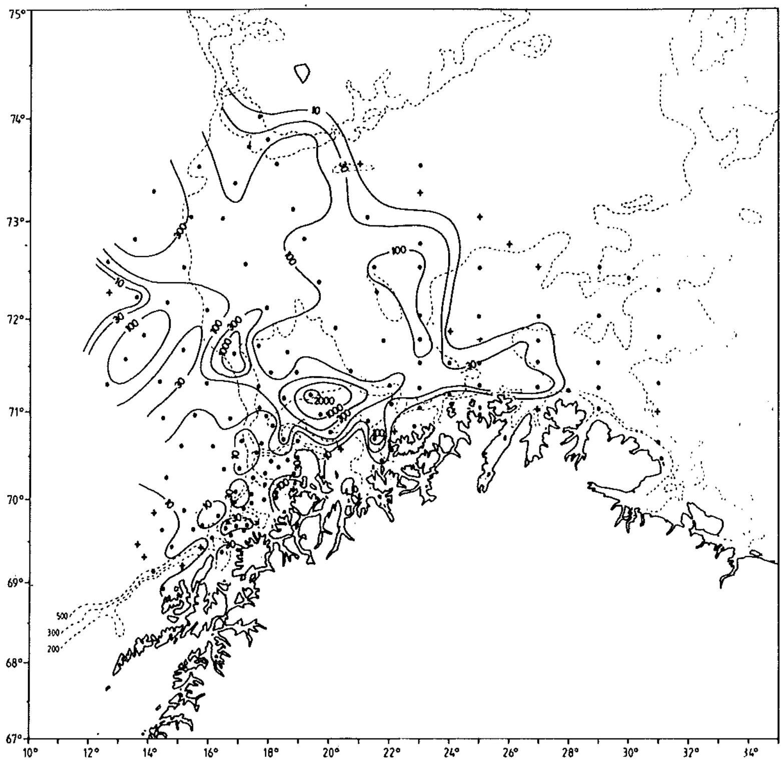

Fig. 5. Distribution of postlarval cod 24 June- 20 July 1984. Number per trawl hour.

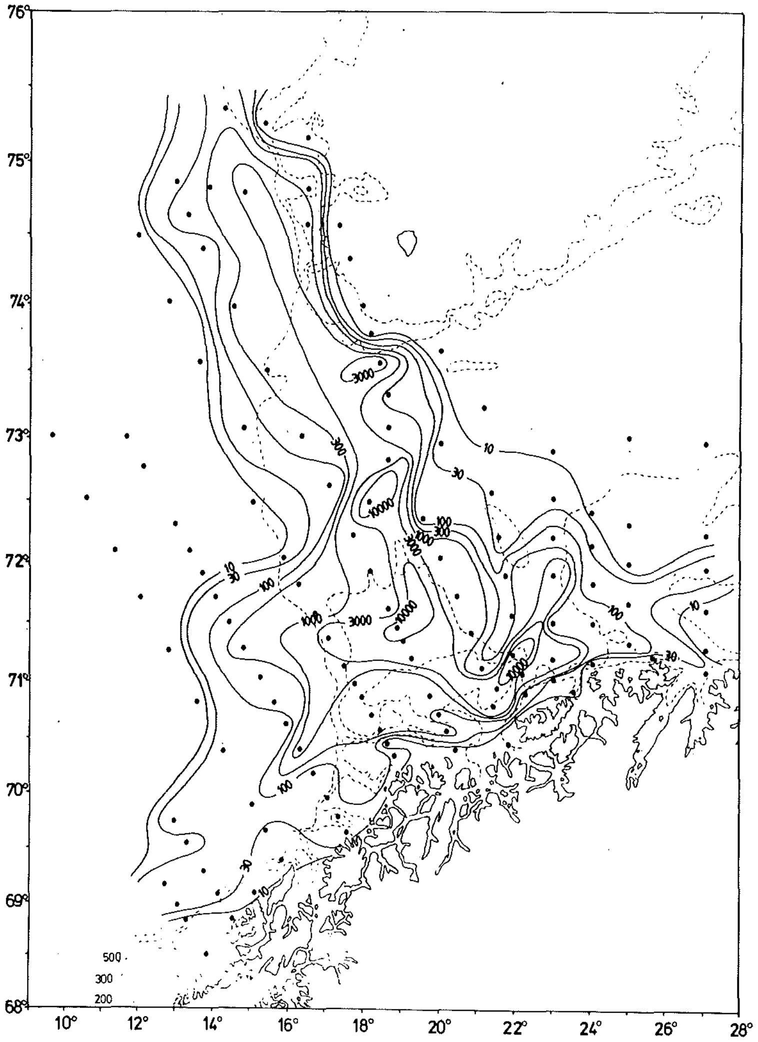

Fig. 6. Distribution of postlarval cod 21 June-15 July 1985. Number per trawl hour.

A general feature common for all the six years is the high concentrations found at Tromsøflaket (Fig. 17). Another is that postlarval cod is mainly found in the coastal waters of salinity less than 34.9^{o}/oo. However, there are also certain features that are specific for each year: In 1983 extremely high concentrations were found at Tromsøflaket. This year 88 percent of the larvae was found within the 300 m isobath at Tromsøflaket. This coincided with the area of salinity 34.4-34.6^{o}/oo S. The distribution in 1984 and 1985 differed to some extent from the 1983 distribution. Both years a fairly large fraction of the total larval number was found in the western and northern areas. Nevertheless, also these years a large fraction of the larvae was found at Tromsøflaket, 45 percent and 57 percent respectively. The large fraction of cod larvae found at Tromsøflaket is due to anti-cyclonic circulation above the bank which greatly reduces the diffusion of the larvae confined to the upper layer.

Fig. 7 shows the fraction of cod larvae at different salinity regimes (A), the geographical extent (in 1000 km^{2}) of the different salinity regimes where cod larvae are found (B), and the mean concentration of cod larvae in the different salinity regimes (C). From the figure it is clear that the distribution in 1983 was special in the way that a large fraction of the larvae was confined to the salinity 34.4-34.6^{o}/oo S. This coincided with the area of Tromsøflaket.

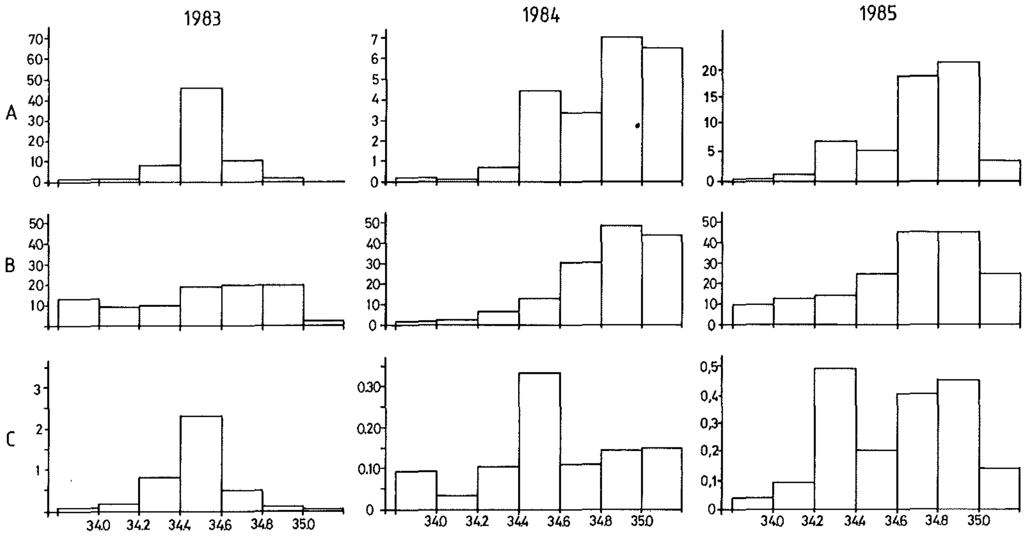

Fig. 7. (A) Abundance indices of postlarval cod at different salinities in 20 m depth. (B) Area (in 1000 km^2) of different salinity regimes where postlarval cod where found. (C) Mean concentration of postlarval cod in the different salinity regimes (A/B, abundance index per 1000 km^2).

In 1984 and 1985 the salinity within the area of the postlarvae was considerably higher, which can be seen from Fig. 7 (B). In 1984 about 8 percent of the area where cod larvae were found had a salinity less than 34.4‰ S, and in 1985 about 25 percent. These two years the postlarval cod were also more widely spread. Especially in 1984 large numbers of larvae were found in the northwestern part, in the Norwegian Sea and towards Spitsbergen. Fig. 5 also shows that the Spitsbergen area was not sufficiently covered. Also in 1985 a relative large fraction of the larvae was found in the northwestern parts towards Spitsbergen. However, this year the northwestern parts were more completely covered. The relative large fraction of larvae in the northwestern parts in 1984 and 1985 may be due to the increased spawning observed at the Vesterålen banks in these years (SUNDBY and BRATLAND 1987). Transport of larvae from these spawning sites tend to have more westernly drift patterns.

Figs. 8-16 show distribution of the cod larvae in three length groups, <30 mm, 30-40 mm, and >40 mm for the years 1983, 1984, and 1985. The lengths refer to the same point of time. A growth rate of 0.5 mm/day was used to adjust for the time lag between the stations. The figures show that the larger larvae are found more frequent in the southern and western parts, while the smallest larvae tend to have a more easternly distribution. This is also shown in Table 1 where the fractions of postlarvae in four subareas are listed for each length group. The four subareas are shown in Fig. 17.

The table shows that the smallest larvae are more abundant in the northern (1) and the eastern (4) areas, whereas the largest larvae are more abundant in the western area (2).

Assuming that the larvae in the eastern parts have been subjected to a longer driftroute from the spawning grounds, and hence are older larvae, one should expect that they should be larger than the larvae closer to the spawning grounds. However, when the results here show that the larger larvae tend to

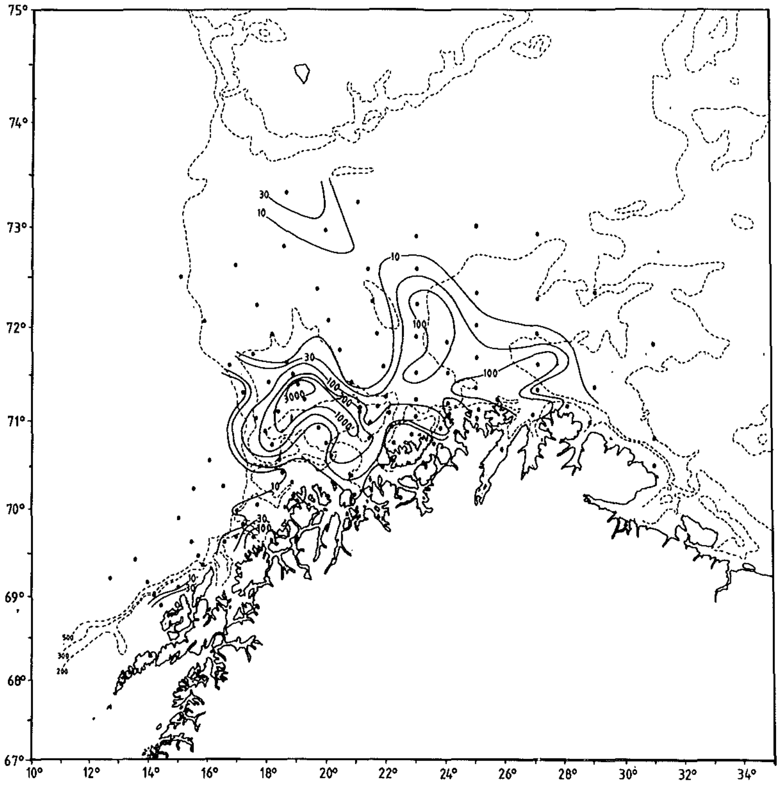

Fig. 8. Distribution of postlarval cod of lengths <30 mm. 1983. (See text).

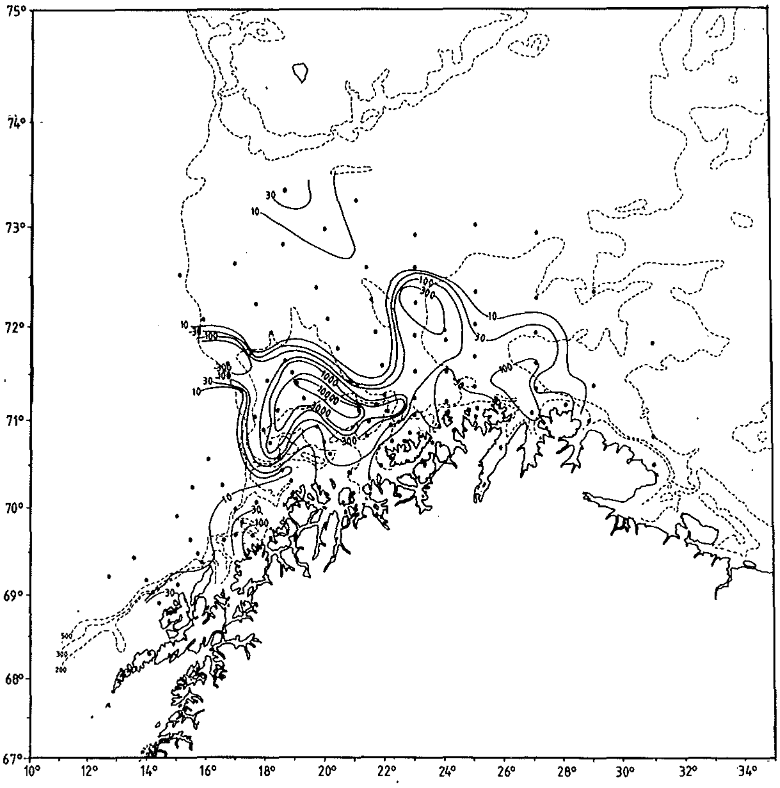

Fig. 9. Distribution of postlarval cod of lengths 30-40 mm. 1983. (See text).

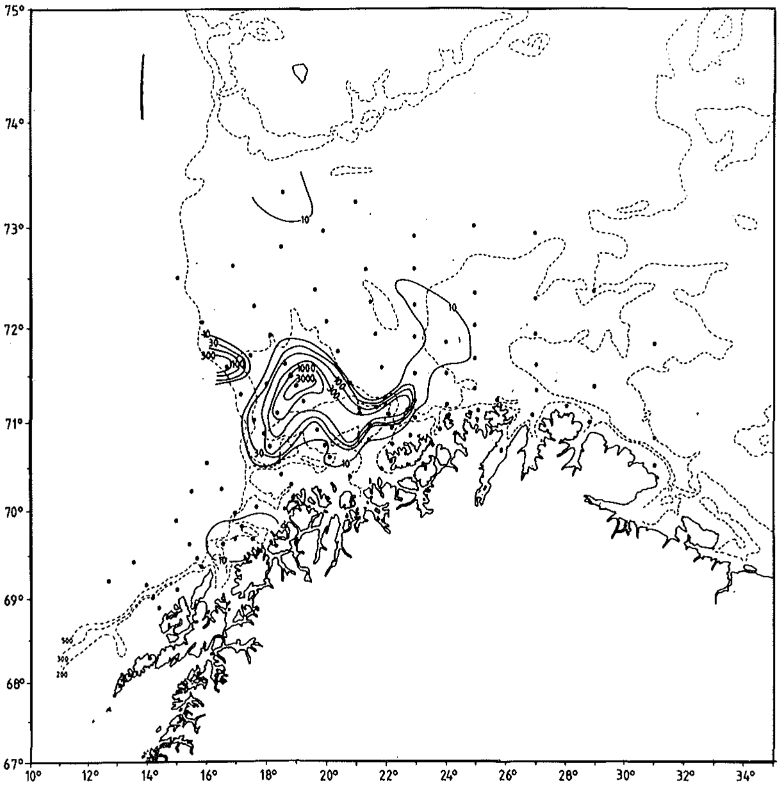

Fig. 10. Distribution of postlarval cod of lengths >40 mm. 1983. (See text).

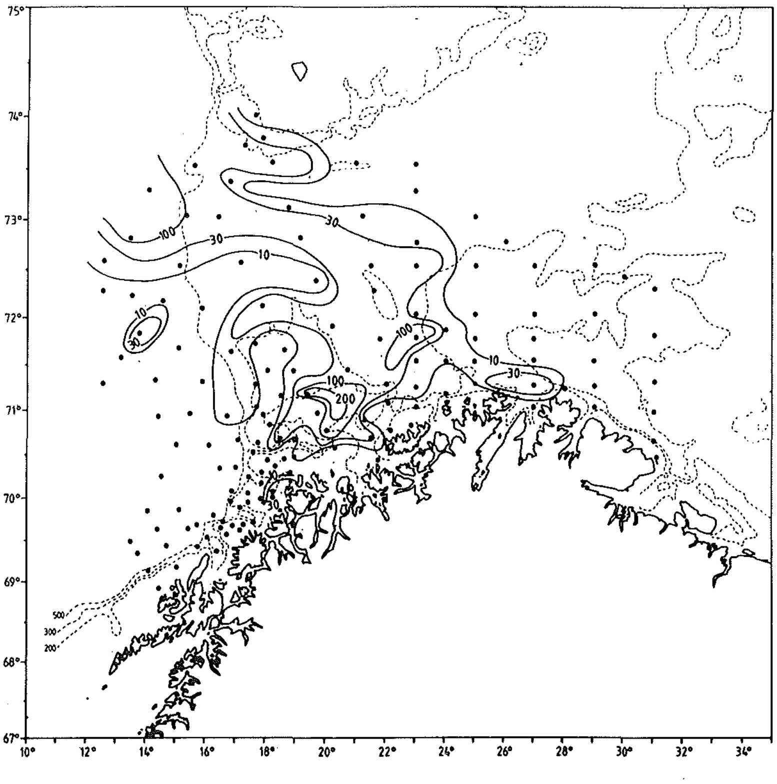

Fig. 11. Distribution of postlarval cod of lengths <30 mm. 1984. (See text).

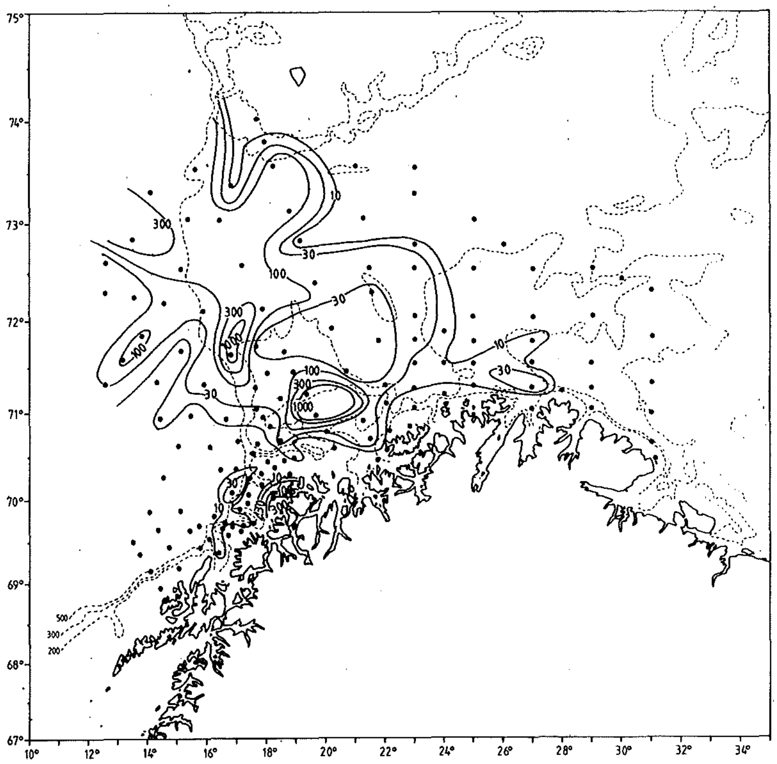

Fig. 12. Distribution of postlarval cod of lengths 30-40 mm. 1984. (See text).

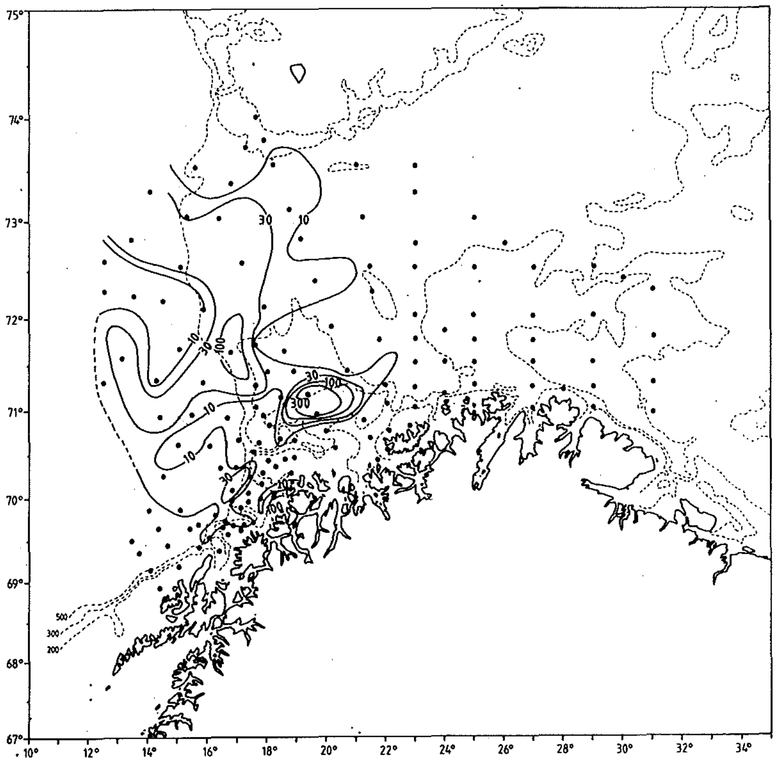

Fig. 13. Distribution of postlarval cod of lengths >40 mm. 1984. (See text).

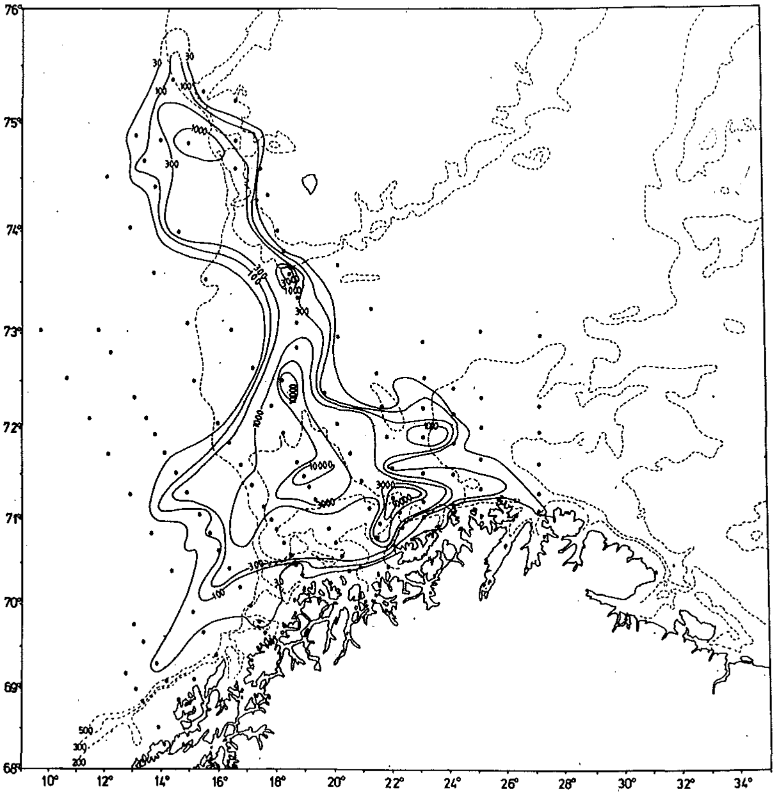

Fig. 14. Distribution of postlarval cod of lengths <30 mm. 1985. (See text).

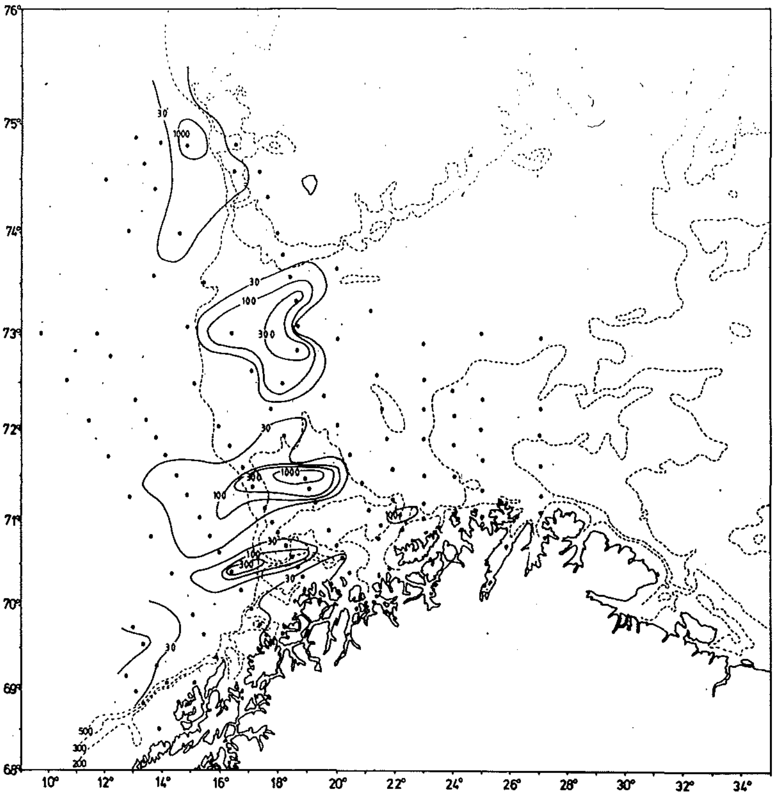

Fig. 15. Distribution of postlarval cod of lengths 30-40 mm. 1985. (See text).

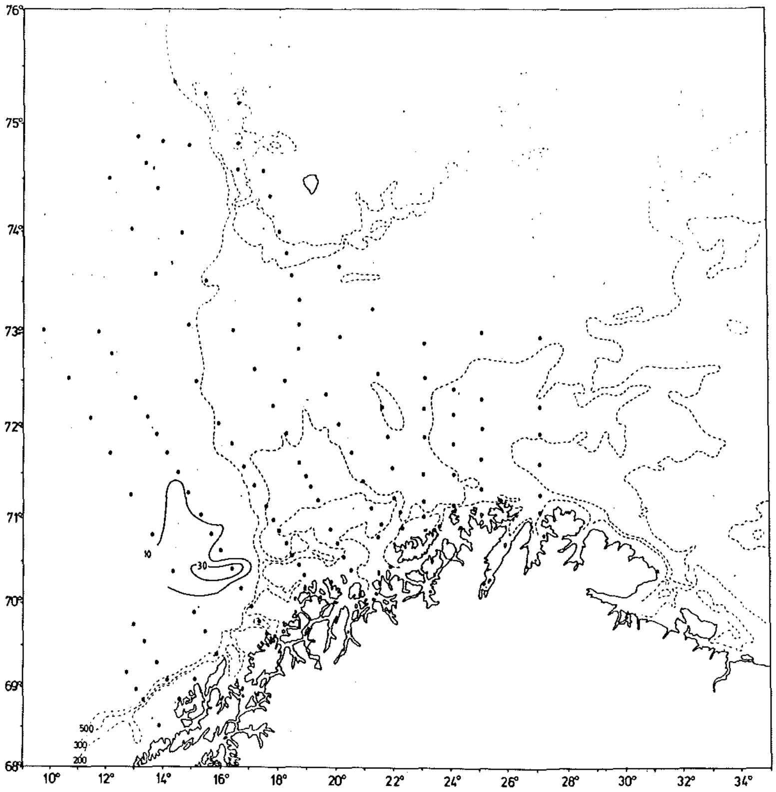

Fig. 16. Distribution of postlarval cod of lengths >40 mm. 1985. (See text).

have a more westernly distribution, it is more likely to believe that they have experienced a warmer life history, and hence subjected to a higher growth rate.

Comparison of the postlarval cod and 0-group cod horizontal distributions 1979-1981 and 1983-1985

During the six years 1979-1981 and 1983-1985 the first three years period had typical weak year classes while the second period had strong year classes. Fig. 18, showing the 0-group distributions, originates from the international 0-group surveys (ANON. 1979b, 1980, 1981, 1983, 1984a, and 1985). The 0-group distribution in 1979 (Fig. 18) must be considered as typical westernly. A very large fraction of the 0-group was then distributed to the west of the shelf edge of the Barents Sea and at the western coast of Spitsbergen. Also in 1984 and 1985 large numbers of 0-group cod were found at the western coast of Spitsbergen, but these years high concentrations were also found in the central parts of the Barents Sea.

Table 1. Percent of postlarval cod in four subareas for three length groups. The sub-areas are shown in Fig. 17.

Length (mm)	1983				1984				1985			
	Subarea				Subarea				Subarea			
	1	2	3	4	1	2	3	4	1	2	3	4
<30	0	3	82	15	7	28	40	25	7	11	77	5
30-40	0	3	90	7	2	38	50	10	7	29	61	3
>40	0	3	96	1	0	51	47	2	0	100	0	0

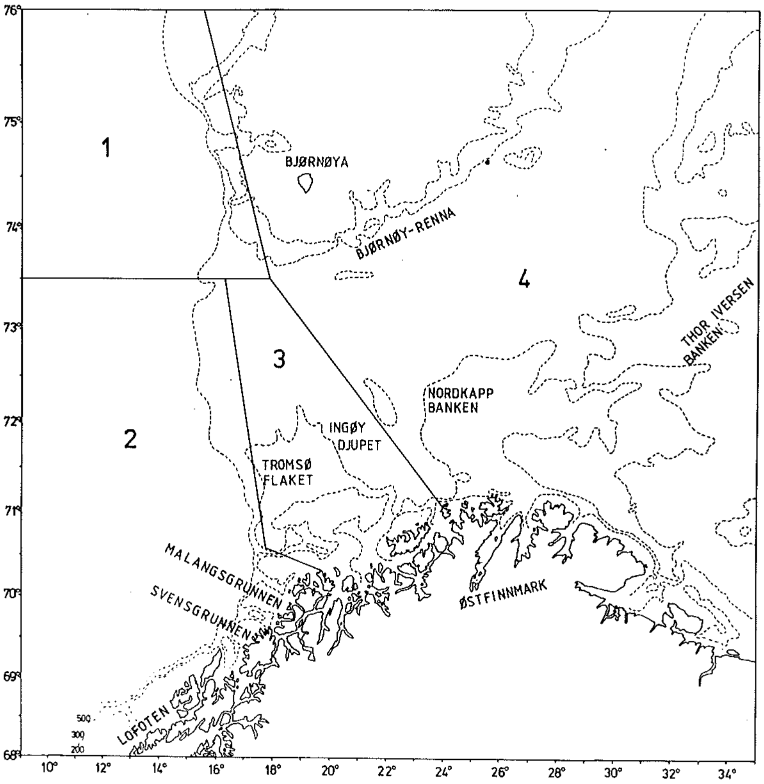

Fig. 17. Four subareas where the abundance of the different length groups are computed (see Table 1) and local names used in the text.

The westernly distribution of 0-group cod in 1979 was even more pronounced during the postlarvae survey showing large numbers of larvae at the southwestern parts of Tromsøflaket and in the Norwegian Sea to the west of the shelf edge. The large numbers of 0-group cod at the western coast of Spitsbergen in 1984 and 1985 can also be predicted from the postlarval distribution which shows high concentrations in the western part of the Bjørnøyrenna and to the west of Bjørnøya.

The very weak 1980 year class had also similar features of distribution during the postlarval and 0-group stages in the way that both stages show a separated northerly and southerly distribution. The postlarvae at the southern parts of Tromsøflaket were advected eastwards showing a distribution from Nordkappbanken and eastwards at the 0-group stage, while the postlarvae in the Bjørnøyrenna were advected northwards showing a distribution along the west coast of Spitsbergen during the 0-group stage.

Abundance indices

Table 2 shows the abundance indices for cod from the postlarvae surveys in June/July and from the 0-group surveys in August/September (ANON. 1985). The latter indices are logarithmic and calculated according to RANDA (1984). Fig. 19 shows the two sets of indices and the regression line.

Assuming that logarithmic transformation normalize the 0-group indices, a Pearson correlation coefficient can be calculated from the data in Table 2. The computed coefficient equals 0.82, significant at the 5 percent level.

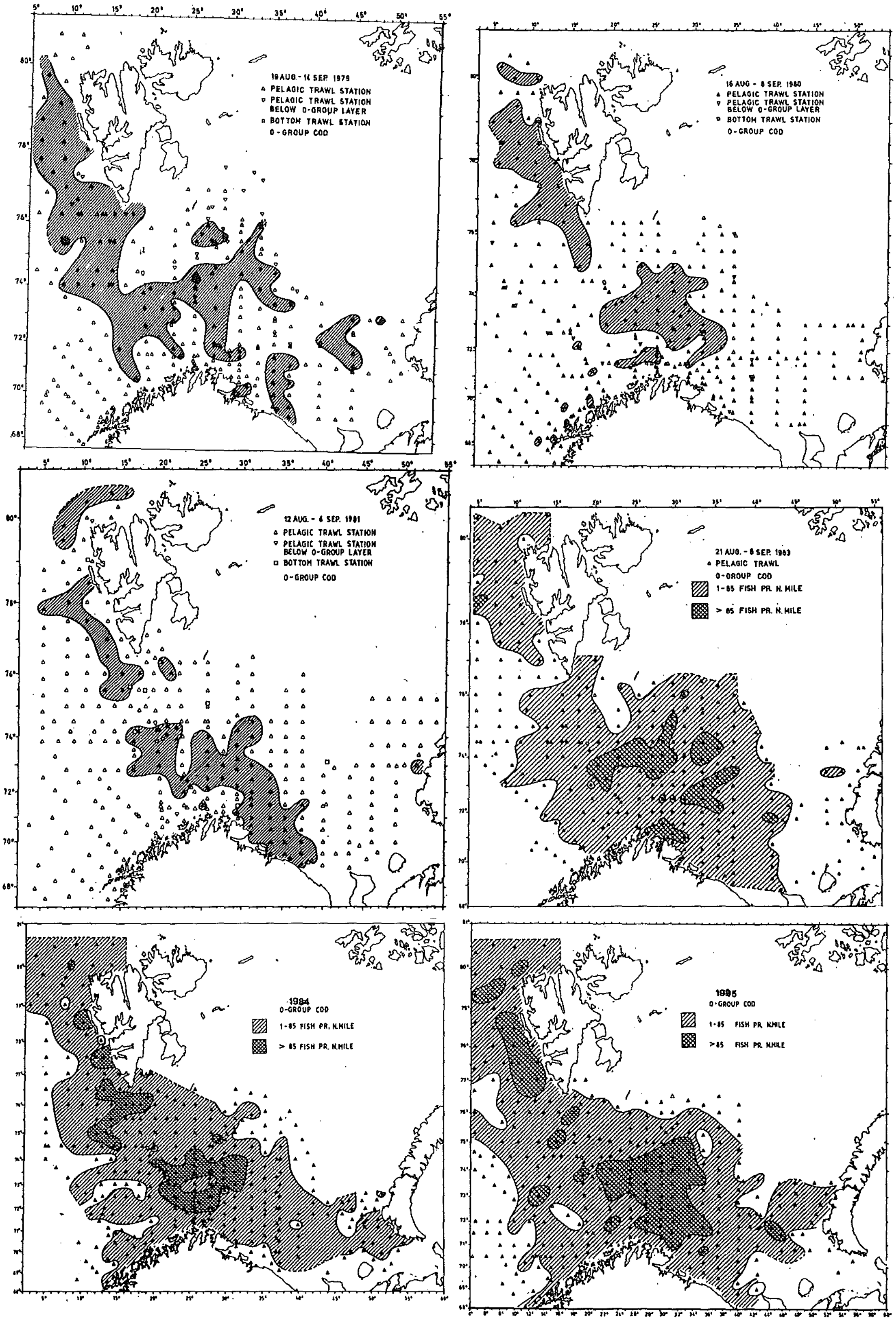

Fig. 18. Distribution of 0-group cod from the international 0-group surveys 1979-81 and 1983-85.

Table 2. Abundance indices for cod from the postlarvae surveys in June/July and from the 0-group surveys in August/September.

Year	1979	1980	1981	1983	1984	1985
Postlarve	7.2	0.4	15.4	74.7	23.5	56.5
0-group (logarithmic)	0.40	0.13	0.10	1.69	1.55	2.46

Both in 1981 and 1983 a very large fraction of the postlarvae index results from the abundance of larvae at Tromsøflaket. Both years the 0-group indices are low compared to the postlarvae indices. The abundance estimates of both these years have been adjusted upwards during the last years (ANON. 1982, 1984b and 1986) and recent estimates from acoustic surveys indicate that the 1981 year class is 1/5 of the 1983 year class. (HYLEN, JAKOBSEN, NAKKEN and SUNNANÅ 1985). This could indicate that the 0-group station grid may fail to record very patchy distributions.

The postlarvae index for the 1984 year class is obviously an underestimate since the northernmost area of distribution was not examined. The direction of these adjustments are indicated in Fig. 19. In view of these factors it is likely that the correlation between the two surveys is better than indicated in Fig. 19. Bearing in mind the improved coverage of the cod larvae distribution since 1983, it seems reasonable to believe that the postlarvae indices produced in July gives a fairly good indication for the year class strength of cod as 0-group.

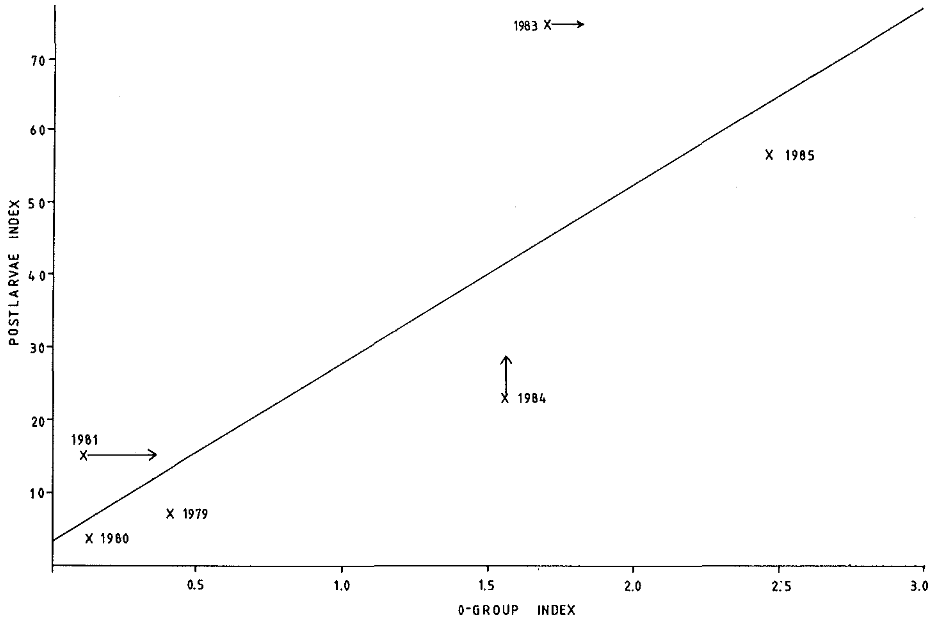

Fig. 19. The regression line between the cod postlarvae and the 0-group indices. Arrows indicate direction of adjustments.

CONCLUSIONS

In June/July a large fraction (45-90 percent) of the year class of cod was found at Tromsøflaket. This was caused by the presence of an anti-cyclonic circulation above the bank that greatly reduces the diffusion of postlarval cod which is confined to the upper layer.

The postlarvae are most years found in coastal water masses of intermediate salinities (34.4-34.8 $^{o}/oo$ S).

The relative large fraction of larvae in the western parts and in the Spitsbergen area in 1984 and 1985 may be due to heavy spawning activity at the more offshore spawning fields Moskenesgrunnen and Eggagrunnen.

There are similar features of the distributions of postlarval and 0-group cod with respect to westernly/easternly distributions.

The postlarvae indices produced in July seem to give a reasonable good indication for the year class strength as 0-group cod in September.

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THE EFFECT OF OCEANOGRAPHIC CONDITIONS ON DISTRIBUTION AND POPULATION
DYNAMICS OF COMMERCIAL FISH STOCKS IN THE BARENTS SEA
Proceedings of the third Soviet-Norwegian Symposium, Murmansk, 26-28 May 1986
Edited by H. Loeng. Institute of Marine Research, Bergen, 1987.

OCEANOGRAPHIC CONDITIONS AND REPRODUCTION OF ARCTO-NORWEGIAN COD OF THE BARENTS SEA IN 1980-1985

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ABSTRACT

The oceanographic conditions in the reproductive zone and drift areas of cod eggs and larvae are considered. To reveal seasonal and interannual variations in the patterns of both the dynamic topographical relief and intensity of the geostrophic circulation, the dynamic charts for the spring-summer period of 1980-1985 have been analysed. The distribution of cod eggs and larvae is reviewed in relation to the dynamic crest of the increased water level, and also to the flow rate and direction of the currents on the watershed between the Norwegian and Barents Seas. The regions of the larval cod transport from the spawning grounds to the areas of the first wintering have been determined.

INTRODUCTION

Early ontogenesis is known to be the most critical period in the life of fish. The long-term experience has revealed the following main factors which limit the strength of year classes during their formation (DEKHNIK, SEREBRYAKOV and SOIN, 1985):

- food availability for larvae,
- predation upon eggs and larvae,
- complexity of hereditary factors,
- influence of oceanographic conditions.

Among the latter, the flow intensity and direction of currents, together with the water temperature, exert much influence on the fish survival during the early period of development (HJORT 1914, CARRUTHERS 1938, CHASE 1955).

The life cycle of the Arcto-Norwegian cod is closely bound up with the Eastern branch of the Norwegian Current and North Cape Current. The spawning grounds of cod on the Lofoten Shoals are located in the region of the increased intensity of the Eastern branch of the Norwegian Current and adjacent waters. According to SEREBRYAKOV and ALDONOV (1984), in the area of the Lofoten Islands, there are three categories for the location of the spawning grounds:

a) main spawning grounds, which are located on the banks near to the coast;

b) on both the banks and the shelf slope;
c) only outside the Norwegian Sea shelf region and on the Malangen Bank.

The spawning intensity in these areas varies from year to year. This is basically associated with the structure of the spawning stock. The mature cod of the older age groups spawn primarily in the inner waters of the Lofoten Islands (in the Vestfjord). The younger fish do so in the areas more northward and at later time than the older fish (NAKKEN 1984). The spawned and fertilized cod eggs (consequently larvae) are carried by the current. Consistent with its direction, some of them are transported into the Bear Island/Spitsbergen area, but a greater number drift with the North Cape Current into the Barents Sea.

The drift of cod during the stage of early ontogeny have been studied by many explorers. Thus, according to some authors (MASLOV 1944, RASS 1949, BARANENKOVA and KHOKHLINA 1959, 1961, BARANENKOVA, SOROKINA and KHOKHLINA 1976, KISLYAKOV 1961), the transport of young cod into the Barents Sea depends on the rate of flow of the currents. CORLETT (1965) has found that intensification of the southerly winds contributed to the transport of eggs and larvae into the northern Barents Sea. Apart from the current flow rate, the distribution of cod eggs in the surface layer is significantly influenced by the crest of the increased water level which extends northward from the Norwegian coast (KISLYAKOV 1964).

The survival of cod fingerlings, which determines the year class abundance, is known to be much higher in the southern part of the Barents Sea than in the northern part (PONOMARENKO 1982). It is, therefore, important to know in what areas of the Barents Sea the bulk of eggs and larvae are transported every year. Eggs of the abundant 1963, 1969, 1970 and 1975 year classes drifted principally with the coastal branch of the North Cape Current into the southern Barents Sea, which undoubtedly favoured the good survival of young cod (ALDONOV and SEREBRYAKOV, 1984). In papers by TERESHCHENKO (1980), and DVININA and MUKHINA (1984) it has been shown that the direction of the drift of cod eggs and larvae in the spring-summer period defines the areas of the first wintering of young fish. To estimate correctly the spawning efficiency and routes of transport of fish eggs and larvae, there is the necessity for (LYNN 1984, POWER 1984):

- knowledge of the location of the spawning grounds and dates of spawning;
- reliable taxonomic identification of different stages of the fish development in the early ontogenesis;
- knowledge of the plankton phase duration;
- correct data on the abundance of larvae;
- regular observations of hydrographic conditions in the survey area.

The present paper considers the effects of the geostrophic circulation and flow rate of the eastern branch of the Norwegian Current and North Cape Current upon the distribution of cod eggs and larvae on the spawning grounds and during their subsequent drift.

MATERIAL AND METHODS

The paper presents data of the ichthyoplankton surveys in the north-eastern Norwegian and south-western Barents Seas which were carried out during

April-May and June-July for 1980-1985. The survey route and trawl stations are given in Fig. 1. The sampling and processing of the materials have been done by standard methods as adopted by PINRO (BARANENKOVA and KHOKHLINA 1959, 1961). This was except for 1985 when the assessment survey of cod eggs and larvae in the coastal waters of the Lofoten Shoals started one month later than usual.

To study the flow intensity of the currents with the dynamic method (ZUBOV and MAMAEV 1956), the depths on each station and relative values of the flow rate of the geostrophic circulation between two adjacent stations have been calculated. The 200 m depth has been taken as the reference level.

The identification of eggs and larvae of Gadidae has been made visually with the MBS-1 binocular according to the nomenclature of developmental stages, suggested by RASS (1946). To define the spawning area, the charts of the density distribution of eggs of the first developmental stage (division stage) have been plotted. The area of the intensive spawning have been defined by concentrations of eggs of the first developmental stage, exceeding 100 species per haul.

RESULTS

During spring (April-May), the cod eggs of the first developmental stage are distributed over a fairly broad area, but the distribution of density varies from year to year. Intensive spawning was observed on the Vesterålen and Malangen Banks during 1980 and 1981, Andøy Bank in 1982, Vesterålen Bank

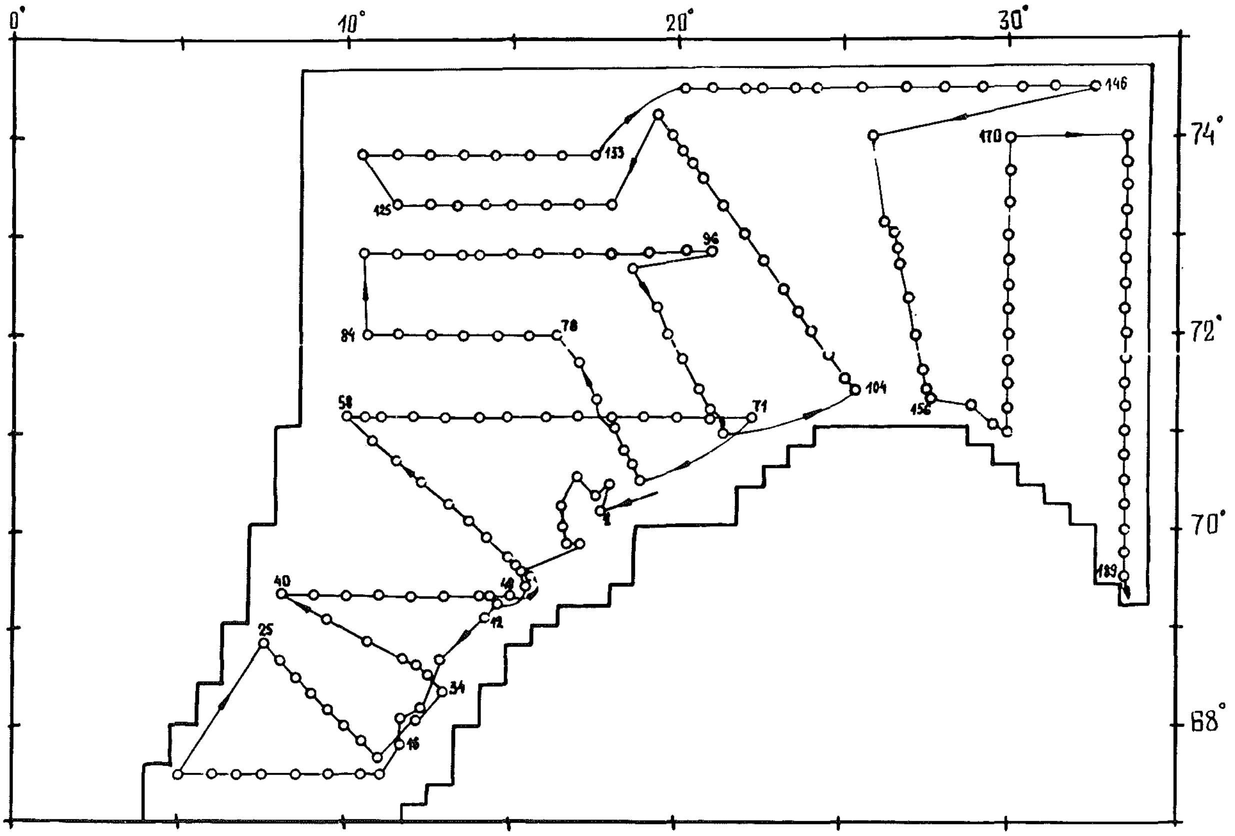

Fig. 1. Route and station grid of the ichthyoplankton survey during 1980-1985.

in 1983, Malangen and Andøy Banks during 1984 and 1985 (Figs 2A-7A). Variations in the distribution of eggs in the surface layer, and also their abundance in the survey area depend much upon peculiarities of the hydrographic regime during the spawning, particularly, upon the dynamics of the currents. The grounds of intensive cod spawning are located in those areas having a higher flow rate of the eastern branch of the Norwegian Current, and tend to be separated from each other. During spring of 1980-1985, the flow rate of the waters in the coastal areas of the Lofoten Shoals ranged within 7-18 cm$\cdot$s^{-1}. With the flow rate of the surface water masses of 13-18 cm$\cdot$s^{-1} (observed in 1981-1983), the isolation of these areas was especially notable. By contrast, a lowering of the flow rate (e.g. 7-10 cm$\cdot$s^{-1}), caused the boundary between the areas of egg distribution to become less marked, as was the case in 1984 (Figs 3A-7A). Hence, we may suggest that the flow rate of water masses in the surface layer can be a reason for eggs to concentrate in one or another area. The increase of the flow rate likely promotes formation of cyclonic gyres in the surface layers, which causes the eggs to be concentrated. The eggs are thus held on the spawning grounds, where no sharp variations of the environmental conditions occur, and this favours subsequent survival of the eggs.

The distribution of eggs is much influenced by the crest of the increased water level, originating from the considerable run-off of the continental waters. Our observations have confirmed the conclusions made by KISLYAKOV (1964), that the more the crest is developed, the more northward of the coastal areas of the Lofoten Shoals the eggs of the early developmental stages are transported, and the larger is the area of the egg distribution. The location of the northern boundary of the spawning grounds in the period of the observations varied annually: in 1980, 1981 and 1985 the eggs of the first developmental stage did not occur north of latitude 72°50'N, during 1982 and 1984, north of 72°00'N, and during 1983, north of 71°45'N (Figs 2A-7A).

For certain years (1983-1984), the drift of eggs was also influenced by cyclonic gyres forming between latitudes 71°N and 73°N, and hampering the northward transport of eggs (Figs 5A-6A).

The hatching of cod larvae in the survey area begins during late April - early May. At this time, the larvae drift passively with the surface flow. The relationship between the dynamics of the water mass and the distribution of larvae during spring has not been revealed because of their low abundance. During years of poor abundance (1981-1982), the drift of larvae cannot be traced, even during summer, and only a probability for the direction of their transport can be indicated. We have found that, while for spring the larvae keep on the spawning grounds (as in 1981, 1983 and 1985), that during summer they are transported mostly into the southern Barents Sea. When in spring the larvae were caught outside the spawning grounds (most commonly in the Tromsøflaket area), it meant that their summer drift had been directed primarily northward into the Bear Island - Spitsbergen area. This was the case in 1984.

During summer (June-July), as compared to spring, the crest of the increased water level on the watershed between the Norwegian and Barents Seas is the most pronounced, but the degree of its development in the surveyed years has been different. The highest development was observed during 1980 (north to latitude 74°00'N); the lowest one was during 1984 (north to 72°30'N). The analysis of the distribution of cod larvae and degree in the development of the crest in the summer period has shown that the transport of larvae into the Barents Sea is decisively influenced not by the

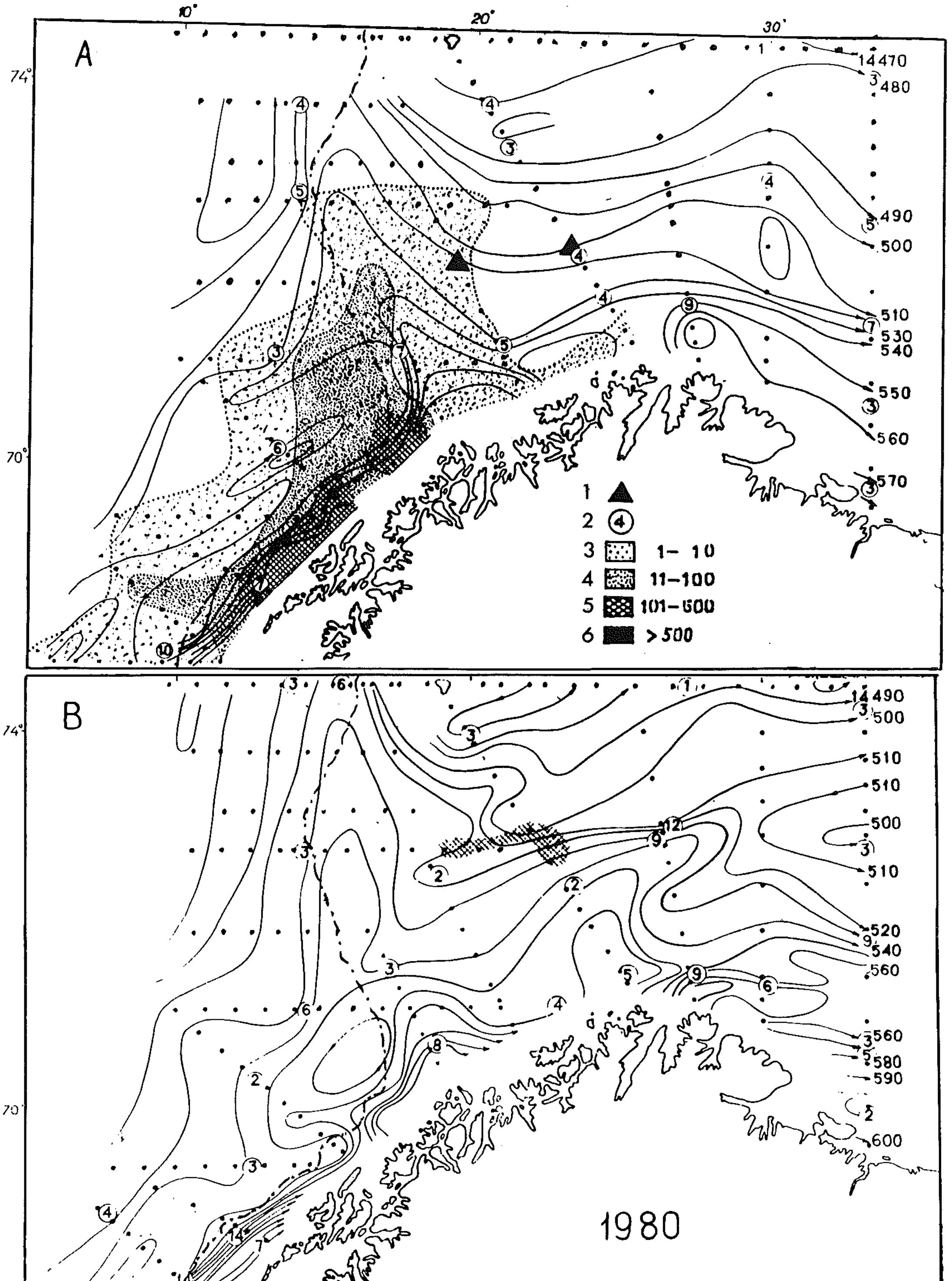

Fig. 2. Spawning area of cod and distribution of larvae during 1980 compared to dynamic topography (decibars).

A. spring situation
B. summer situation

(1) distribution of larvae
(2) mean flow rate (cm.s^{-1}) in the 0-10 m layer
(3-6) number of eggs per haul. 3 : 1-10 ; 5 : 101-500
4 : 11-100; 6 : above 500

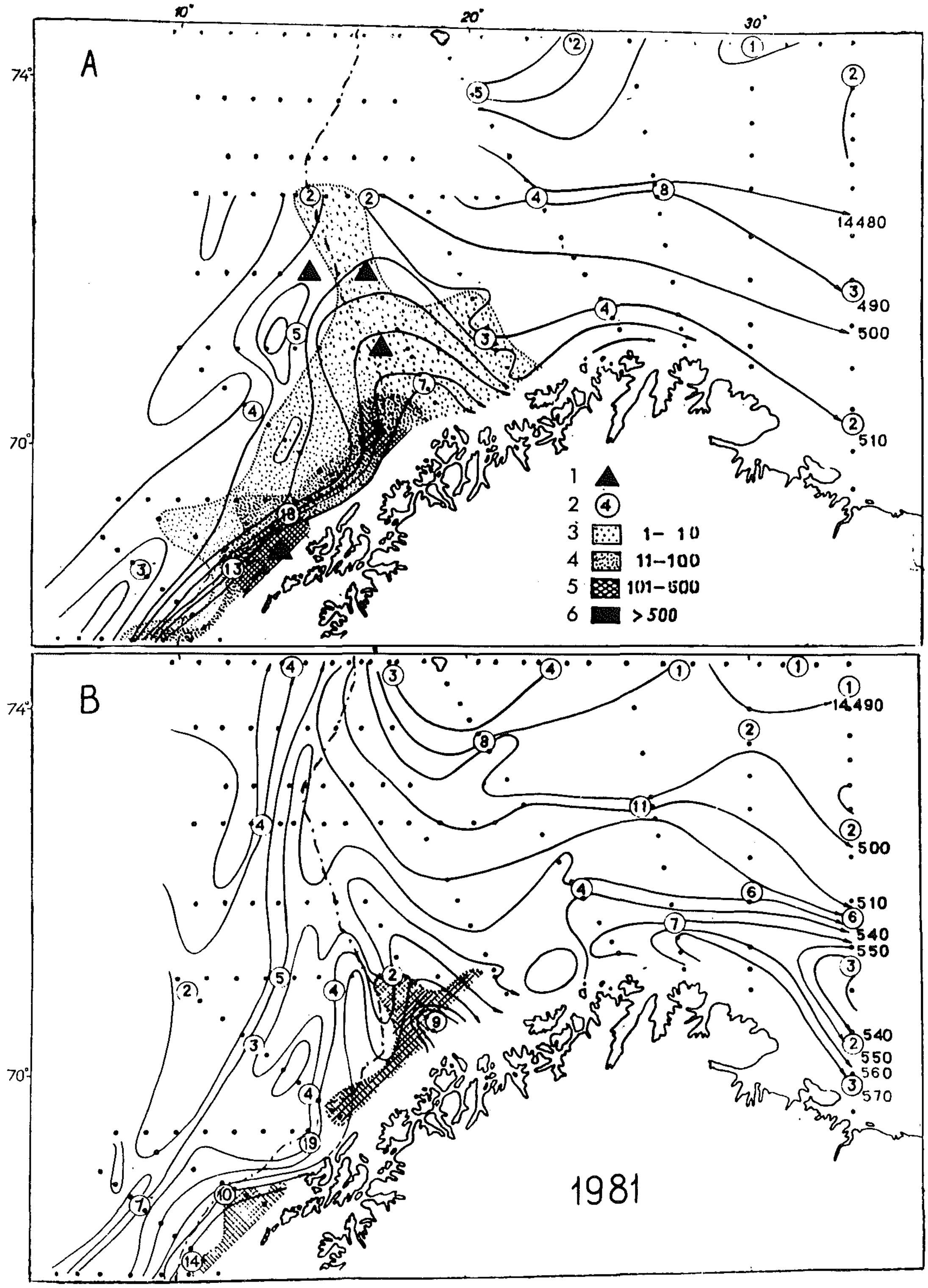

Fig. 3. Spawning area of cod and distribution of larvae during 1981 compared to dynamic topography (decibars).

A. spring situation
B. summer situation

(1) distribution of larvae
(2) mean flow rate (cm.s^{-1}) in the 0-10 m layer
(3-6) number of eggs per haul. 3 : 1-10 ; 5 : 101-500
4 : 11-100; 6 : above 500

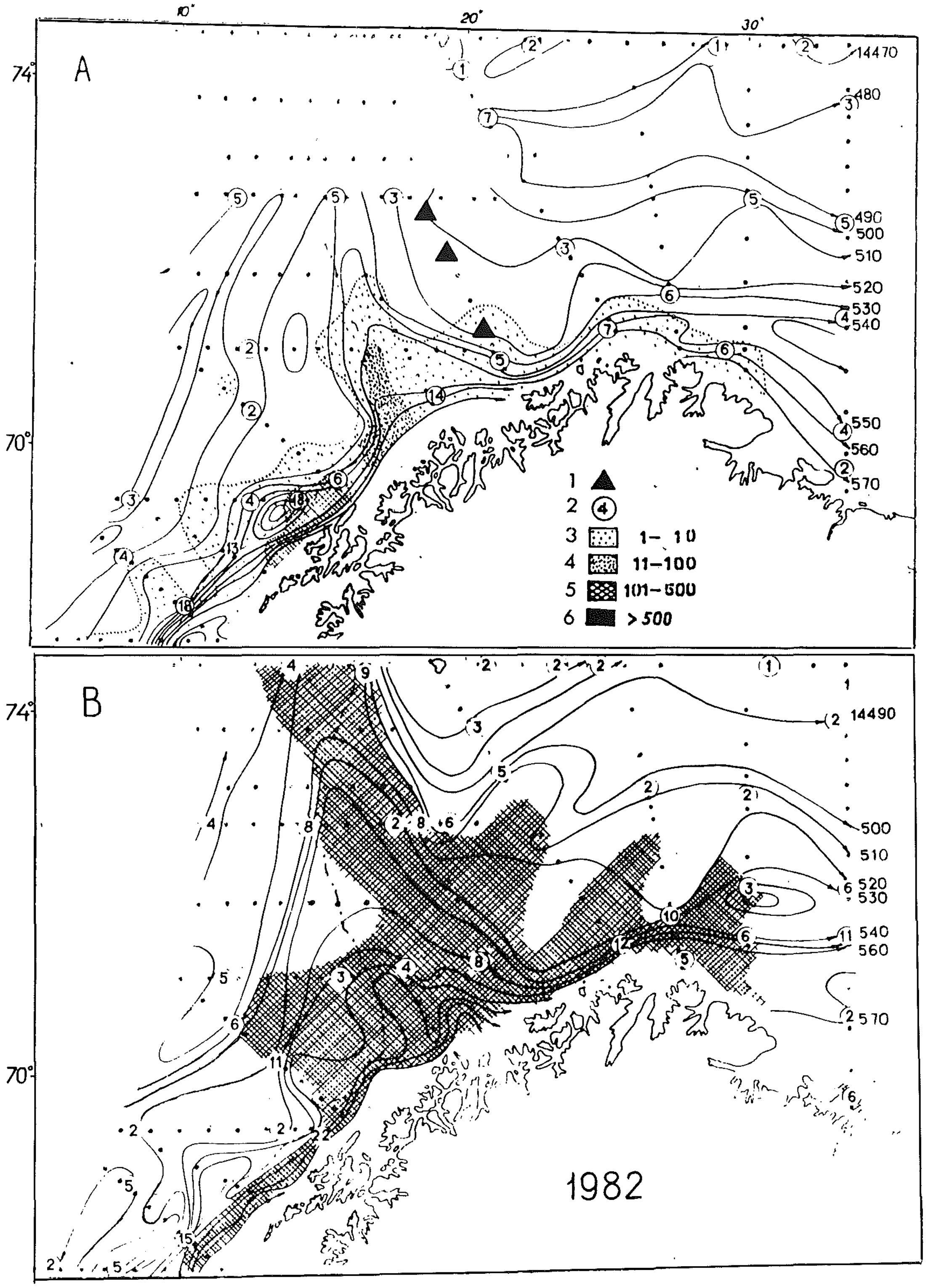

Fig. 4. Spawning area of cod and distribution of larvae during 1982 compared to dynamic topography (decibars).

A. spring situation
B. summer situation

(1) distribution of larvae
(2) mean flow rate ($cm.s^{-1}$) in the 0-10 m layer
(3-6) number of eggs per haul. 3 : 1-10 ; 4 : 11-100; 5 : 101-500; 6 : above 500

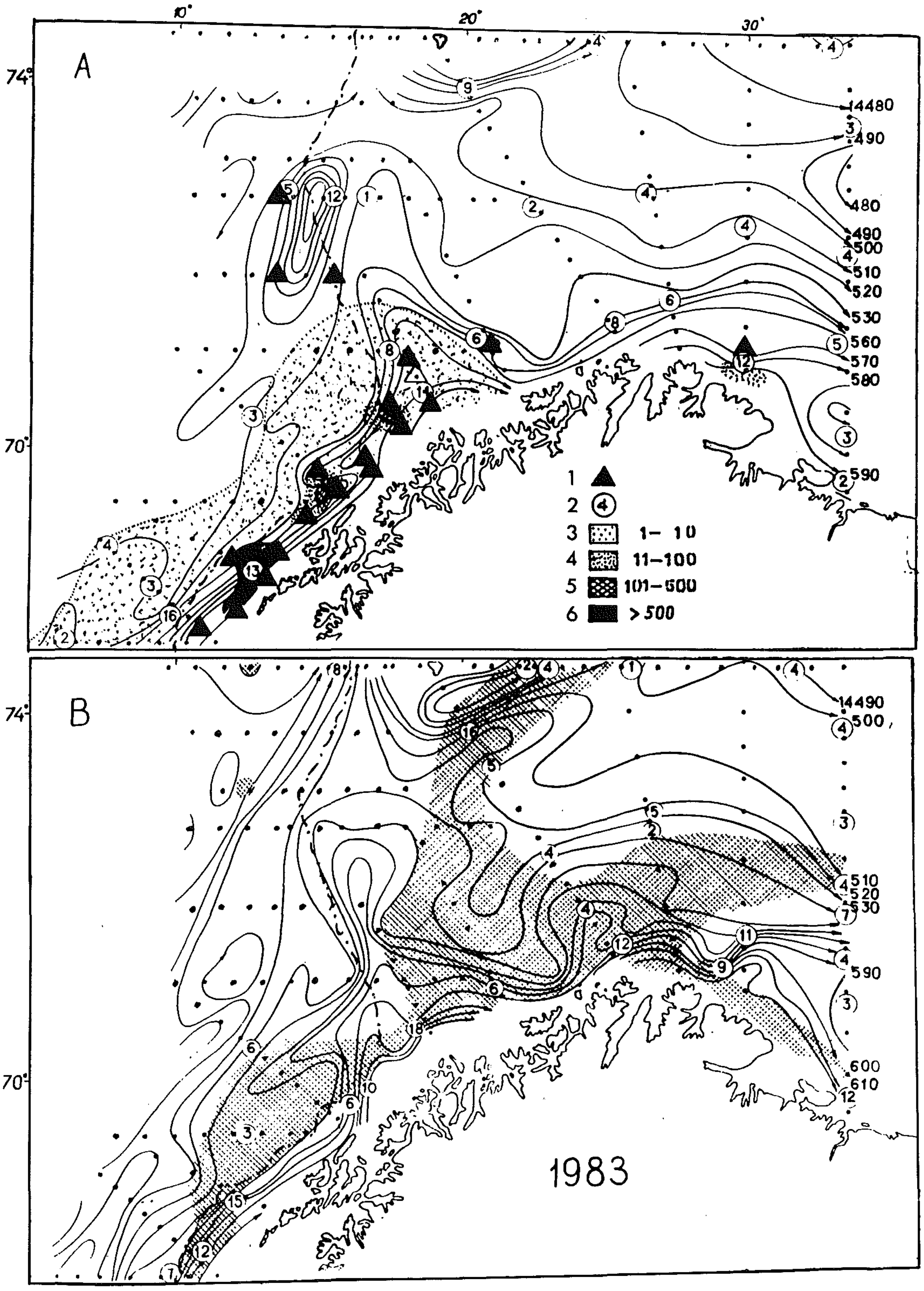

Fig. 5. Spawning area of cod and distribution of larvae during 1983 compared to dynamic topography (decibars).

A. spring situation

B. summer situation

(1) distribution of larvae

(2) mean flow rate ($cm.s^{-1}$) in the 0-10 m layer

(3-6) number of eggs per haul. 3 : 1-10 ; 5 : 101-500
4 : 11-100; 6 : above 500

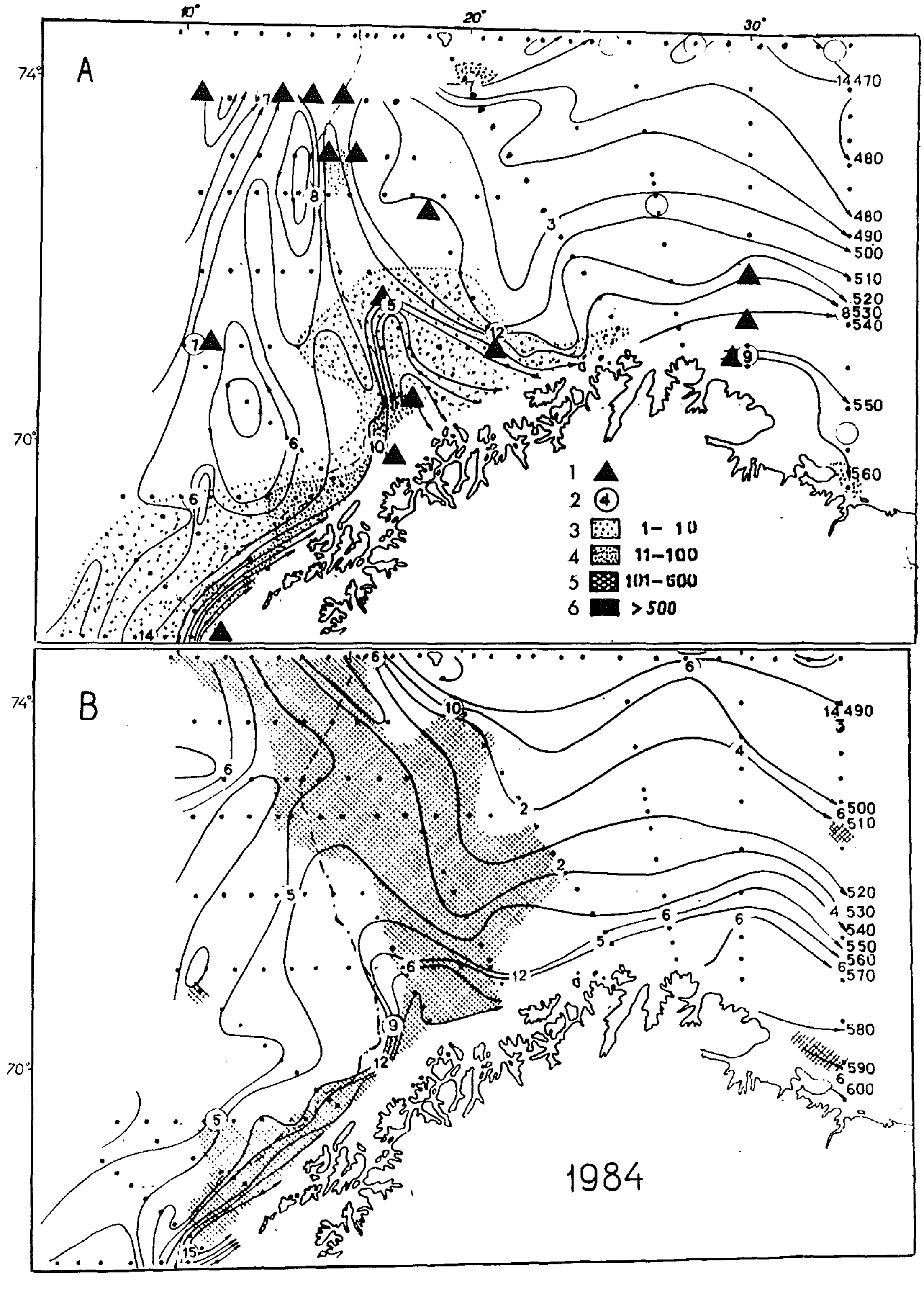

Fig. 6. Spawning area of cod and distribution of larvae during 1984 compared to dynamic topography (decibars).

A. spring situation
B. summer situation

(1) distribution of larvae
(2) mean flow rate (cm.s^{-1}) in the 0-10 m layer
(3-6) number of eggs per haul. 3 : 1-10 ; 5 : 101-500
4 : 11-100; 6 : above 500

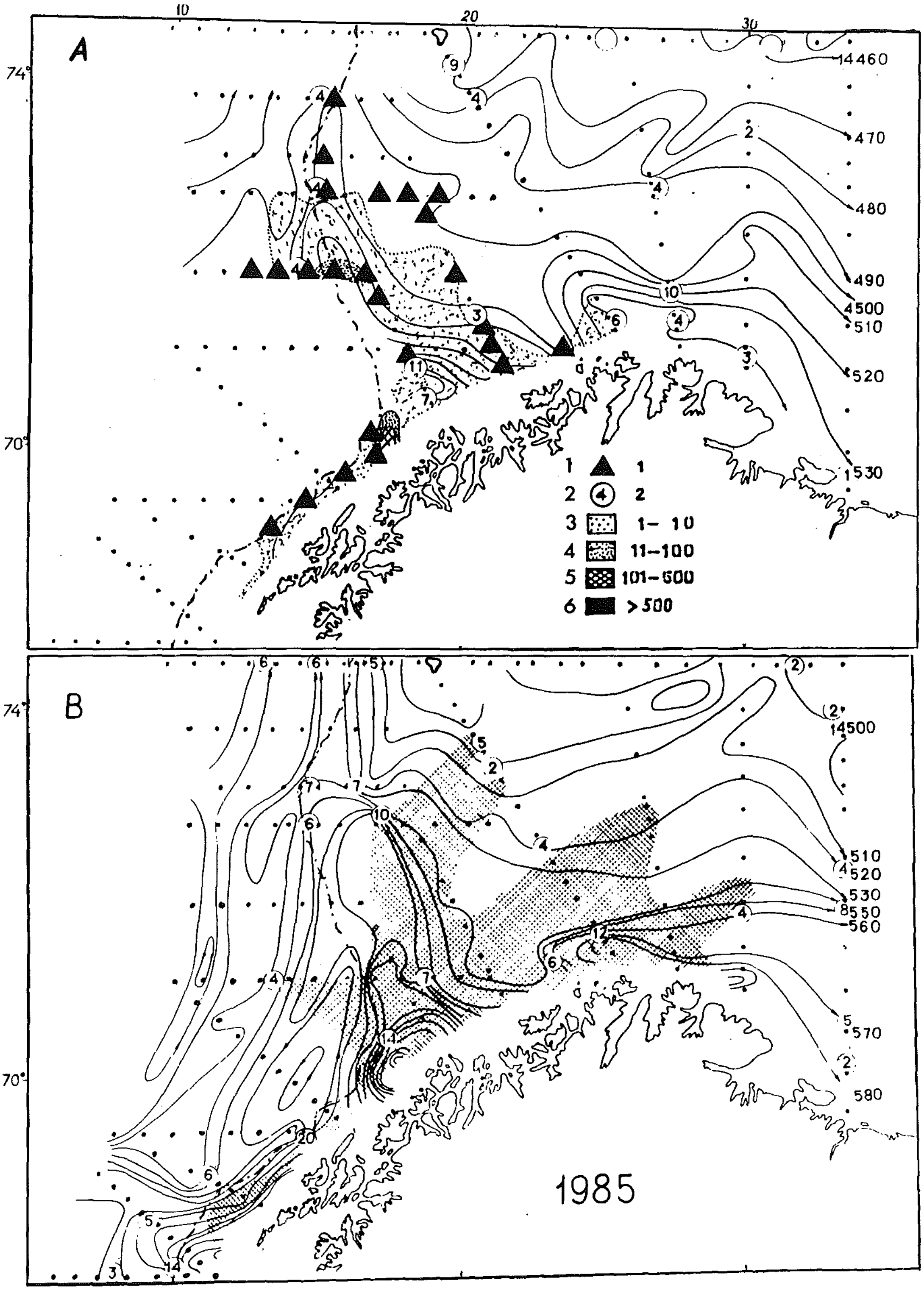

Fig. 7. Spawning area of cod and distribution of larvae during 1985 compared to dynamic topography (decibars).

A. spring situation
B. summer situation

(1) distribution of larvae
(2) mean flow rate (cm.s^{-1}) in the 0-10 m layer
(3-6) number of eggs per haul. 3 : 1-10 ; 4 : 11-100; 5 : 101-500 6 : above 500

crest itself, but rather by the intensity of water circulation in the area mentioned. The same conclusion was made by TERESHCHENKO (1980) who studied the effect of hydrometeorologic conditions on the drift of the Lofoten cod eggs and larvae into the Bear Island/Spitsbergen area. As our findings show, the flow rate of the eastern branch of the Norwegian Current has ranged from 12 to 22 cm$\cdot$s^{-1}. The highest flow rate was recorded in 1982 and 1985, the lowest one in 1980 (Figs 2B, 4B and 5B). Variations of the current flow rate off the southern Lofoten Islands have a significant bearing upon the distribution of cod larvae over the whole Lofoten Shoals. Thus, at the flow rate of 14-22 cm$\cdot$s^{-1} for the surface layer, the transport of larvae from fjord into the open sea is hampered, while their concentration in the coastal areas (RØst and Vesterålen Banks) increases. Such a distribution was observed during 1981, 1982 and 1985. With the flow rate of the eastern branch of the Norwegian Current equalled to 10-15 cm$\cdot$s^{-1} (as for 1983 and 1984), we observed in the area of the Lofoten Islands an appreciable drift of cod larvae into the open sea, outside the shelf area (Figs 5B-6B). Intensification of the water flow in the area of the Lofoten Shoals contributes to formation of anti-cyclonic gyres in the more eastern regions of the Norwegian coast. According to BJØRKE and SUNDBY (1984), the extremely high concentrations of cod larvae which were registered during June-July, 1983, in the gyres along the TromsØ and North Cape Banks, where they had been held due to anti-cyclonic whirls. This was confirmed by satellite data of a drifting buoy. From our observations, during 1983, the water flow rate in the area of these banks constituted 18 cm$\cdot$s^{-1}.

To determine the grounds of the first wintering, the drift rate of cod larvae is of particular interest, as well as the direction of the drift along the branches of the North Cape Current. It is known that if the discharge of water through the section between the North Cape and Bear Island is low, the transport of cod larvae into the northwestern Barents Sea is more probable (MUKHIN and DVININA 1978). The inverse relationship has also been revealed between the flow intensity of the North Cape Current and abundance of cod fingerlings in the Bear Island - Spitsbergen area (TERESHCHENKO 1980). By comparison of the charts on the dynamic topography and distribution of cod larvae during June-July, it has been found that larvae are transported into various parts of the Barents Sea with those brances of the North Cape Current. These have a most marked flow intensity. Thus during 1982, the highest flow rate was recorded in the Spitsbergen Current (9 cm$\cdot$s^{-1}) and Coastal branch (12 cm$\cdot$s^{-1}) of the North Cape Current, where the main drift of cod larvae was observed (Fig. 4B). During 1983, the drift was basically directed into the southwestern Barents Sea along the coastal (12 cm$\cdot$s^{-1}) and northern (16 cm$\cdot$s^{-1}) branches of the North Cape Current (Fig. 5B). During 1984, the intensity of the water flow through the section between the North Cape and Bear Island was insignificant. Cod larvae were primarily transported, therefore, with the Spitsbergen Current (10 cm$\cdot$s^{-1}) into the Bear Island/Spitsbergen area (Fig. 6B). In 1985 the larvae drifted mostly with the coastal (12 cm$\cdot$s^{-1}) and main (10 cm$\cdot$s^{-1}) branches of the North Cape Current into the Barents Sea.

Comparison of the values of flow rate for the North Cape Current by years, one may notice that the higher values have the young cod transported further eastward. For instance, during 1983 the intensity of the North Cape Current was very high which promoted the wide spread of not only young cod, but also other commercial fishes at the pelagic devlopmental stage in the Barents Sea (ANON. 1983).

CONCLUSIONS

The areas of the intensive cod spawning on the Lofoten Shoals are located in the region of the higher flow rate of the eastern branch of the Norwegian Current. The increase of the flow rate favours concentration of eggs in the limited area of the spawning grounds and their arrest there. The horizontal distribution of cod larvae of the first developmental stage (and, hence, the area they are distributed over) is determined by the degree of development of the crest of the increased water level on the boundary between the Norwegian and Barents Seas. The more extensive a crest, the more northward from the coastal areas eggs are transported during early stages.

In summer the character and direction of the drift of cod larvae depend mainly on the flow rate of the Norwegian and North Cape Currents. The increase of the flow in the eastern branch of the Norwegian Current (to 14 cm • s^{-1} and above) hampers the transport of larvae from fjords into the open sea and promotes their concentration in the coastal areas off northern Norway. During summer, cod larvae drift into various parts of the Barents Sea along those branches of the North Cape Current, the flow intensity of which was the most pronounced in the year observed.

The appearance of the cod year-classes of higher abundance is favoured by the following factors:

- southern location of the spawning grounds;
- water flow intensity of the eastern branch of the Norwegian Current, which hampers in spring the transport of eggs and larvae from fjords into the open sea;
- summer transport of larvae mostly into the southern Barents Sea.

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THE EFFECT OF OCEANOGRAPHIC CONDITIONS ON DISTRIBUTION AND POPULATION
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Proceedings of the third Soviet-Norwegian Symposium, Murmansk, 26-28 May 1986
Edited by H. Loeng. Institute of Marine Research, Bergen, 1987.

THE ABUNDANCE OF YEAR CLASSES OF THE BARENTS SEA CAPELIN AND PECULIARITIES OF THE DISTRIBUTION OF THE YOUNG IN RELATION TO HYDROGRAPHIC CONDITIONS

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ABSTRACT

The dynamics of the capelin year class strength is considered in relation to various factors. No statistically significant relationship was discerned between the year class strength on one hand and the parent stock numbers and ambient conditions on the other. However, poor year classes appear more often in cold years.

The analysis of the water thermal state in the Barents Sea for the recent 20 years indicated that a large scale decrease of water temperature in 1977-1982 had a great effect on the migration pattern of spawning capelin. In these years the spawning of fish only occurred near the northern coast of Norway. No displacement of spawning sites eastwards in connection with higher recorded water temperatures in the subsequent years was observed. The spawning of capelin off Finnmark in recent years (1981-1984) entailed a westward distribution of the young capelin favourable for their survival and for the formation of rich year classes in these years.

INTRODUCTION

The capelin stock size is determined by the abundance of coming year classes. In turn their abundance depends on the total effect of different factors, amongst which are the temperature at spawning grounds and drift routes, parent stock size, population fecundity and predation (NIKOLSKY 1974).

Elucidation of the relationships between the year class abundance and factors determining it, as well as monitoring of the total stock status, are required in the working-out of scientific advice for the rational fishing of capelin.

MATERIAL AND METHODS

The paper uses data from observations for the distribution of capelin and temperature conditions on spawning grounds during 1971-1984. Information about areas and conditions of spawning off Finnmark for the period is taken from HOGNESTAD (1972, 1973), GJØSÆTER and SÆTRE (1973), GJØSÆTER et al. (1974), GJØSÆTER and MARTINSEN (1976), HAMRE and RØTTINGEN (1977), DOMMASNES, MONSTAD and NAKKEN (1978), DOMMASNES (1978), HAMRE and MONSTAD (1979, 1980), ALVHEIM (1985) and others.

The water temperature on the spawning grounds was analysed using the data from areas off Murman (information of the PINRO Laboratory of Fisheries Oceanography) and Finnmark (SÆTRE 1973).

The strength of capelin year classes and the distribution of fingerlings were evaluated based on the results of annual Soviet/Norwegian 0-group survey in the Barents Sea and adjacent waters (ANON. 1976-1984). The spawning stock is estimated by capelin acoustic surveys (DOMMASNES and RØTTINGEN 1985) and the numbers of fish in separate age groups are determined from revised acoustic estimates (USHAKOV and GALKIN 1983).

RESULTS AND DISCUSSION

The analysis of water thermal conditions in the southern Barents Sea made by Norwegian scientists indicated a series of alternating periods of warming and cooling (SÆTERSDAL and LOENG 1984). Over the past 20 years the water temperature was below normal during 1965-1969 and 1977-1982 (cold years) and exceeded the long term mean during 1970-1976 and 1983-1984 (warm years). The same periods are given in the paper by OZHIGIN and LUKA (1985).

Observations conducted by Soviet and Norwegian scientists allowed determination of the location for the main spawning grounds during 1971-1984 (Fig. 1). The figure shows that the location of the main spawning grounds off the northern coast of Norway and near the Murman coast changed due to varying oceanographic conditions. Thus, during the period of warming from 1970-1976, the spawning grounds were observed to be displaced eastward, with most easternly spawning in 1975 (Fig. 1). The massive spawning of capelin that year occurred in coastal areas from the North Cape to 36-37°E. Owing to cooling which started in 1977, the fish were found to go further west for spawning. During 1979-1981 the western boundary of the spawning area reached 18-20°E, and in the east the fish spawned near the northwestern coast of the Varanger Peninsula. No massive spawning of capelin was observed near the Murman coast from 1977 to 1984.

Soviet and Norwegian observations demonstrate that the spawning of capelin occurs at water temperature from 1.5 to 5.0°C (POZDNYAKOV 1958, PROKHOROV 1965, OLSEN 1968, DRAGESUND, GJØSÆTER and MONSTAD 1973).

According to PINRO data the long term mean temperature off the Murman coast in March-April is 1-2°C. The massive spawning of capelin occurred in these areas only in periods of warming, when the temperature increased by 1° or more and reached 2-3°C. In the coastal area from Vardø to Nordkyn, spawning capelin were regularly observed during all years. The long term mean water temperature there during March-April constitute 2.5-3.0°C. Spawning grounds located west of the North Cape were occupied by the fish primarily during periods of considerable cooling in the southern Barents Sea, with the water temperature in the coastal area Nordkyn - Revsbotn - Lopphavet constituting 2.0-2.5°C. It appears from the above that the temperature of 2-3°C is most optimal for spawning capelin. Thus, the data which are presented confirm the results of previous investigations aimed at determining the optimal spawning conditions for capelin. Any considerable

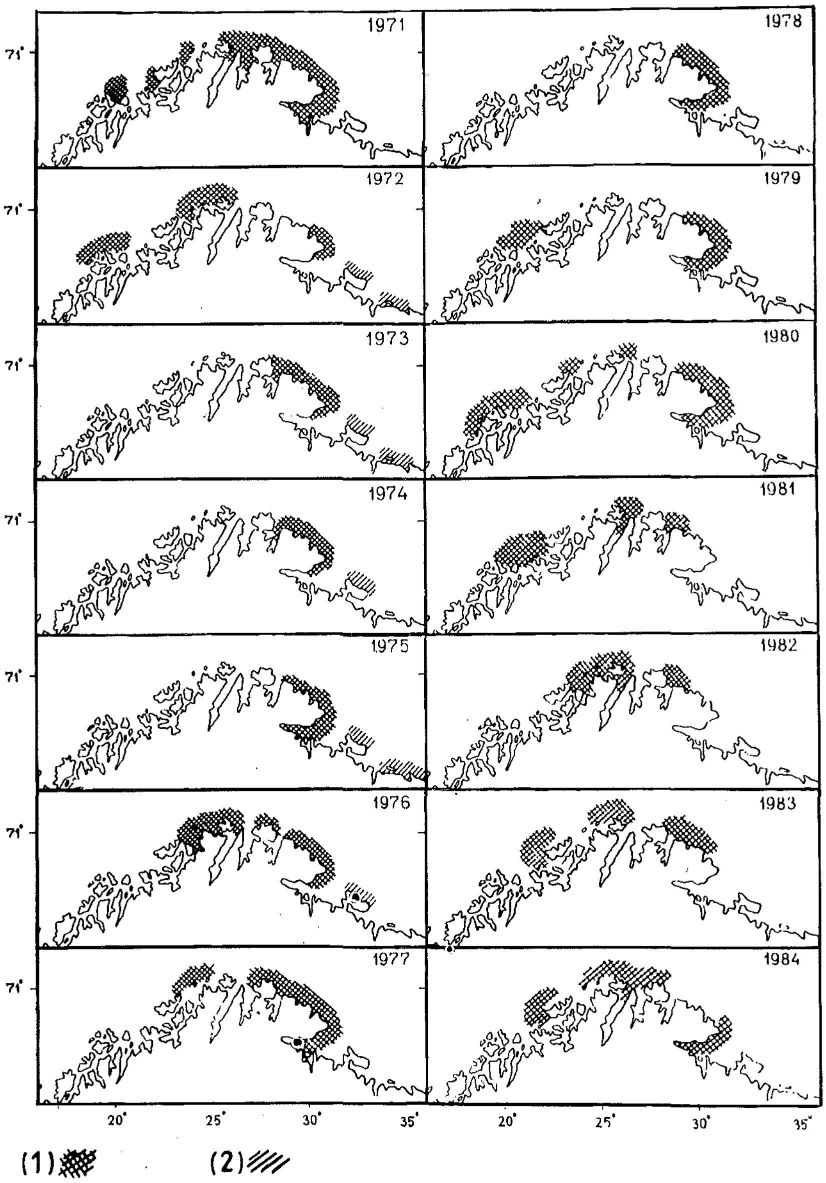

Fig. 1. Positions of capelin spawning sites during 1971-1984. (1) Norwegian data; (2) results of PINRO surveys.

anomalies in the water temperature, both positive and negative, are, apparently, unfavourable for the fish and cause certain changes in the fish behaviour and, particularly, entail a displacement of areas of massive spawning.

However, it should be noted that capelin do not immediately respond to thermal changes in the water. A certain inertness in the displacement of spawning areas due to changes of temperature conditions may be traced. So, after a series of cold years (1965-1969 and 1977-1982) the spawning of capelin in warm years (1970-1971 and 1983-1984) still continued to occur only near the Norwegian coast.

Estimates of the capelin year class strength from the 0-group capelin survey indicated the 1971-1976 and 1979-1984 year classes to be rich (Table 1). Rich year classes appeared more often in the warm period (1970-1976). The parent stock in these years was composed of abundant year classes. Subsequent acoustic surveying of these year classes at age 2+ confirmed previous estimates (USHAKOV and GALKIN 1983, DOMMASNES and RØTTINGEN 1985).

Table 1. Characteristics of the spawning stock and strength of capelin year-classes in 1971-1985.

	Year-class															Mean
	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	
Spawning stock, 10^9 ind.	266	230	138	296	446	320	257	206	182	291	85	108	70	54	18	198
Abundance index for the 0-group fish	151	275	125	359	320	281	194	40	660	592	570	393	589	(400)	110	332
Abundance at age 1+, 10^9 ind.*	290	640	890	470	390	270	600	540	320	340	385	496	515	145	35	422
Abundance at age 2+, 10^9 ind.*	220	180	240	550	340	240	180	370	330	200	195	311	200	184	47	252
Abundance at age 3+, 10^9 ind.*	130	140	80	160	240	140	100	100	110	160	48	63	38	48	21	105

* According to revised data from acoustic surveys (USHAKOV and GALKIN 1983)

Abundant 1979-1982 year classes originated from parents of high (1976), average (1977) and low (1978) abundance and appeared in cold years. But the strength of these year classes at age 2+ was estimated to be at a low level.

Year classes of the average abundance were found to appear in both the warm year of 1973 and the cold year of 1977 originating from parent stocks of different numbers. A poor 1978 year class appeared at lower temperatures and originated from a scanty number of parents.

Thus, the analysis of the spawning stock dynamics in relation to temperature conditions and progeny numbers revealed no pronounced correlation (Fig. 2). Correlation coefficients did not exceed 0.3. A low level of spawning stock was

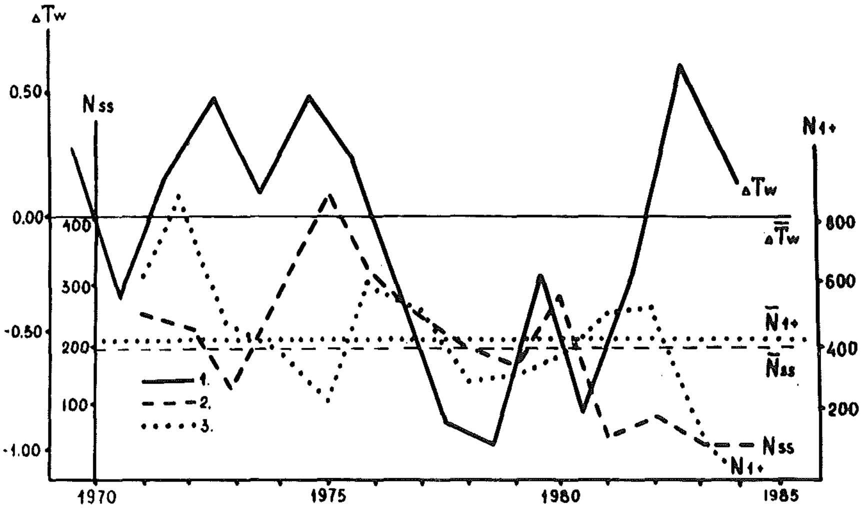

Fig. 2. The changes of water temperature anomalies, spawning stock, and fish abundance at age 1+ during 1970-1984. (1) water temperature anomalies on Kola Section, 0-200 m layer; (2) spawning stock, 10^9 ind.; (3) fish abundance at age 1+, 10^9 ind. (reduced to the year of appearance).

recorded in both warm (1973 and 1983-1984) and cold years (1978-1979 and 1981-1982). Four rich year classes came under such conditions. At the same time poor year classes appeared in 1978 (cold year) and 1984 (warm year) and an average year class in 1973 (warm year) (Table 1).

A high level spawning stock was recorded in both warm (1971-1972 and 1974-1976) and cold years (1977 and 1980). The average year class appeared only in cold 1977, all other year classes were of high abundance (ANON. 1967-1984).

The analysis of the 0-group capelin distribution patterns indicated that the effect of large scale changes in the thermal state of the sea is also manifested in the distribution of fingerlings (Figs. 3-5). For warm 1970-1976 years, the young capelin were found mainly in areas east of 25°E. When the warm period changed for cold ones during 1977-1978, the distribution range of the 0-group capelin was the smallest. After the displacement of spawning grounds

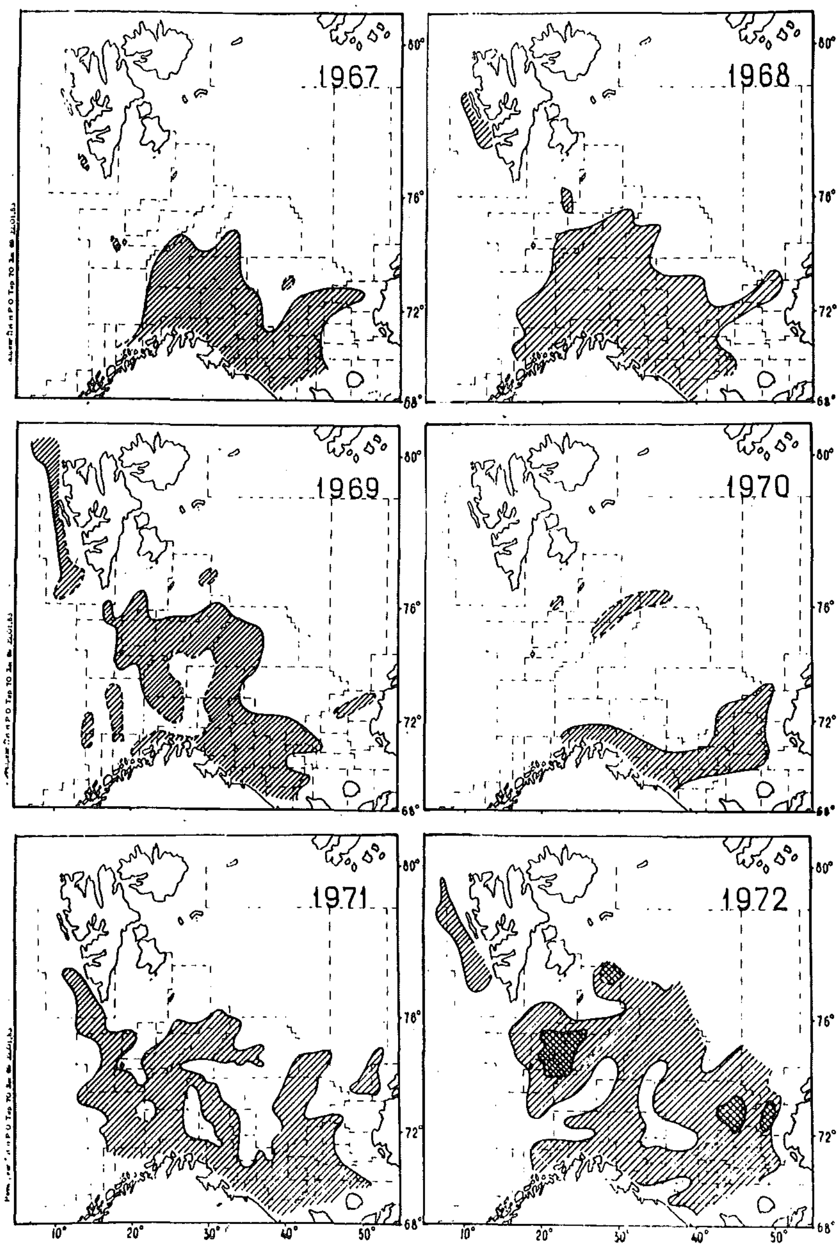

Fig. 3. The distribution of young capelin during 1967-1972 according to data from the International 0-group fish survey.

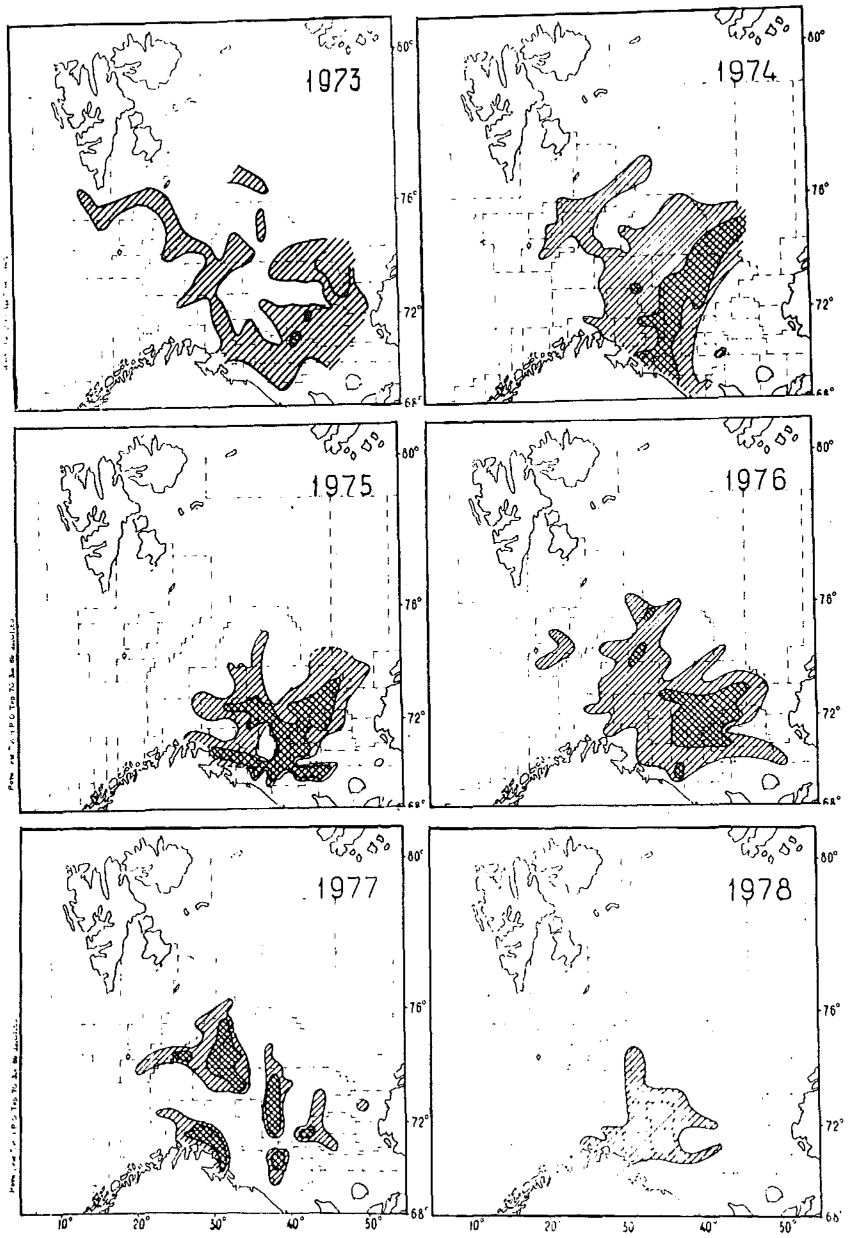

Fig. 4. The distribution of young capelin during 1973-1978 according to data from the International 0-group fish survey.

westward, the distribution area of the young was observed to expand and also shift westward. The 0-group capelin were found to be distributed over a vast area in the western Barents Sea and near West Spitsbergen after the period of cooling during 1983-1984 came to an end. Therefore, we may again speak about the inertness of biological systems.

The distribution of the young in warmer streams of currents in the western Barents Sea during 1979-1984 seemed to favour to a large extent the survival of fingerlings and the higher abundance of year classes which appeared during these years. At the same time a low level spawning stock recorded in recent years was responsible for a poor abundance of subsequent year classes.

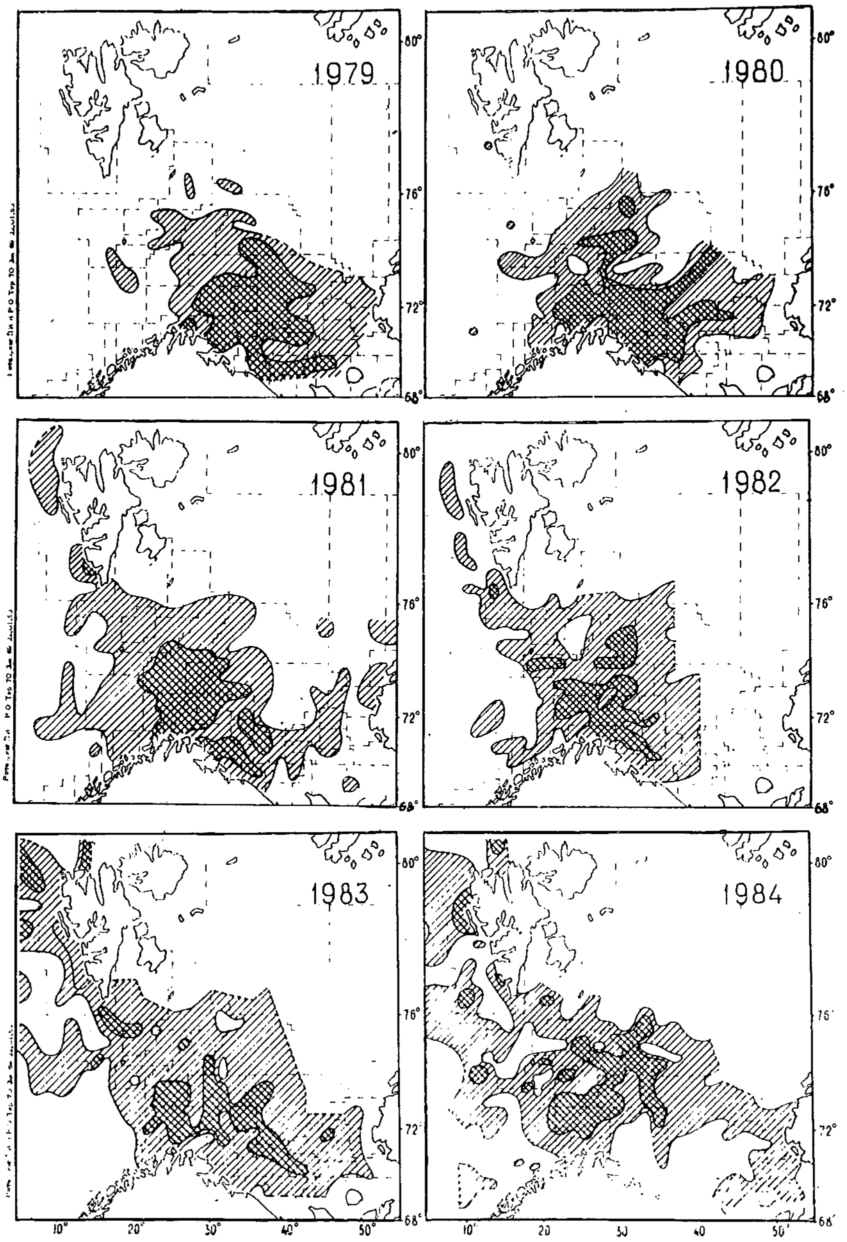

Fig. 5. The distribution of young capelin during 1979-1984 according to data from the International 0-group fish survey.

CONCLUSIONS

The analysis demonstrates that abundant year classes of capelin may appear both at low and high levels of the spawning stock as well as in both warm and cold periods. Poor year classes are more frequent in cold years and originate from low level parent stocks. However, no quantitative statistical relationship between the year class abundance and variations of oceanographic parameters and spawning stock size was discovered in the present study.

Large scale variations of water temperature in areas inhabited by capelin entail changes in the location of spawning grounds and distribution of the young, which just seems to regulate the year class abundance and eventually to determine the survival of the species under unfavourable environmental conditions. There is a 1-2 year delay in the response of fish to these influences. Year classes of scantiest number come in the periods of drastic changes in the environment, under which, the ecological adjustment of the population seems to occur.

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EFFECT OF OCEANOGRAPHICAL FACTORS ON THE ABUNDANCE OF THE BARENTS SEA POLAR COD YEAR CLASSES

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ABSTRACT

The results of the investigations carried out during 1977-1984 demonstrated that the ice coverage in the eastern Barents Sea over the polar cod spawning areas during January to June promoted a high survival of eggs and larvae during incubation and hatching.

A close relationship between the abundance of polar cod during early ontogeny and hydrometeorological factors (wind, water temperature, ice) on the main spawning grounds was elucidated by correlation analysis.

INTRODUCTION

Polar cod is one of coldwater gadoid fishes. The entire life cycle of this species is closely related to severe conditions of the Arctic. Being a typical representative of the Arctic ichthyofauna, polar cod occur in the circum-polar area and is the major species for all areas of the Arctic Ocean (KISELEV 1940, JENSEN 1948, ANDRIYASHEV 1954, BURMAKIN 1957, KRAVCHUK 1958, PONOMARENKO 1963, 1968, QUAST 1974, CHERKASOV 1976).

The adaptability of polar cod to spawning under the ice in water when favourable conditions (lack of predators, abrupt changes in temperature, sea wave, etc.) are formed for the extruded eggs promoted greatly such a vast area of fish distribution. It is known that the fecundity of this species is low, and the eggs are large and most delicate (PERTSEVA 1936, SHLEINIK 1978).

Polar cod are known to spawn in the Barents Sea from November-December to March, but mass extrusion of eggs takes place during January-February (RASS, 1934, 1941, POKROVSKY 1936, MANTEIFEL 1943). The duration of spawning varies by year and depends on oceanographic conditions (SHLEINIK 1973, SOKHNOV 1975, BORKIN 1979).

Polar cod spawning occurs at a negative temperature and, as a rule, in the presence of ice. This was first pointed out by KLUMOV (1935), and others later on (MANTEIFEL 1943, YUDANOV 1976, PONOMARENKO 1964, ALTUKOV 1979). Eggs are extruded and fertilized pelagically after which they gradually ascend to the surface layers (ALTUKHOV et al. 1958, PONOMARENKO 1964, ALTUKHOV 1979). In case the ice is present in spawning areas, eggs become accumulated under it, and incubate for a long time (2-5 months).

The freezing of polar cod eggs in the laboratory has always resulted in inviability. Under natural conditions, however, a close to zero buoyancy prevents eggs from freezing within ice. The lower surface of ice in the sea is not smooth, but represents an extremely heterogeneous ice formations different in shape and structure (RYBAKOV 1981).

Larvae hatch from April to July (KAZANOVA 1949, BARANENKOVA, PONOMARENKO and KHOKHLINA 1966, RASS 1968, ALTUKHOV 1979), however, during May-June it is most intensive. Our investigations throughout a number of years (1977-1984) indicate that the hatch of polar cod larvae occurs during the destruction of ice, and its intensity has a direct relationship to the sea temperature. The analysis of the age-length composition of larvae indicates that larvae of minimum length (4-6 mm; BORKIN 1980, 1981, 1983) were always caught in the zones of the ice edge and broken ice during spring. Under experimental conditions the age of such larvae would amount to 1-5 days (MAKHOTIN 1982).

During the first days of life, larvae are distributed in the 0-5 m surface layer. When developing, they descend to the 5-10 m layer, and to 20 m or rarely to 30 m later on (SEKERAK 1982, BORKIN 1983, 1984a, 1984b). During August, a considerable portion of the larvae enter the stage of fry. At the end of a month, most fingerlings are distributed at 20-30 m. During September, they are abundant at 30-40 m to 50 m depths and sometimes deeper.

Thus, at the first stage of their existence, the survival of polar cod eggs depends, to a large extent, on water temperature and ice regime. At the second stage (larvae and fry) the formation of the polar cod abundance may be greatly determined by a direct effect of such environmental parameters as wind waves and water temperature.

MATERIAL AND METHODS

The data for the ichthyoplankton surveys were obtained in the east of the Barents Sea during 1977-1984. In addition, materials of the International 0-group surveys of the Barents Sea commercial fishes conducted during August-September were used (Table 1).

Table 1. Indices of polar cod abundance and hydrometeorological parameters in 1977-1984

Year	No. of larvae, 10^9 ind.	0-group index (ANON. 1984)		No. of days with wind over 10m/s in SE of the sea (June)	Surface temp. at Northern Kolguev station °C(July)	Ice cover, % (68-70°N 40-60°E), Jan-June
		west of the sea	east of the sea			
1977	773	157	70	10	8.0	61.2
1978	1474	107	144	6	2.9	70.7
1979	-	23	302	5	1.6	90.2
1980	-	79	247	2	4.0	62.3
1981	-	149	73	4	5.2	74.2
1982	808	14	50	10	6.5	67.0
1983	342	48	39	10	7.3	61.3
1984	107	115	16	12	9.2	45.7

For the first years of investigations (1977-1978), the surveys were conducted between April and August to determine the duration of appearance of the polar cod larvae in ichthyoplankton, and the optimal period for performing the investigations. Because of difficult ice conditions during the summer of 1979, the larval survey failed. For 1983-1984, a vast part of the Barents Sea, from the Novaya Zemlya Islands, to the West Spitsbergen, was covered by ichthyoplankton surveys.

Spatial distribution of larvae was analysed by the catches of the IKS-80 egg net made of kapron gauze No. 140 with an 80 cm diameter. At each station, vertical tows in the layers of 50-0, 30-0 and 20-0 m, as well as in the layers of 0-3 and 10-15 m, were made during 10-minute circulation of the ship. To determine the vertical distribution of larvae by layers, a number of tows were made at separate stations for different depths from 80-50 m to the surface. During fishing for larvae, the speed of the trap net was 1-1.2 m/s. Larvae were fixed in 2% formalin. Lengths were measured with an accuracy of 0.1 mm.

When plotting charts of larval distribution by densities, a standard method of isolines (AKSYUTINA 1970) was used. Mean-weighted abundance of larvae for each station was calculated according to the formala:

$$N_o = \frac{N_v \cdot h + N_h \cdot L}{h + L} \qquad (1)$$

where N_o - abundance of larvae per area unit (ind•m^{-2}) at each station;

N_v - abundance of larvae per area unit during vertical fishing (ind•m^{-2});

N_h - abundance of larvae per area unit during horizontal fishing (ind•m^{-2});

h - layers of fishing during a vertical tow (m);

L - distance covered during horizontal fishing (m).

Estimation of larval abundance at each station during horizontal and vertical fishing was made after the formulae:

$$N_v = \frac{N}{S \cdot K_f} \qquad (2)$$

$$N_h = \frac{N}{V \cdot K_c \cdot K_f} \qquad (3)$$

where: N - amount of larvae per haul (spec.);

S - area of net opening (m^2);

K_c - fishing efficiency of nets (0.8 ± 0.1);

K_f - coefficient of net filtration (0.62) (SHAPIRO 1971);

V - volume of water filtered during horizontal fishing (m^3).

When analysing larval abundance by years, the indices for 1980-1981 were excluded because they were not representative. This is because during 1980, while carrying out the ichthyoplankton survey during late June, an extremely intensive phytoplankton bloom was encountered. The egg nets became constantly clogged with phytoplankton which yielded rather low efficiencies for the IKS-80 net. During 1981, the survey was conducted too early so that it was impossible to determine the area of main concentrations, as well as the total range of larvae. Therefore, the data for 1980-1981 were not used for statistical processing.

To estimate the abundance of fingerlings, 0-group indices during August-September were used (ANON. 1984). The data on water temperature in the surface layer at the Northern Kolguev Station were used to estimate the thermal state of water in the area of the main polar cod spawning grounds.

Polar cod eggs are also exposed to a mechanical effect from a strong sea wave activity. Therefore we considered the number of days during which the wind was over 10 m/s for a particular month in the southeast of the sea (a number of stormy days). This data was based on the data from Murmansk Territorial Administration on Hydrometeorology and environmental Control as an indirect index of the dynamical state of the sea. Ice cover in the southeast of the sea in the first half of the year (as calculated in % for the area between 68-70^{o}N and 40-60^{o}E) was regarded as a factor protecting the polar cod eggs from the mechanical effect of the sea wave.

RESULTS

Taking into consideration the duration and relative stability of the effect produced by environmental factors on polar cod during their early ontogeny, we tried to determine the degree of their effects on the year class strength.

First, the effect of temperature was considered. It was observed that abundant year classes of polar cod larvae appeared, as a rule, during cold years. Long term investigations of 0-group fish during August-September (ANON 1977-1985) indicated that the abundant year classes of fingerlings were distributed over a vast area for cold years. In contrast, the areas of hatching, and respectively, the ranges of larvae and fingerlings moved to the east for warm years (Figs. 1, 2, 3 and 4).

The statistical analysis showed that the abundance of polar cod larvae correlates mostly with water temperature at the Northern Kolguev Station in July (r= -0.91)*. The index of polar cod 0-group abundance (r=0.87) correlates well with water temperature during July.

The wind produces indirectly a mechanical effect on organisms by generating waves (BERNIKOVA 1980). According to calculations, the correlation between the number of stormy days in the southeastern sea in June and the abundance of larvae is rather significant (r=-0.93). The formation of polar cod abundance at the 0-group stage apparently depends on the sea wave regime as well. The correlation between the number of days with the wind over 10 m$\cdot$s^{-1} in June and the number of fingerlings in August-September constituted -0.76 (Table 2).

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* The coefficients of correlation between the larval abundance and hydrometeorological indices are valid at p=0.05, if they exceed 0.88. For the indices of abundance at the 0-group stage at the same level of validity they must exceed 0.71.

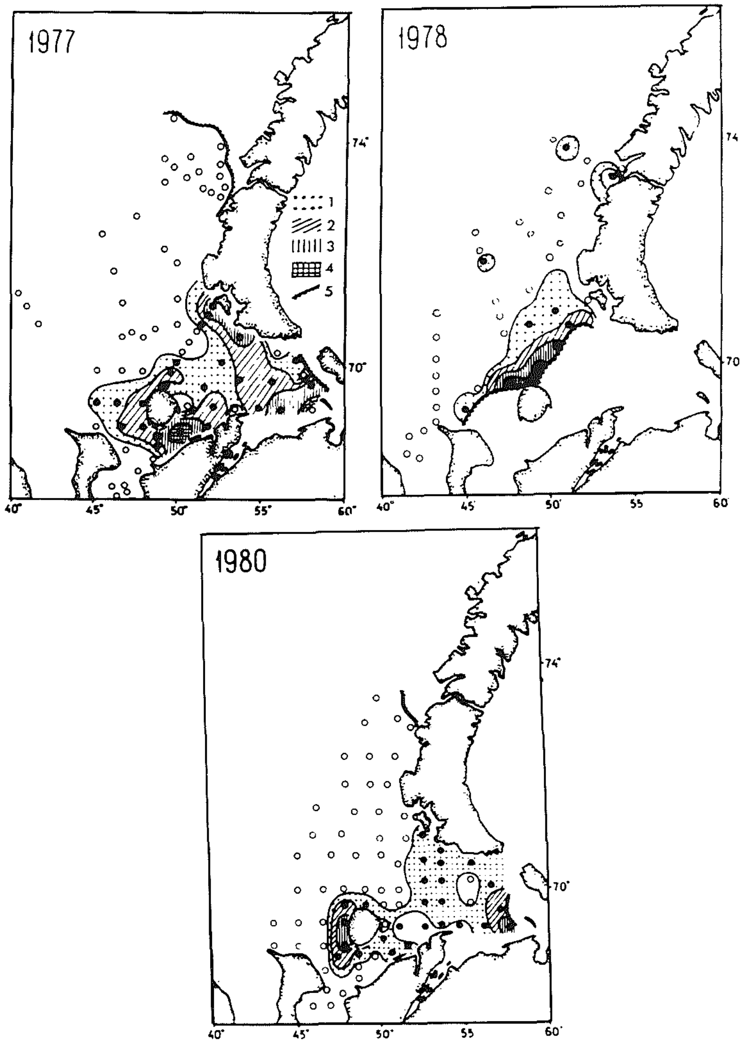

Fig. 1. Distribution of polar cod larvae in June-July 1977-80.
1) 0.1-1.0 ind•m^{-2}
2) 1.1-10.0 ind•m^{-2}
3) 10.1.-100.0 ind•m^{-2}
4) over 100.0 ind•m^{-2}
5) ice edge.

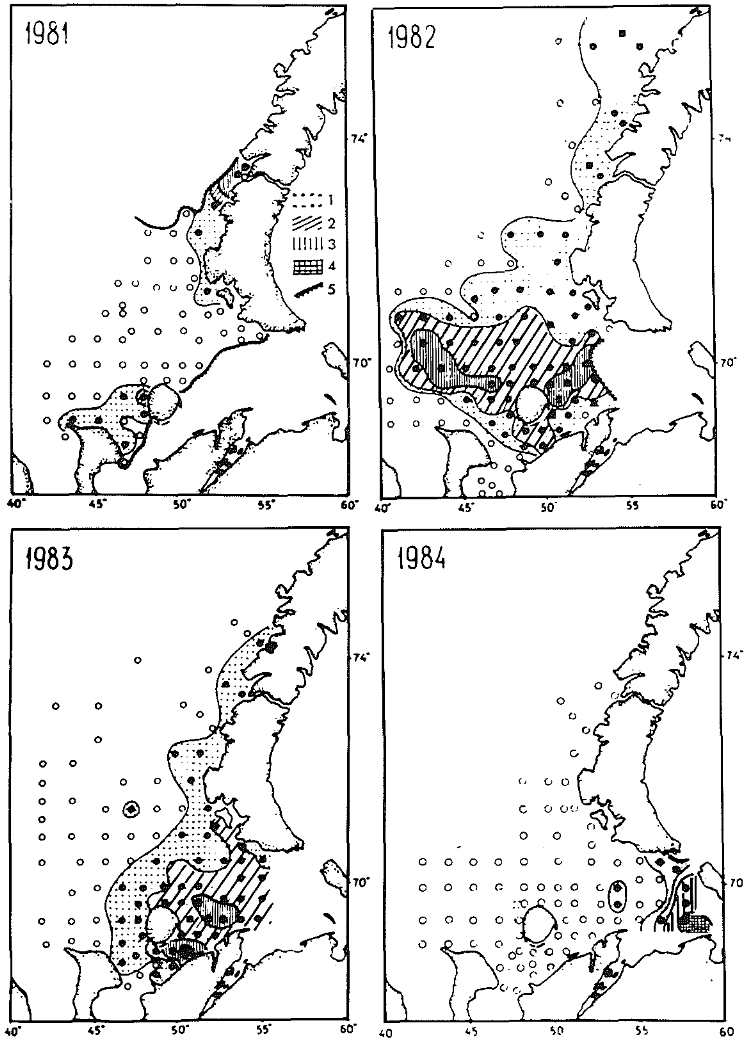

Fig. 2. Distribution of polar cod larvae in June-July 1981-84.
1) 0.1-1.0 ind•m^{-2}
2) 1.1-10.0 ind•m^{-2}
3) 10.1.-100.0 ind•m^{-2}
4) over 100.0 ind•m^{-2}
5) ice edge.

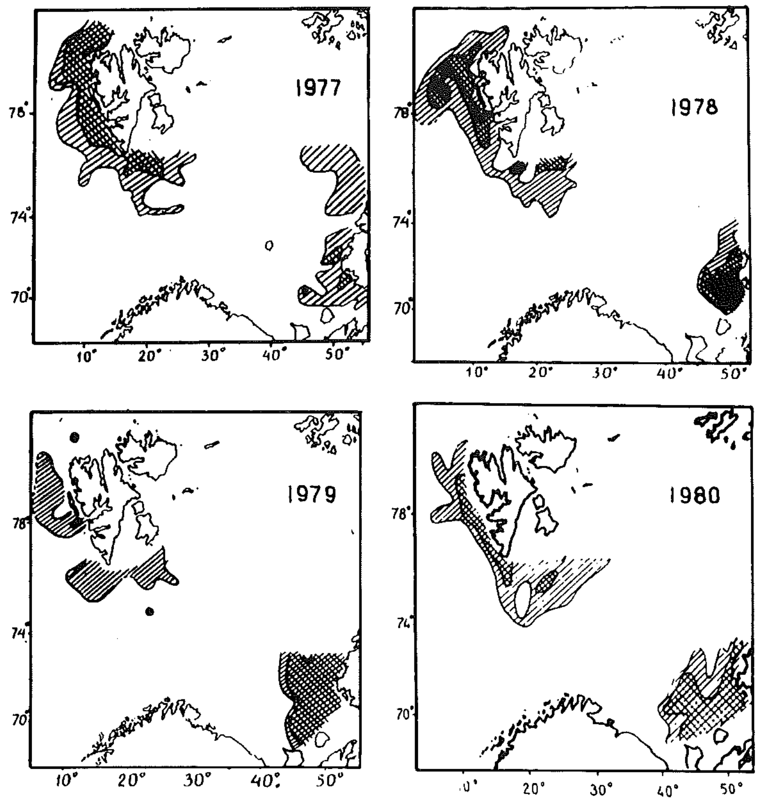

Fig. 3. Distribution of polar cod fingerlings in 1977-1980 according to the data from the International 0-group fish survey.

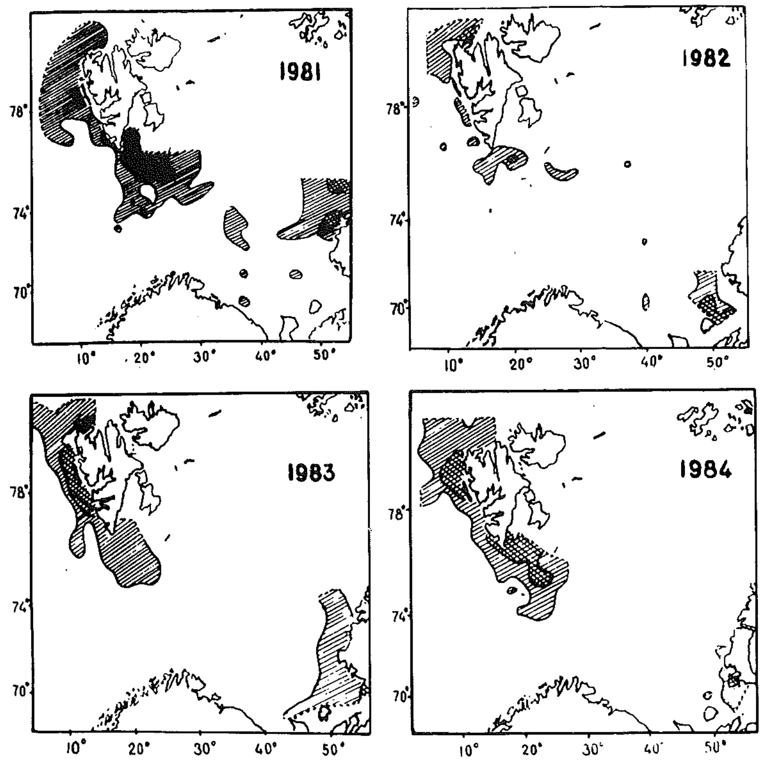

Fig. 4. Distribution of polar cod fingerlings in 1981-1984 according to the data from the International 0-group fish survey.

The ice cover may also be important for the survival of the early developmental stages of polar cod. Frequent storms are known to occur often during spring. Thus, the probability of egg or larval death increases essentially with the destruction of ice in the spawning areas. A heavier ice cover promotes both the survival of polar cod during the earliest stages of life, and the high abundance of their year classes. Ice cover in the southeast of the sea during the first half of the year became the most important effect of ice on the appearing year class abundance. The effect of this index on the abundance of polar cod year classes proved to be rather significant. The correlation for this was, with the larval period, 0.86, and for the stage of fry, equal to 0.68 (Table 2). Thus, ice cover, wind and water temperature are the main environmental factors which determine the formation of polar cod abundance during their early stages of development.

Table 2. Correlation coefficients between young polar cod abundance and hydrometeorological parameters in the southeastern Barents Sea.

Parameters of environment	Indices of abundance	MONTH				
		I-VI	V	VI	VII	VI+VII
No. of days with the wind over 10 m/s	larvae	-	-0.39	-0.93	-0.61	-0.84
	0-group	-	-0.20	-0.76	-0.40	-0.66
Temperature at the sea surface	larvae	-	-	-0.74	-0.91	-0.94
	0-group	-	-	-0.14	-0.87	-0.76
Ice cover, %	larvae	0.86	0.80	0.77	-	-
	0-group	0.68	0.45	0.50	-	-

Annual international investigations of the 0-group commercial fishes in the Barents Sea indicate that isolated ranges of young polar cod in the Northwest and southeast of the sea are steadily preserved throughout a number of years (ANON. 1977-1984). The results of ichthyoplankton investigations carried out during 1983-1984 also indicate the independence of two ranges of polar cod larvae off the Novaya Zemlya and West Spitsbergen, thus indirectly proving independent spawning grounds (Figs. 5 and 6).

It should be noted that the problem of a self-reproductive polar cod group in the northwest of the Barents Sea was partially considered by some investigators (MOSKALENKO 1964, PONOMARENKO 1968, HOGNESTAD 1968). However, the facts proving most convincingly the existence of an isolated population off Spitsbergen were presented quite recently (GJØSÆTER 1973, BORKIN 1984a, 1984b, 1985).

The analysis of indices of the 0-group polar cod abundance calculated for each of these areas testifies to the existence of a definite phase opposition in the year class abundance. During the years for appearance of abundant year classes off the Novaya Zemlya, the number of fingerlings off Spitsbergen, as a rule, were at a low level and vice versa (Fig. 7).

The reason for phase opposition lies, apparently, in the peculiarities of heat redestribution due to the streams of the Atlantic waters between the western and eastern parts of the sea.

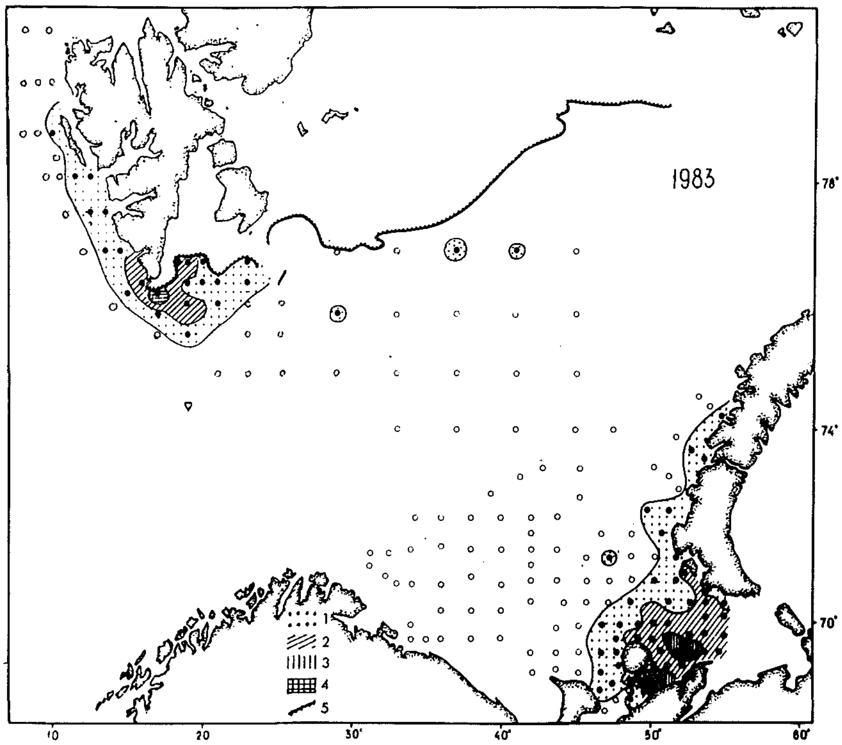

Fig. 5. Distribution of polar cod larvae in the Barents Sea in 1983. For symbols see Fig. 1.

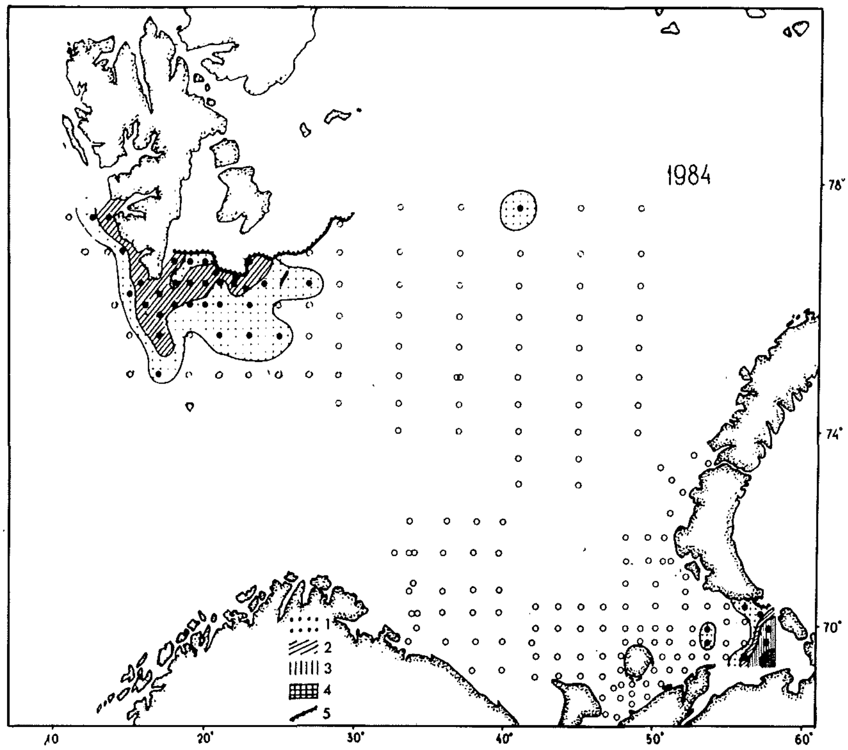

Fig. 6. Distribution of polar cod larvae in the Barents Sea in 1984. For symbols see Fig. 1.

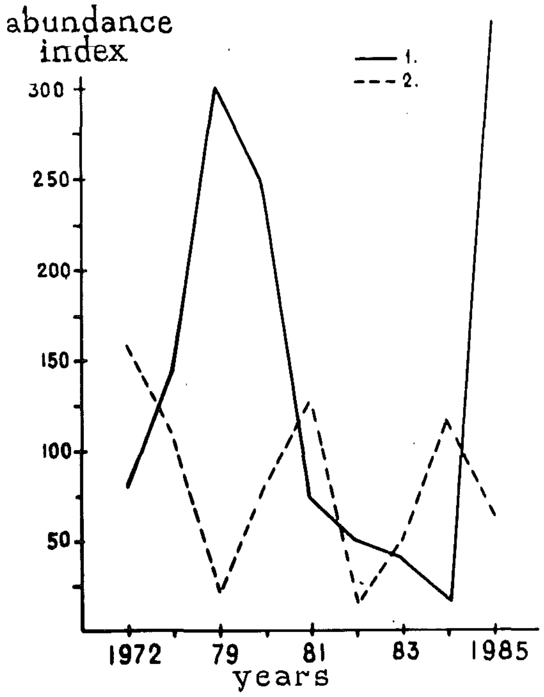

Fig. 7. Indices of polar cod abundance in the eastern (1) and western (2) Barents Sea according to the data from the International 0-group fish survey.

CONCLUSIONS

A number of hydrometeorological factors, variations of which rather closely depend on the fluctuations in abundance of polar cod year classes were elucidated by correlations analysis. A direct relationship between the ice coverage on the southeast of the sea during January-June and the indices of the abundance of young polar cod at the stages of larvae and fry was determined. This gave reason to conclude that the availability of ice in spawning areas throughout the period of egg incubation played a protective role. During the post-spawning period, ice serves as insulation to temperature which prevent eggs from overcooling, while during the period of larval hatch, it protects them from a mechanical effect of the sea wave.

During June, when mass hatching of larvae is usually observed, sea waves affect the abundance of the young polar cod. Wind force can be used as an indirect index of sea wave action. A close inverse relationship between the number of days with the wind speed over 10 m/s in the southeast of the sea during June and the indices of abundance of polar cod larvae and fry was detected. For the years with higher recurrences of strong wind in the spawning areas, the reduction in abundance of polar cod year classes was registered. In contrast, abundant year classes were found for the years with low indices for strong winds.

The close relationship between the abundance of polar cod and the thermal state of the sea indicates that during the post-hatching period (July), water temperature becomes important. When the temperature of the surface layer of the spawning grounds rises to 6-8°C during July, a great decline in the abundance of young polar cod was found. Thus, the year classes of polar cod are formed during the egg incubation under the influence of ice, under that of sea wave action during the hatch, and under that of water temperature during the first months of larval life.

The analysis of the abundance of polar cod year class in the northwest and southeast of the sea confirmed the availability of phase opposition in fluctuations of the young fish abundance. With the appearance of abundant year classes in the east of the sea off the Novaya Zemlya, the reduction of the abundance of young polar cod is usually registered at the western part off Spitsbergen. The causes for phase opposition will be the object of future investigations.

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THE EFFECT OF OCEANOGRAPHIC CONDITIONS ON DISTRIBUTION AND POPULATION
DYNAMICS OF COMMERCIAL FISH STOCKS IN THE BARENTS SEA
Proceedings of the third Soviet-Norwegian Symposium, Murmansk, 26-28 May 1986
Edited by H. Loeng. Institute of Marine Research, Bergen, 1987.

DISTRIBUTION AND BEHAVIOUR OF DEMERSAL FISHES IN THE BARENTS AND NORWEGIAN SEAS, AND THE FACTORS INFLUENCING THEM

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ABSTRACT

The results of the Soviet investigations carried out in 1978-83 for assessing the young fish abundance and demersal fish stocks in the Barents and Norwegian Seas are summarized and analysed. The influence of temperatures, year-class strength, length-age composition of populations and rate of maturation on cod and haddock distribution in April/May of cold years is discussed.

INTRODUCTION

The distribution of cod and haddock in the Barents and Norwegian Seas with respect to the environment, year class strength, age composition, and rate of maturation, has been dealt with in a number of papers (MASLOV 1944, 1968, KONSTANTINOV 1964, MILINSKY 1967, SONINA 1969, MARTI 1980, LEE 1952, MIDTTUN 1965). The interaction of these factors formed peculiarities for individual year classes by affecting both the trophic and reproductive milieu and thus contributed to the survival of the species as a whole.

In the present paper the distribution of the 1974-1981 cod and haddock year classes during April/May 1978-83 was analysed. These years were characterized by the decreases from the average level of 2.5 mill. tonnes to the minimum level of 0.8 mill. tonnes in commercial stock of cod, and from 300 to 120 thousand tonnes for haddock (ANON. 1985). Cod and haddock stocks were recruited in 1978-83 with one rich and five below average to poor year classes. The spawning stock of these species was at a very low level, especially during 1979-81.

MATERIAL AND METHODS

The data on distribution and age composition of cod and haddock were collected during the course of trawl surveys carried out in the southern Barents Sea and adjacent waters of the Norwegian Sea during April/May 1978-83. The methods and results of trawl surveys were published by SHEVELEV (1981, 1983, 1984, 1985).

In the present paper the "limit" of cod and haddock distribution is given as the position of a line of catches equal to 1 spec. per trawling hour. All estimates of the cod and haddock year-class strength as well as those for heat content of water masses cited in this paper, apply to the southern Barents Sea (Subarea I).

The qualitative assessments of abundance of the 1974-1979 and 1981 cod and haddock year classes at the age of 3 were given according to a 7-division scale (MELYANTSEV and SALMOV 1985). Taking into account an increased growth rate, the assessment of abundance of the 1980 cod year class was revised from "poor" to "below average". Mean catches of 3 year old cod and haddock per trawling hour were published in Annales Biologiques (MELYANTSEV 1986). The data on water temperature in the 0-200 m layer at standard sections of the southern Barents Sea in 1978-83 were used. The water heat content was estimated according to a 5-division scale. Mean values of water temperature for 1951-80 were assumed to be the normal.

RESULTS AND DISCUSSION

The heat content in the southern part of Barents Sea was at a low level in 1978, 1979 and 1981, with the water temperature in the 0-200 m layer of the North Cape and Murman Currents being 0.7-1.5°C below normal. During 1980 and 1982, the water temperature of these currents was at, or somewhat below normal. The year 1983 may be classified as warm. The water temperature of the North Cape and Murman Currents was by 0.5-0.9°C above normal. The heat content of the 0-200 m water layer at Kola Meridian section for the first half of the years 1978-83 is given in Table 1.

During April and May, cod and haddock occurred in wintering and spawning areas distributed along the jets of these currents. They were found widely scattered in the streams where the water temperature was most favourable.

Table 1. Abundance and position of the eastern limit of distribution* of the 1974-1980 year classes of cod and haddock at various ages in May 1978-83.

Year class	Cod							Haddock					
	3 year olds				6 year olds			3 year olds			5 year olds		
	Mean catch, ind./hour	Abundance assessment	Heat content, I half	East limit, °E	Mean catch, ind./hour	Heat content, I half	East limit, °E	Mean catch, ind./hour	Abundance assessment***	East limit, °E	Mean catch, ind./hour	Heat content, I half	East limit, °E
1	2	3	4	5	6	7	8	9	10	11	12	13	14
1974	6	-average			1	N 1980	34	14	average		1	-C 1979	32
1975	93	+rich	C 1978	41	3	-C 1981	33	59	rich	38	10	N 1980	36
1976	4	-average	-C 1979	34	<1	C 1982	27	4	poor	34	3	-C 1981	33
1977	2	-average	N 1980	35	<1	W 1983	25	<1	-poor	34	<1	C 1982	32
1978	1	poor	-C 1981	34				1	-poor	34	<1	W 1983	18
1979	<1	-poor	C 1982	34				<1	-poor	34			
1980	1/7**	-average	W 1983	36				<1	-poor	34			

*Eastern limit of distribution area are given with an accuracy of 1°

**In the numerator - the mean catch is calculated according to standard methods (only for fishes below 36 cm), in denominator - the mean catch is calculated with help of summarized series and age samples of young and adult fishes.

***The water heat content in 1978-83 for 3 year old haddock coincided with that given in column 4: -C=abnormally cold, C=cold, N=normal, W=warm.

For cold years, only cod of the poor year classes, but haddock of all year classes wintered in the Barents Sea. A local grouping which preferred the northwestern coast of Norway were distributed along the main branches of the North Cape and Murman Currents (Fig. 1). The smaller the abundance of a year class or age group, the more discrete and close to the northwestern coast of Norway were they found (Figs 1, 2 and 3). This was most pronounced for haddock of older age groups, the bulk of which was distributed in the territorial waters of Norway in cold years and inaccessible during the survey.

Cod of nearly poor 1976 year class older than 3 years were during April and May 1978-83 distributed along the northwestern coast of Norway in a zone varying from 200 nautical miles (nm) in the west to 120 nm in the east. Haddock of the rich 1975 and poor 1976 year classes older than 2 years were distributed in a zone from 80 to 110 nm off the Norwegian coast. The presented indices were stable and did not change during the short-term variations of temperature (Fig. 1 b, c).

The eastern limits of distribution for different sized cod and haddock year classes during May of cold years are given in Table 2 which indicates that the fishes of numerous younger age groups were the most widespread in the Barents Sea. The wintering area shifted westward as the fish grew older, to become the spawning area. The extent of this displacement depended on a variety of factors, such as heat content of water masses and rate of growth

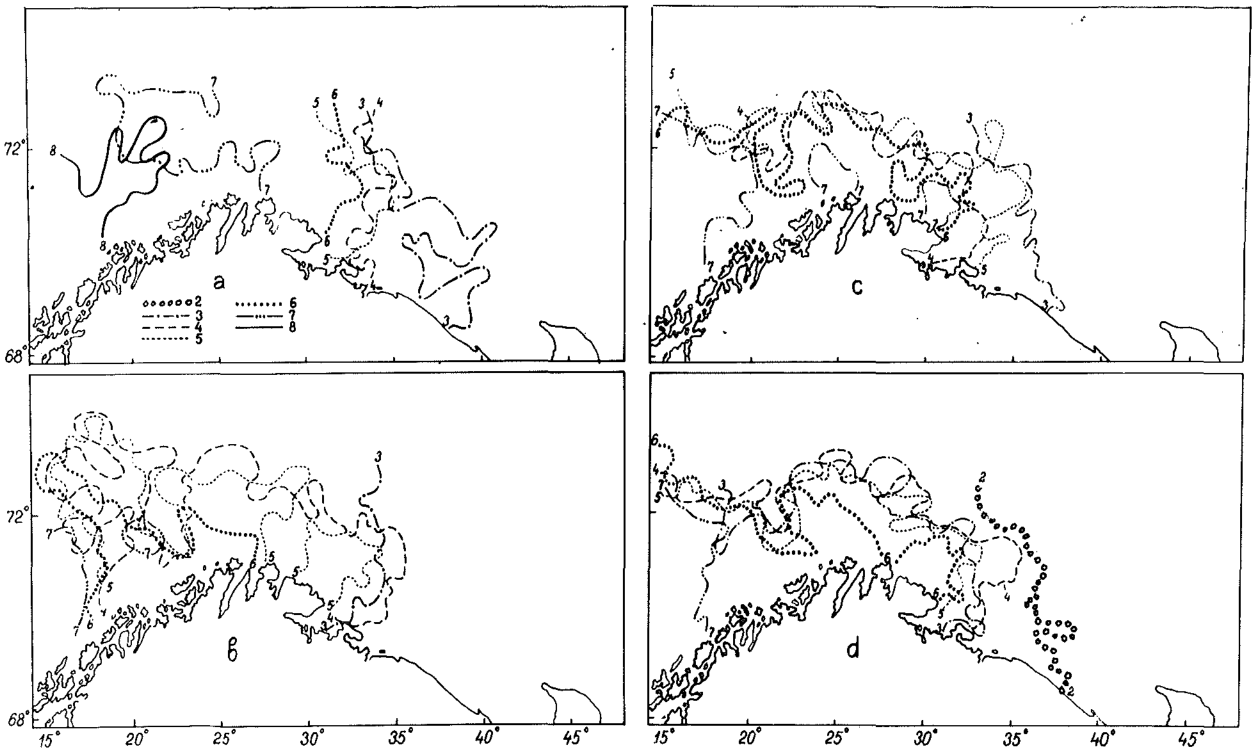

Fig. 1. Distribution of different sized year classes of cod and haddock at various ages (2-8) during April and May 1978-83.

(a) the 1975 year class of cod, very rich;
(b) the 1976 year class of cod, below average;
(c) the 1975 year class of haddock, rich;
(d) the 1976 year class of haddock, poor.

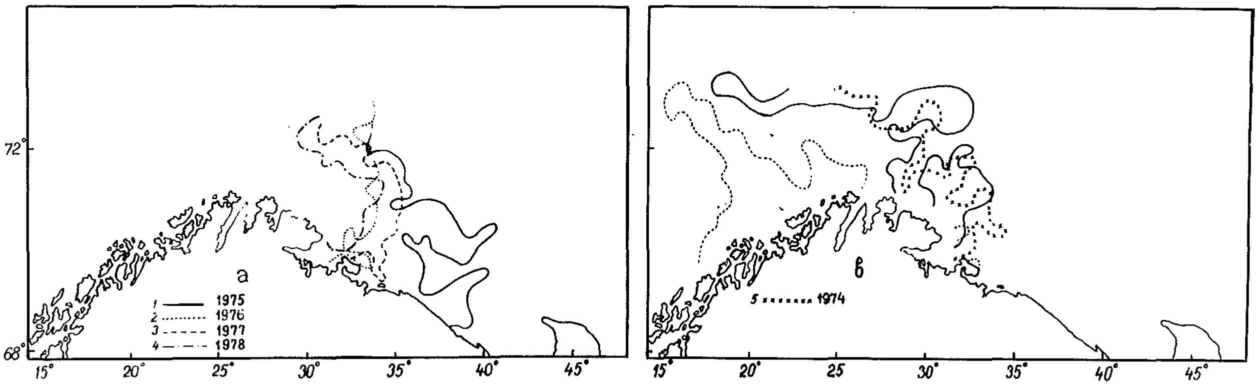

Fig. 2. Distribution of different sized year classes of cod at the age of 3 (a) and 6 (b) during April and May 1978-82.

(1) very rich;
(2) below average;
(3) below average;
(4) poor;
(5) below average.

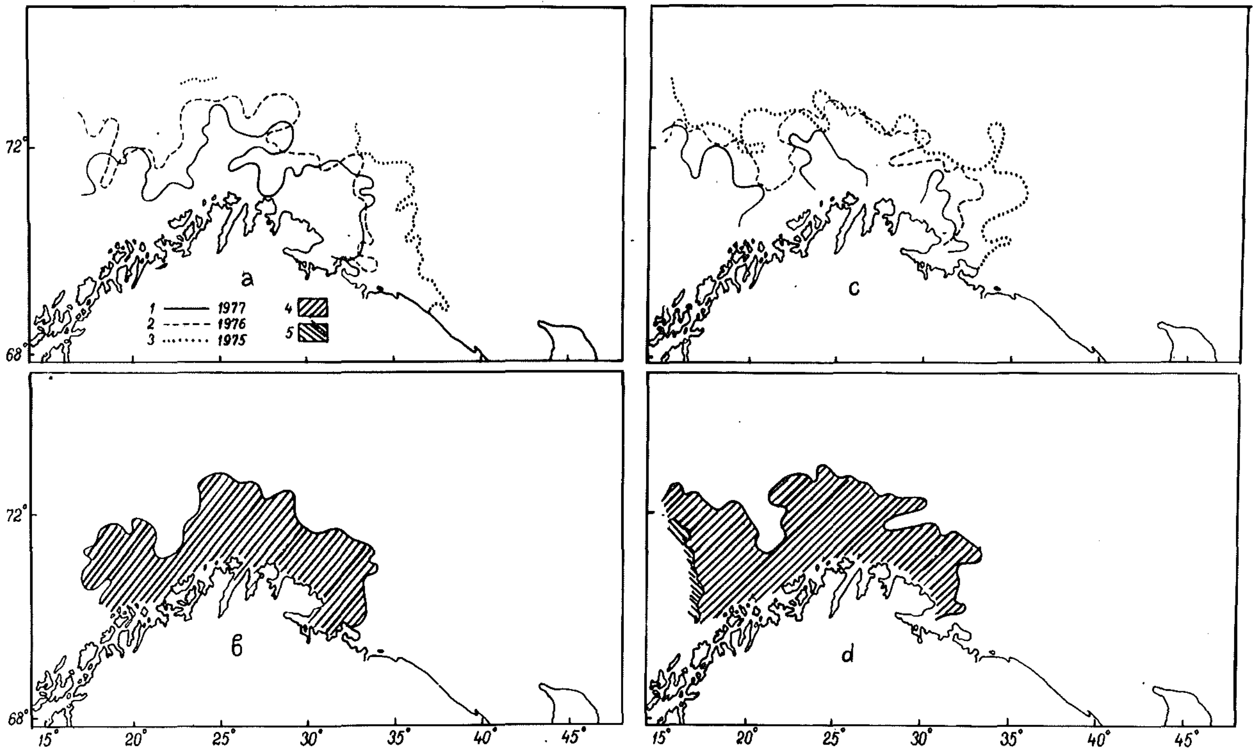

Fig. 3. Distribution of different sized year classes of haddock at the age of 3 and 5 during April and May 1978-82.

(a) different sized year classes at the age of 3;
(b) poor year classes at the age of 3;
(c) different sized year classes at the age of 5;
(d) poor year classes at the age of 5.
(1) very poor year class;
(2) poor year class;
(3) rich year class;
(4) wintering area of poor and nearly poor year classes;
(5) distribution of very poor 1978 year class at the age of 5.

Table 2. Eastern limits of distribution of different sized cod and haddock year-classes at various age in May of cold years.

Age, years	Cod		Haddock	
	Very rich 1975 year-class	Below average 1976 year-class	Rich 1975 year-class	Poor 1976 year-class
2				39°E
3	41°E	34°E	38°E	34°E
4	35°E	36°E	34°E	36°E
5	35°E	34°E	36°E	33°E
6	33°E	27°E	33°E	32°E
7	29°E	22°E	21°E	19°E
8	22°E			19°E
Average annual west displacement in nautical miles of wintering areas with increasing age	76	64	76	80

and maturation (MASLOV 1944, SONINA 1969, LEBED, PONOMARENKO and YARAGINA 1983, SÆTERSDAL and LOENG 1984).

The eastern limits of wintering area of 3 to 7 year old cod and haddock were displaced westerly with increasing age, with an average of 60 and 40 miles per year for cod and haddock respectively. The maximum displacement of wintering area was observed for fishes of the younger age groups (Fig. 1, Table 2).

Cod and haddock began to mature and migrate to spawning areas at the age of 6 and 7 years, with haddock maturing earlier than cod (MASLOV 1944, SONINA 1969).

The maximum westernly migrations for rich cod and haddock year classes were observed at the age of 7 or 8. Those of poor years were at the age of 6 or 7 years and was an indirect characteristic of an acceleration in maturation rate. Similar phenomenon have been mentioned by others (SONINA 1969, PONOMARENKO, PONOMARENKO and YARAGINA 1985).

The rate of maturation of different sized cod year classes (that of poor ones in particular) increased in 1982-84 compared to the 1960s and 1970s (Table 3). Fifty percent of the cod matured formerly at the age of 8 or 9 years (PONOMARENKO et al. 1985). Beginning from 1982, the portion of mature fishes increased in all the age groups, the 50% maturation was observed at the age of 7 or 8 years, and at the age of 6 or 7 years in 1983. The growth rate of cod was unusually high in 1982 and 1983 (LEBED and PONOMARENKO 1985) which resulted from scattering of the population, a better food supply, and perhaps, from the selective influence of an intensive fishery on the cod population structure (BORISOV 1978).

With the fish age increasing from 3 to 8 years, the cod year class migrated west on the average by about 80 nm per year. Fish of rich year classes migrated slower than of poor ones. This was accounted for by both the regulating influence of high abundance and maturation rate which was lower in rich year classes than in poor ones.

At first appearance it seemed that the rate of western displacement of the poor 1976 cod year class did not agree with our hypothesis (Table 2).

However, this discrepancy was due to lack of data on the fish distribution of this year class at 8 years. The rate of west migration of the 1975 cod year class at the age of 3 to 7 years was 60 nm, and that of the 1976 year class 64 nm. Thus, distribution and position of wintering areas for cod and haddock depended on abundance, age composition and maturation rate of the year classes which formed the population.

The effect of water temperature on the rate of west displacement of wintering area with respect to an increased fish age may have been observed in 1980 in the southern Barents Sea. The first half of that year was close to normal and much warmer than the first half of 1979, which was estimated as very cold (Table 1). As a result of the rise in water temperature, the cod of the rich 1975 year class did not migrate west in 1980, but stayed in those areas where they had wintered at the age of 4 (Fig. 1 a, Table 2). The wintering areas for the 1976 cod and haddock year classes at the age of 4, and the 1975 haddock year class at the age of 5, were located 40 miles further east than the wintering areas of these year classes when of the age of 3 and 4 (Fig. 1 b, c, d, Table 2). The similar response of other cod and haddock year classes of younger age groups to the change of water masses heat content may be followed in Figs 2 and 3.

The effect of water temperature on the distribution of fishes older than 6 years was not demonstrated from our data. So, despite the fact that 1983 was warm, during April and May, nearly all the fishes above the age of 6 years were distributed in the western marginal area of the Norwegian Sea near the spawning grounds (Fig. 1, Table 2). The physiological state of a fish, in particular the maturity of gonads, seemed to be a decisive factor for this age and during this season (Table 3). Accordingly, the distribution of cod and haddock during April and May depended on the water heat content, year-class strength, size-age composition and physiological state of fishes.

The stock size and distribution of spawning capelin (the main food item of cod and, to a lesser extent, of haddock during spring) were also of great importance. During 1979-83 capelin approached the coast further west and at earlier periods than usual. Cod fed most intensively on capelin from February to April off the coast of Norway and Murman (from the Fugløya to Rybachya Bank; YARAGINA 1984, 1985) which favoured the migration of cod further west. Capelin were of little significance to feeding haddock for that period.

Table 3. Maturation of cod year-classes (% of mature fishes at different age) (after PONOMARENKO 1984, LEBED and PONOMARENKO 1985).

Year-class	Age, years					
	5	6	7	8	9	10
1973	0.7	5.3	9.0	35.5	73.2	95.5
1974	0.9	2.1	17.2	56.2	64.7	100
1975	0.4	6.1	46.2	59.8	98.9	100
1976	2.0	26.3	50.0	89.5	91.6	
1977	10.8	20.1	55.9	85.4		
1978	7.1	31.4	58.6			
1979	18.4	32.6				
1980	9.6					
Portion of mature fishes at different age for 1959-81	2.0	5.6	15.9	36.8	61.0	79.3

The distribution of haddock differed from that of cod by being further west, and more in the coastal areas. In addition, the haddock had a quicker displacement toward west compared to cod with an increasing age of fish.

It follows from the data presented in Figs 2 and 3 and in Table 1 that during April and May of cold years, the wintering areas of poor to nearly poor year classes of cod and haddock at 3 years were located west of 34°E, and partially coincided with each other. As far as the comparison of various data permitted, the wintering areas of haddock during 1978-83 were located slightly farther west compared to the 1950s and 1960s (SONINA 1969). That was indicative of a continued western displacement of the species range during the 1970s and 1980s. With the rise of the year class abundance or water temperature, however, the distribution range was expanded eastward. In our opinion, interspecific differences of cod and haddock relative to the heat content of the Barents Sea were characterized by exceptions from this rule. Thus, in the course of the short-term rise of water temperature in 1980, the 1977 cod year class, despite a smaller abundance than that in the 1976 year class, expanded its range compared to the latter one.

Regardless of warming, haddock of the 1977 year class at the age of 3 years did not change their wintering areas (Figs 2 and 3, Table 1). A similar response occurred for the 1980 cod and haddock year classes with respect to the variation of temperature during 1983 which was warm.

It may be concluded that cod responded to the water temperature variations faster than haddock. This is deduced from the immediate changes of cod wintering areas while this was not apparent for haddock. To explain these differences, the following working hypothesis is proposed. The interspecific differences in time response to the changes of water temperature occurred as a response to the food supply. Cod feed mainly on organisms (necton) which respond quickly to changes of environment. The main item of the haddock diet is benthic, which changes under the ambient environmental conditions.

Thus, in addition to the factors directly influencing the population at each moment, the indirect effect of environment also took place during the course of a year class life cycle. For our data, this was apparent as a sluggish pattern of distribution of the population in space despite the variations of temperature.

CONCLUSIONS

Since the problem was large and involved many aspects, both the volume of data analysed and the range of questions under study had to be restricted. Nevertheless, a number of examples demonstrated a dependence of distribution for cod and haddock on the abundance, age composition of population, maturation rate, and temperature conditions in the course of the year class life cycle. These examples agreed and supplemented other investigations.

The effect of the environment on the population and its range is complex. It is impossible to point out a universal factor which influenced the fish distribution during the course of the whole life cycle. Therefore, the series of regularities which occurred over a period of years which have been used successfully for the prediction of distribution and the efficiency of fishery (ELIZAROV 1959; KONSTANTINOV 1961, 1964; KONSTANTINOV and MUKHIN 1964, 1965) were ineffective in other years. From this point of view the use in prognosis of such a predictor as fish distribution, which already contains both the result of interaction of the whole complex of biotic and abiotic factors, and the operative receipt of which does not present difficulties, is of great interest.

A specification of wintering areas of different sized cod and haddock year classes during the periods of cold, and definition of the extent of western displacement with the increasing fish age are of practical importance for both planning the researches and predicting the fishery. The conclusions about the western migrations of haddock in cold years (1978-82), compared with the previous 1950s and 1960s, is one of the main findings of this report.

The lag in distribution of haddock observed with variations of the water heat content is of great practical value for a long-term prediction. In our opinion, such a phenomenon is peculiar to cod as well, but to elucidate this question, other methods and a more accurate analyses should be used.

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DYNAMICS OF COMMERCIAL FISH STOCKS IN THE BARENTS SEA
Proceedings of the third Soviet-Norwegian Symposium, Murmansk, 26-28 May 1986
Edited by H. Loeng. Institute of Marine Research, Bergen, 1987.

PECULIARITIES OF FEEDING MIGRATIONS OF THE LOFOTEN-BARENTS SEA COD IN THE SOUTHERN BARENTS SEA IN RELATION TO VARIABILITY OF ENVIRONMENTAL CONDITIONS

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ABSTRACT

Historical data (1950-1983) demonstrate that during years when the frontal zone is observed to increase at the bottom layer at the end of the hydrological winter, the feeding migration of cod is along the main branch of the Murman Current. If the heating of waters off the Murman coast during April and May is intensive, the distribution area of wintering cod will be displaced considerably eastwards, and the migration during June-August passes through coastal areas.

INTRODUCTION

Cod from the Lofoten-Barents Sea area exhibit extensive feeding, wintering and spawning migrations in the southern Barents Sea during the year. Peculiarities of fish behaviour at each stage of the migrational cycle (beginning, extent, route, speed) are determined primarily by the heat content of the water masses and secondly by seasonal variations of abiotic factors (MASLOV 1944, 1968a, 1968b, KONSTANTINOV and MUKHIN 1964, MILINSKY 1967, SARYNINA 1980). During the hydrographic spring, when the lowest seasonal temperature is succeeded by higher water temperatures, the cod start a migration from the wintering and spawning grounds to the feeding grounds. These feeding grounds are located in the eastern and southeastern Barents Sea with relatively warm currents. The principle migration routes pass along the main or coastal branches of the Murman Current (Fig. 1). In this area there have been summers when the industrial fleet takes up to 80% of the total cod catch from the southern Barents Sea.

For each particular year, peculiarities of environmental conditions in the southern Barents Sea determine which of the principle routes will be chosen by the cod during their massive feeding migration. This is because during this period, the behaviour of migratory fish is determined by abiotic factors rather than the physiological state, as during their spawning migrations (MARTI 1980). The distribution of cod in summer is, in a way, influenced by the size-age composition of the population. This is because the sensitivity and response to adequate fluctuations of environmental factors for fish of different age vary. The routes and timing of the migration seem to be dependent on nutritional factors, that is the times and sites of settling, and aggregation of euphausiids, young fish, shrimp etc., which are, in turn, determined by abiotic conditions.

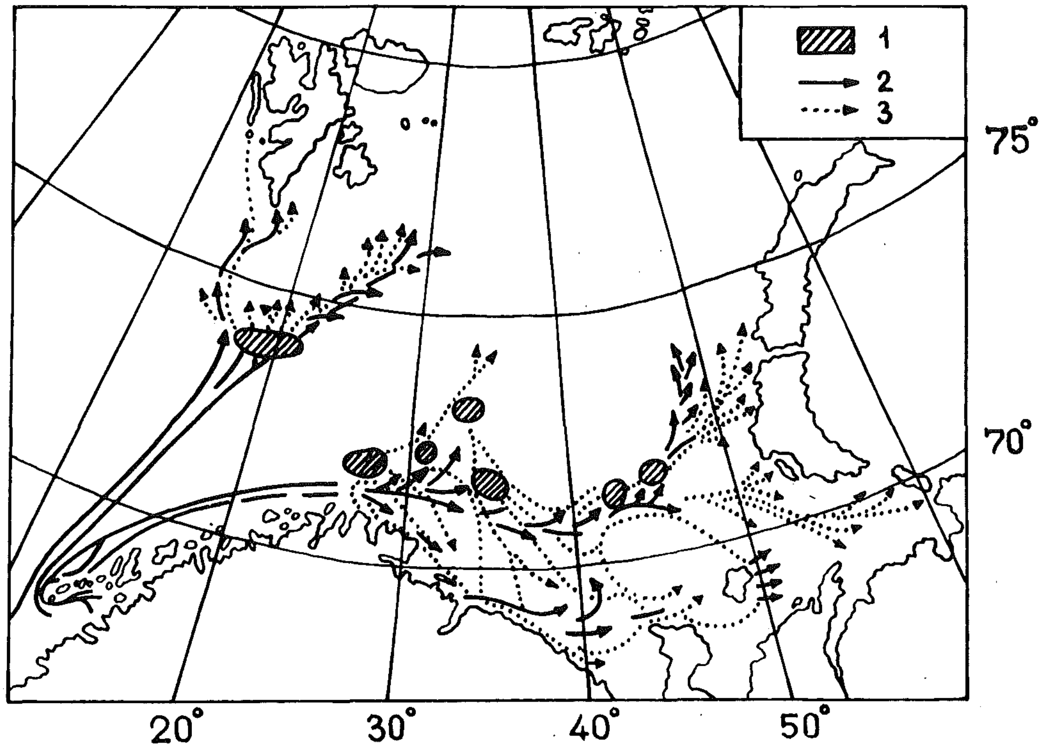

Fig. 1. Routes of the eastward migration of the Lofoten-Barents Sea cod (according to MASLOV 1944)

1 - wintering areas of immature cod
2 - migrations of mature cod
3 - migrations of immature cod

MATERIAL AND METHODS

The location of the studied area, close to the fishing ports makes it possible for scouting vessels to carry out regular observations over cod migrations. Therefore, we think it allowable to take the fishing areas for range of the actual (massive) distribution for cod. The total catch of cod from the Kildin Bank and west-coastal area (the group of coastal areas, Fig. 2) may be used as a relative index for the number of cod which have passed in the period of their feeding migration during June-August along the coastal branch of the Murman Current. The catch from the North-Central area (the group of central areas) can be used for the number of fish which have passed along the main branch. Positions and names for the areas are given in ANON. (1957). A comparison of cod number indices for the two groups of areas is used to estimate which portion of the cod stock has passed eastwards along the coast of Murman and which one along a more northerly route. To eliminate the effect of interannual variation of the stock size as well as differences in fishing effort per fish number index, a frequently used parameter (weight of an area in the fishery) expressed as a percentage ratio of the catch for a certain time period from each group of areas to the total catch during the same period from the southern Barents Sea was used. The time series of data which were obtained illustrate major peculiarities in cod feeding migrations during 1950-1983.

The most informative factors influencing the migrational behaviour of cod during their period of feeding, were selected amongst the temperature of deep

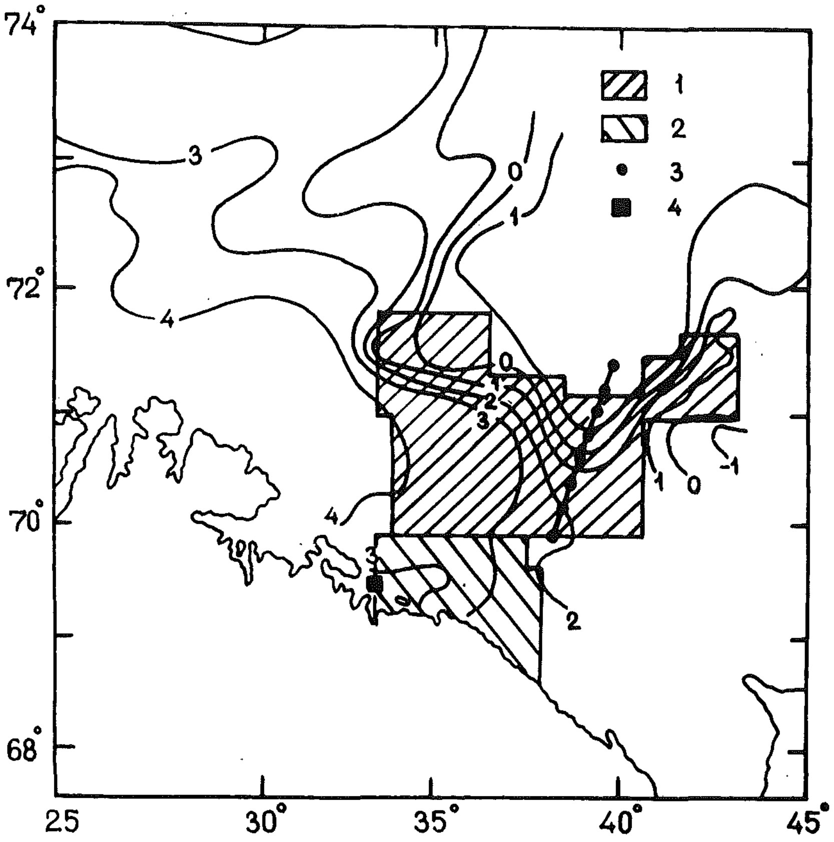

Fig. 2. Distribution of water temperatures in the bottom layer in April 1983.

1 - central areas,
2 - coastal areas,
3 - hydrographical stations in the frontal zone,
4 - station No.1 on the Kola Meridian section.

waters, horizontal and vertical gradients of water temperature, rate of heating of water masses on some standard sections, areas in the southern Barents Sea with near bottom waters above 2°C, and a number of other estimated parameters averaged for different time intervals. Using correlation and regression analyses, a check was made of the coherence between interannual variations of the relative index of cod numbers in the two groups of areas during summer (Fig. 2). From 17 factors which described the environment, the two most effective factors were selected. These were

(1) the maximal horizontal gradient of water temperature in the bottom layer on the northern slope of the Murman Shoal during April (in °C per nautical mile), and

(2) the difference between mean water temperatures at 150 m at Station No. 1 on the Kola Meridian section during May and April (in °C).

The first characteristic indicated the development of the frontal zone dividing warmer Atlantic waters and cooler Barents Sea waters in the southern Barents Sea. The second was a relative value for the variation of water heat content in the Murman coastal zone during hydrographic spring (Fig. 2).

The industrial cod stock is known to be composed of fish of different ages, the migration routes of which partially coincide. As the fish grow, their feeding migrations become more extensive and their wintering grounds are displaced westward (MASLOV 1957). Therefore, interannual variations in the proportion of different age groups in the stock may, to a certain extent, influence the behaviour of cod during migrations. Historic data on the size-age composition of the cod stock in the southern Barents Sea and relative indices of the number of cod at different ages were used in this paper.

RESULTS AND DISCUSSION

The analysis of cod feeding migrations in the southern Barents Sea for the years 1950-1983 indicate that only during 1955-1958 and 1976-1977 the amount of fish in coastal areas were much higher than in areas located along the main branch of the Murman Current. For all the other years, the group of central areas was the dominant or the two groups were nearly equally important (Fig. 3). The same route may be taken by cod for the massive migration in both hydrographicly warm and cold years. Therefore, variation of thermal state of the sea does not always seem to be a determining factor for the orientation of cod migrational routes during summer. This is confirmed by a low correlation (r=0.1±0.2) between interannual values (1951-1980) for the weight of groups of coastal areas and central areas during June-August, and mean water temperatures in the 150-200 m layer at Stations No. 3-7 on the Kola section during April and May (the period preceding the feeding migration). This is probably due to the fact that the migrational behaviour of cod is determined by a complexity of factors (both abiotic and biotic), which influence differently the distribution of fish in the surveyed area during different years.

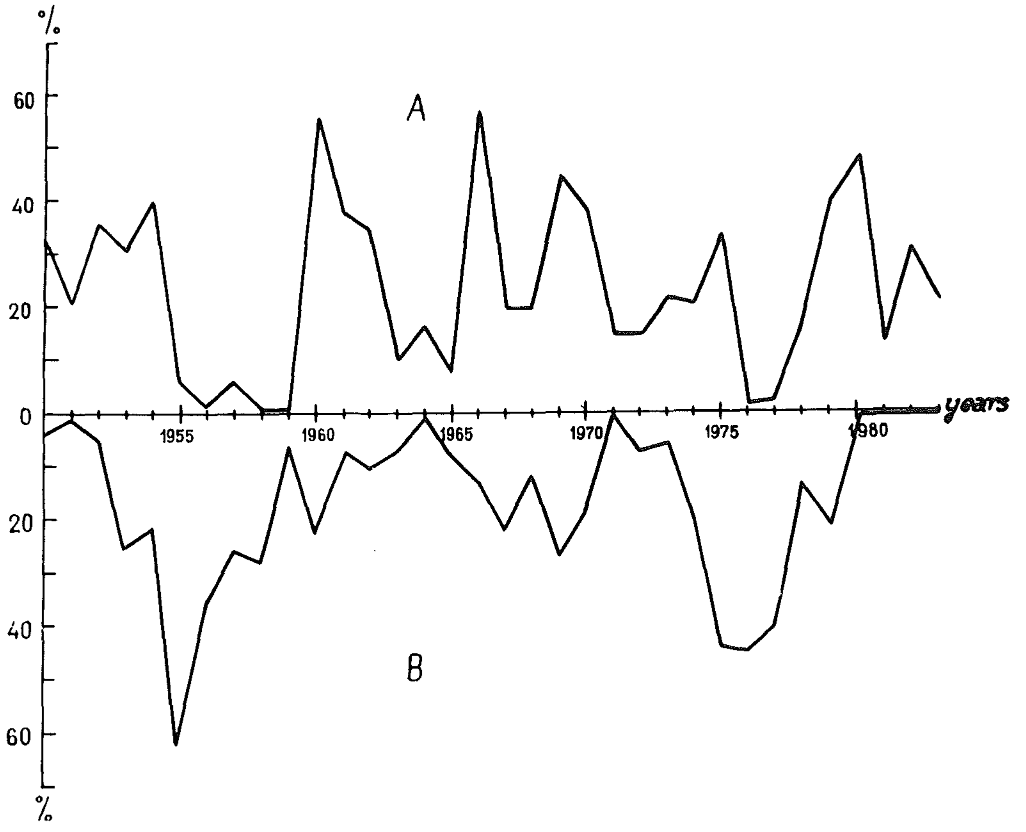

Fig. 3. Variation in the percentage catch of cod from the central areas (A) and from the coastal areas (B) in June-August during the period 1950-1983.

Some scientists consider cod behaviour to be influenced by the rate of variation rather than by absolute value of temperature (KHANAICHENKO and KOZLOVA 1961, SARYNINA 1980). For the southern Barents Sea, the water temperature for the whole water column usually attains its yearly minimum during April. However, in some years, seasonal minimum may be recorded in the bottom layer during May, or even June. A subsequent rise in temperature occurs at various rates which depend on the intensity of the heat displacement from midwater into the bottom layer, as well as on dynamic processes which regulate the influx of heat from horizontal advection of the water. The time when the temperature minimum occurs in the bottom layer and the rate of the water heat content increase during hydrographic spring, seem to be the crucial factor for the start of cod feeding migrations. A check on the relation between the weight of the group of coastal areas in the fishery and the difference between water temperatures in May and April at 150 m at Station No. 1 on the Kola Meridian section gave the correlation coefficient $r=0.509$ ($p=0.995$). Using a position of the eastern boundary of the distribution range of wintering cod in the southern Barents Sea as the second determining factor, a linear equation for multiple regression was derived ($R=0.808$ at $n=33$):

$$y = 44.28x + 2.46z - 19.19$$

where y - the weight of the group of coastal areas in the fishery in June-August (per cent);

x - difference between water temperatures at 150 m at Station No. 1 on the Kola Meridian section in May and April (^{o}C);

z - distance (in degrees of longitude) from the 20^{o}E meridian to the eastern boundary of the cod distribution range in March.

Wintering areas of fish from different size-age groups do not coincide: larger fish are distributed farther west (MASLOV 1952, 1960, MILINSKY 1967). MIDTTUN, NAKKEN and RAKNES (1981) demonstrated with an example from the 1975 year class of cod that in the southern Barents Sea, 10-20% of the young cod (aged 3 to 5 years) moved west of 30^{o}E during a year. Therefore, the larger the percentage of young fish in the stock, the further east their wintering grounds are located. The fish formed a kind of reserve for approaches to the coast of Murman before migrating to feed. Probably for this reason, there is an actual positive correlation between the weight of coastal areas in the fishery during summer and the relative number of 51-70 cm cod in the stock ($r=0.500$; $n=37$). In support of this conclusion was observations that the number of fish in coastal areas increased during summer for 4 to 6 years after rich year classes of cod (1950, 1963, 1964 and 1970) had appeared (Fig. 3).

During their migration along the main branch of the Murman Current the cod pass the areas, in which the hydrographical regime is influenced by a narrow frontal zone. Therefore, in order to estimate the most informative factors that influence the distribution of cod during summer, a number of characteristics that describe the intensity of the development of the frontal zone dividing Atlantic and Barents Sea waters as well as illustrate its time-spatial variability were examined. A correlation analysis indicated that, for the group of central areas, the magnitude of horizontal gradients of bottom temperature in the frontal zone in April (the extent of its increase during this period, Fig. 2), is most important. Intensification or weakening of the hydrographical front appeared to influence the distribution of prey in the area adjacent to the gradient zone, and hence, on the cod migration pattern in central areas. The correlation coefficient for the discovered relationship was $r=0.788$ ($n=28$). The relationship is approximated by the following equation:

$$y = 428.27x - 6.02$$

where y - the weight of the group of central areas in the fishery in June-August (per cent);

x - maximal horizontal gradient of water temperature in the bottom layer on the northern slope of the Murmansk Shoal in April (^{o}C per nautical mile).

Thus, in those years when the frontal zone in the southern Barents Sea is intensified at the end of hydrological winter, the cod primarily pass through fishing areas located along the main branch of the Murman Current for feeding. When the rates at which water is heated near the Murman coasts from April through May is intensified and the stock contains higher numbers of younger fish, a notable eastward displacement of wintering grounds occurs, and the concentration of cod located in coastal areas increases during the summer.

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THE EFFECT OF OCEANOGRAPHIC CONDITIONS ON DISTRIBUTION AND POPULATION
DYNAMICS OF COMMERCIAL FISH STOCKS IN THE BARENTS SEA
Proceedings of the third Soviet-Norwegian Symposium, Murmansk, 26-28 May 1986
Edited by H. Loeng. Institute of Marine Research, Bergen, 1987.

CONDITIONS FOR THE FORMATION OF PRESPAWNING AND SPAWNING GREENLAND HALIBUT CONCENTRATIONS OF THE NORWEGIAN-BARENTS SEA STOCK

By

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ABSTRACT

An effect of biotic and abiotic conditions in feeding areas on a density of prespawning and spawning Greenland halibut concentrations was examined. The effect of temperature in feeding areas upon the rate and terms of maturation of Greenland halibut reproductive products, which had influenced the terms of fish feeding and mass approach to the spawning grounds, have been estimated. Accelerated development of reproductive products resulted in an active spawning fish migration. This caused a large quantity of specimens at the maturity stage IV to be simultaneously accumulated in the spawning grounds, and promoted the formation of steady concentrations of Greenland halibut.

INTRODUCTION

An interrelationship between the organisms and biotic and abiotic factors of the environment is a most important problem when studying fish behaviour. It is known that abiotic factors essentially alter the biotic relationships. For example, a physiological state of specimens is considered to be a main factor determining the stability, mobility and period of the existence for fish concentrations (DOMANEVSKY 1970). At the same time, fish behaviour (the transition from physiological state into another) closely depends on variations of environmental conditions. Therefore, it is impossible to consider either state separately from each other.

For a long time, investigators were interested in the migrations and distribution of Greenland halibut of the Norwegian-Barents Sea stock (KNIPOVICH 1926, RASS 1934, ESIPOV 1937, 1949, AVERINTSEV 1940, MILINSKY 1944, SOROKIN 1967, NIZOVTSEV 1970, KOEFOED 1909, LUNDBECK 1935). While many aspects on Greenland halibut biology were examined, systematic investigations have only been carried out since 1965.

According to the results of the investigations in 1965-1981, NIZOVTSEV (1985) found inverse relationships between the water temperature in

1) the 0-200 m layer in the North Cape - Bear Island section and a productivity of Greenland halibut fishery, and
2) the 200-500 m layer on the sections 9-c, 10-c, 11-c (located in NIZOVTSEV 1985) and a density of halibut concentrations in September - February.

However, these relationships were observed only for those years when the abundance of the commercial part of Greenland halibut stock was at a level not lower than the mean, i.e. from 1965 to 1976. Furthermore, NIZOVTSEV (1985) suggested that

> "if the abundance of a commercial part of stock is at the level lower than the mean one, as, for example, in 1977-1981, then the dependence considered in these years is not registered and distributed on the whole during the entire period of observations (1965-1981)".

The aim of the present paper is to elucidate factors on which the formation of prespawning and spawning Greenland halibut concentrations at a low stock status depend.

MATERIAL AND METHODS

Data on fishery, the results of mass measurements made on board the research vessels, and also the results of fish tagging for 1975-1984, were used to examine the distribution and migration of Greenland halibut.

To judge the conditions of Greenland halibut feeding, a fullness of stomach (mean degree of stomach fullness) was estimated according to a 5-point scale with a condition factor on the average per month. A condition factor was determined according to NOSKOV (1950). The terms of fish maturation were judged from stages of maturity for gonads, which were determined according to a 6-point scale (SOROKIN and GRIGORYEV 1968, FEDOROV 1968).

The positions of standard sections in the Norwegian and Barents Seas, and the location of the main Greenland halibut spawning grounds, are given in Fig. 1.

Mean values of water temperature from the main and northern branches of the North Cape Current (sections 3 and 29) in the layer of water 50-200 m were used as an index of heat content in the feeding areas of Greenland halibut for the first half of the year. Additionally, water temperature values for the middle branch of the Norwegian Current (in the section along 74°30'N for 200-500 m) during June were also used. The closest relationship between water temperature of this branch was found with the waters washing the continental slope along the West Spitsbergen (TERESHCHENKO 1984).

An analysis of correlation was used for a quantitative estimation of the relationship between the comparable parameters. Coefficients of both partial and multiple correlation at different combinations of abiotic and biotic factors were obtained.

RESULTS

The year-to-year differences of fish migration had an effect on the level of Greenland halibut concentrations. As it is seen from Figs 2 and 3, dense concentrations of Greenland halibut are observed in some years in the Kopytov area (the main spawning area, located between 71°20' - 73°30' N and 14°30' - 22°00' E) during September (1975, 1976, 1981). For other years, fish were scattered (1978, 1980, 1984), or the commercial concentrations absent (1977, 1978, 1982, 1983). In some years, density of aggregations was higher in November or December, and occasionally as early as September-October.

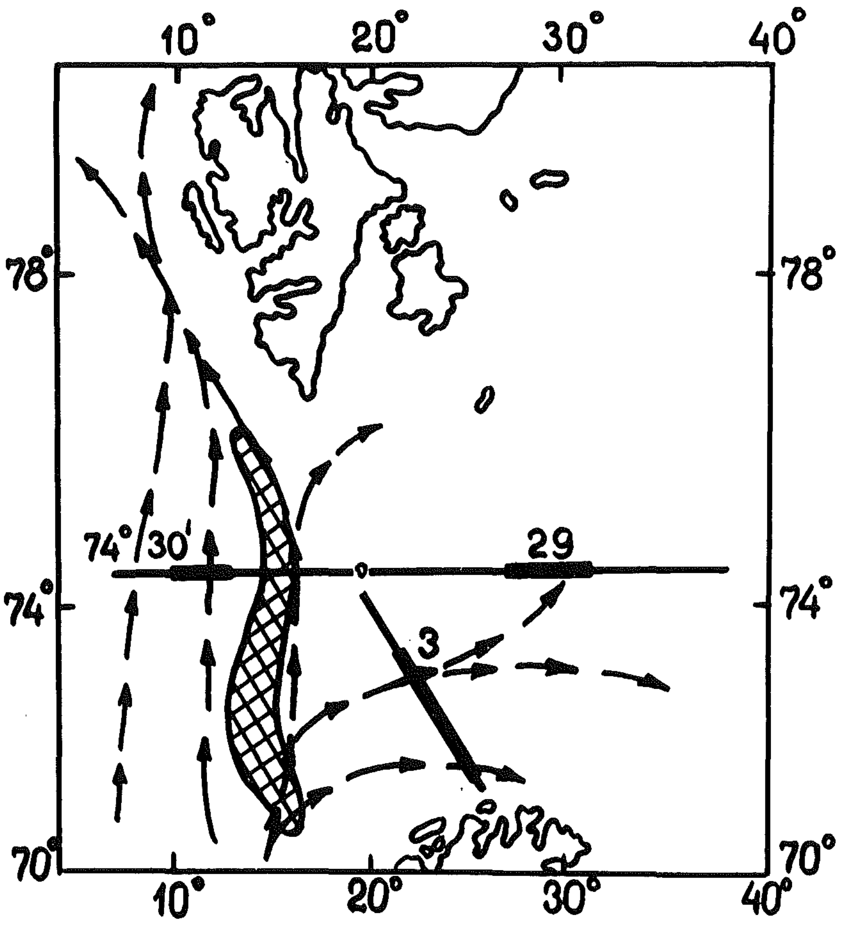

Fig. 1. The position of standard sections in the Norwegian and Barents Seas and the location of Greenland halibut spawning grounds (hatched area).

The time of aggregation depended on the factors for the mass approach of fish to the spawning grounds, a peak of spawning, an extent of the spawning areas, and the environmental conditions.

Thus, to judge from a distribution and a level of concentrations, the timing of approach of mature fish to the Kopytov area are different by years. The occurrence of Greenland halibut in feeding areas is assumed to vary depending on the peculiarities of the hydrological regime. Variations in water temperature caused changes of feeding intensity, the latter may directly influence the Greenland halibut behaviour, or indirectly by either delaying or accelerating the maturation of gonads.

Analyses of the distribution of Greenland halibut during October, 1975-1984, indicated that a density in the spawning grounds by years was not identical (Figs 4 and 5). Mass approaches of mature Greenland halibut to the Kopytov area were registered for some years. During other years, fish were distributed from the West Spitsbergen area to the Kopytov area and the mass approach to the spawning grounds was not observed.

These data indicate that a mass spawning of Greenland halibut occurred over an area of different extent and in different terms. Due to this, the distribution and density of Greenland halibut concentrations in September -

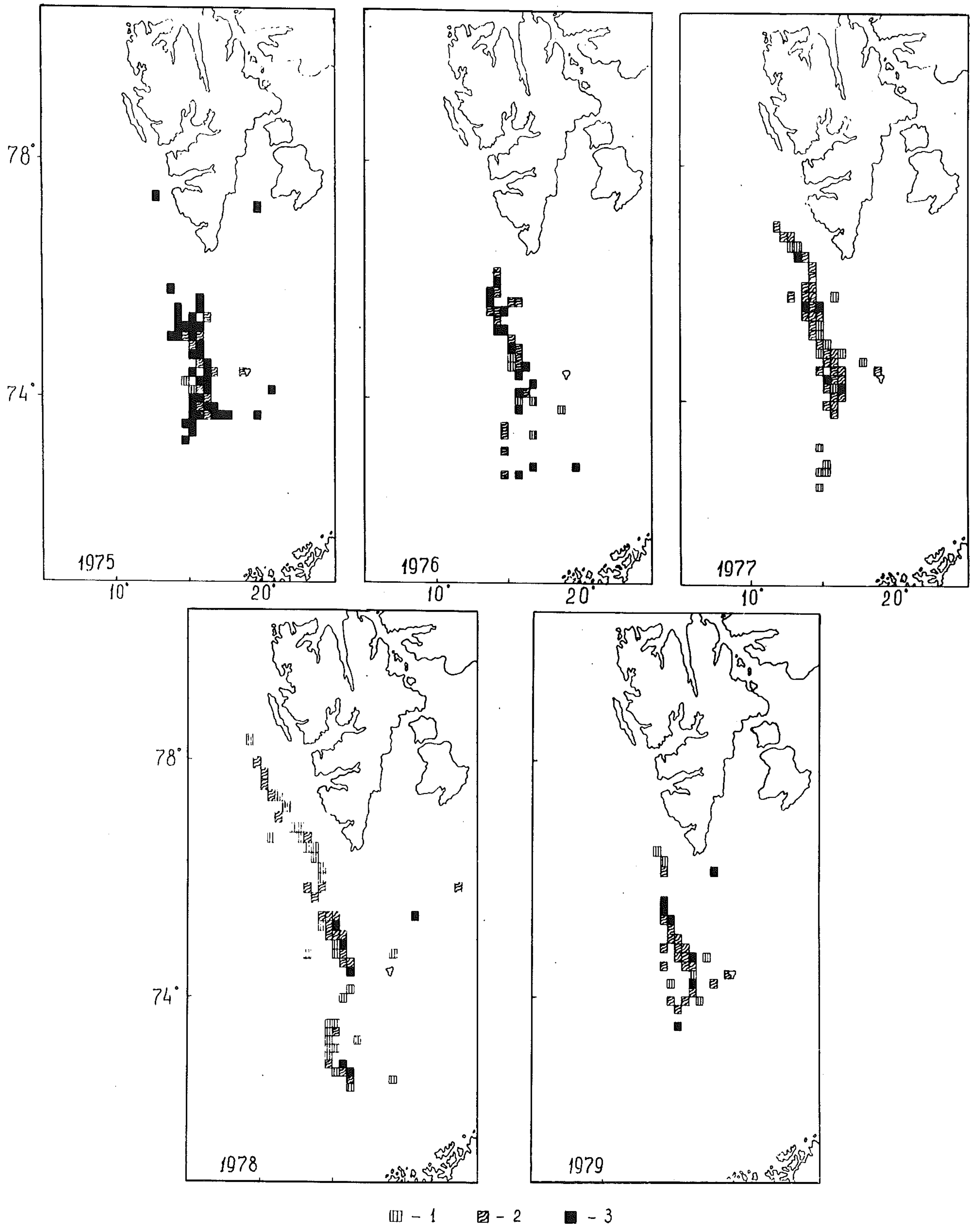

Fig. 2. Distribution and density of Greenland halibut concentrations in September 1975-1979, based on fishery productivity of a medium refrigerator trawler.

1: Catch less than 3.0 tonnes (t) per day of fishing
2: 3.1 t < catch ≤ 5,0 t per day of fishing
3: Catch above 5.0 t per day of fishing

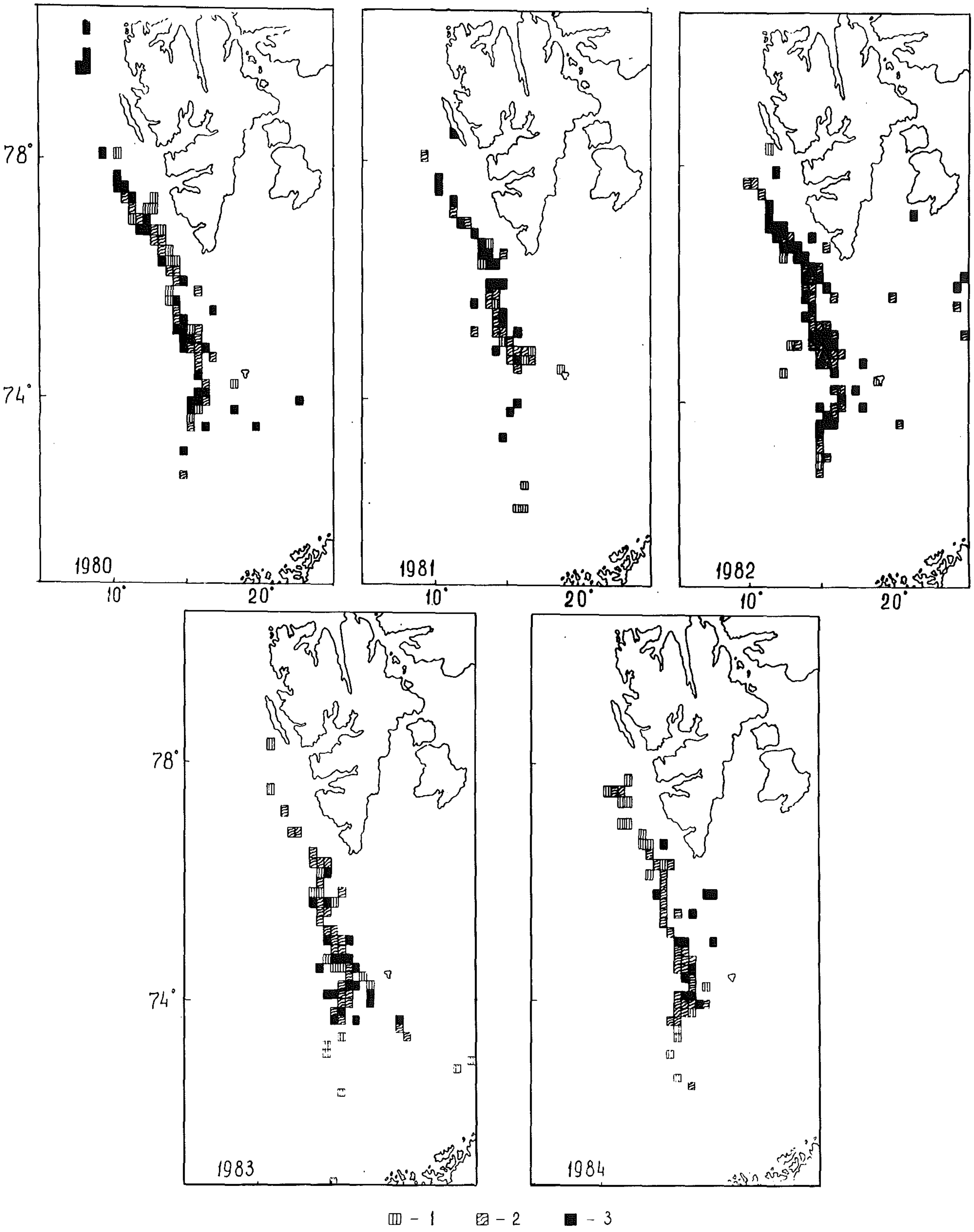

Fig. 3. Distribution and density of Greenland halibut concentrations in September 1980-1984, based on fishery productivity of a medium refrigerator trawler.

1: Catch less than 3.0 tonnes (t) per day of fishing
2: 3.1 t < catch ≤ 5,0 t per day of fishing
3: Catch above 5.0 t per day of fishing

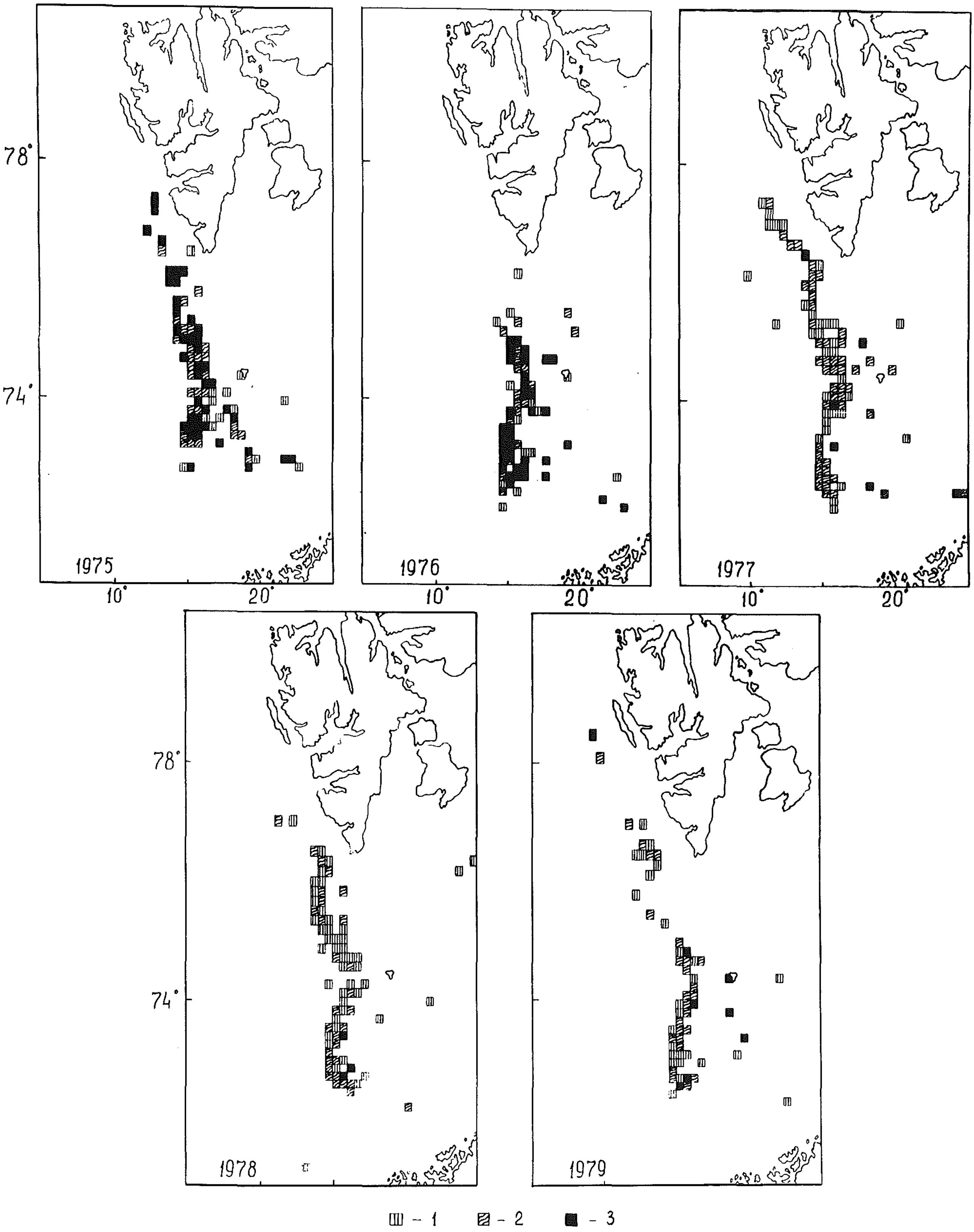

Fig. 4. Distribution and density of Greenland halibut concentrations in October 1975-1979, based on fishery productivity of a medium refrigerator trawler.

1: Catch less than 3.0 tonnes (t) per day of fishing
2: 3.1 t < catch ≤ 5,0 t per day of fishing
3: Catch above 5.0 t per day of fishing

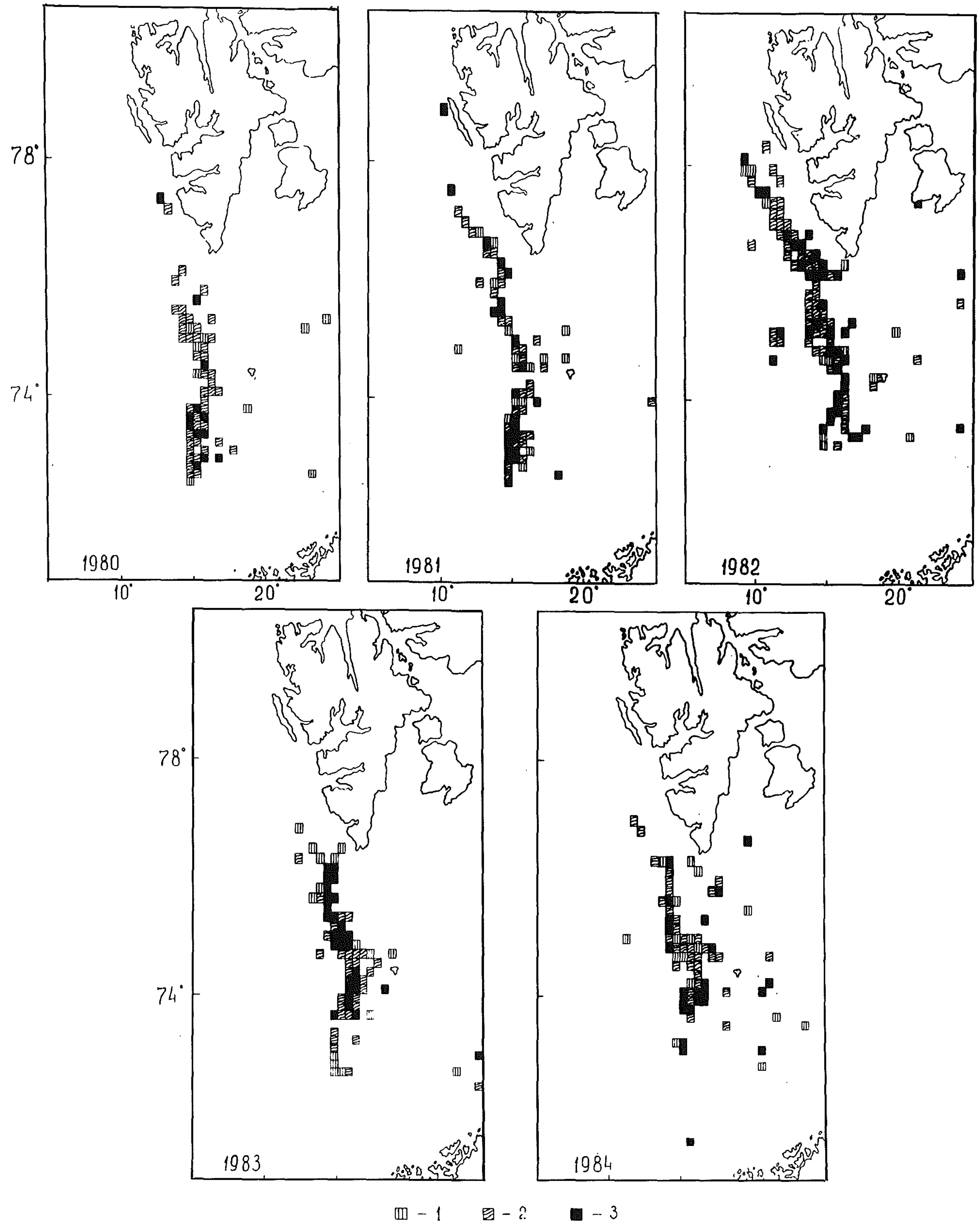

Fig. 5. Distribution and density of Greenland halibut concentrations in October 1980-1984, based on fishery productivity of a medium refrigerator trawler.

1: Catch less than 3.0 tonnes (t) per day of fishing
2: 3.1 t < catch ≤ 5,0 t per day of fishing
3: Catch above 5.0 t per day of fishing

January differ by years. If a regularity for a growth in a level of concentrations and a productivity of Greenland halibut fishery from September to November-December was common to autumn-winter fishing season on the whole, then during separate years, these dynamics may be broken (Table 1).

Table 1. Dynamics of the productivity of Greenland halibut fishery in autumn and winter 1975-1984, tonnes/hour.

Year			Month			
	Sep	Oct	Nov	Dec	Jan	Catch*
1975	0.37	0.35	0.40	0.47	0.36	0.39
1976	0.28	0.38	0.44	0.40	0.27	0.40
1977	0.23	0.27	0.30	0.29	0.18	0.27
1978	0.18	0.19	0.23	0.24	0.21	0.21
1979	0.24	0.22	0.25	0.23	0.20	0.23
1980	0.29	0.26	0.25	0.21	0.15	0.24
1981	0.45	0.32	0.28	0.32	0.27	0.32
1982	0.33	0.26	0.29	0.31	0.40	0.29
1983	0.26	0.30	0.30	0.33	0.26	0.28
1984	0.20	0.35	0.40	0.30	-	0.31
1975-1984	0.28	0.29	0.31	0.31	0.26	0.29

* mean catch per trawling hour for the fishing season

To elucidate the regularities and conditions for the formation of prespawning and spawning of Greenland halibut concentrations, we have considered a complex of factors which may effect their formation as:

- population abundance,
- dynamics of age-length composition,
- year-to-year water temperature variations in feeding and spawning areas,
- feeding conditions,
- variation of rates and timing of gonad maturation depending on hydrographic and feeding conditions,
- the effect of the development time for gonad maturation on the level of prespawning and spawning fish concentrations in the spawning grounds.

According to our investigations, a factor of abundance is of paramount importance concerning the dynamics of year-to-year fishery productivity. However, it is not always a determinant for the formation of dense Greenland halibut concentrations in different months. It is known that fish are also aggregated with a high density of commercial stock during separate seasons of the year and which do not form the dense aggregations. On the contrary, they may be at a low abundance but concentrated within a small area.

It had been elucidated that one of the factors determining the behaviour, distribution, and migrations of Greenland halibut was water temperature. The effect of temperature conditions on the duration of feeding migrations resulted in accelerating or delaying metabolism. This, in its turn, effected the time and rates of gonad maturation, for which accelerated maturity is a main stimulant for the active spawning migration of Greenland halibut.

To confirm the above, we first considered the variation in time for Greenland halibut gonad maturation which depended on the feeding conditions. A comparison between the years during which the feeding conditions were favourable (index of fullness is higher than the long-term mean), indicated that the maturation of gonads in Greenland halibut took place in shorter periods. A number of specimens at the IV and V stages of gonad maturity made up over 50% in the Kopytov area in those years (October). In November-December a considerable amount of males and females were spent. A correlation between a number of specimens in IV and V stages of gonad maturity in October and conditions of feeding in spring-summer was found (correlation coefficient r=0.57, reliable at p=0.10).

To elucidate an effect of water temperature upon the period for gonad maturation of Greenland halibut, we compared the temperature variations of the middle branch of the Norwegian Current at 200-500 m depth during June and a relative amount of Greenland halibut (%) at the IV stage of gonad maturity during October in the spawning area (correlation coefficient r=0.68, reliable at p=0.05). Thus, the rate of maturation of Greenland halibut gonads and the timing of fish approach to the spawning areas may be forecasted in advance as a factor of temperature. A reliable correlation was also obtained between the water temperature at the same section and a relative amount of Greenland halibut males at the IV stage of gonad maturity (r=0.77 is reliable at p=0.01). A positive correlation, (expressed by the correlation coefficient r=0.88 reliable at p=0.001) was registered between the mean water temperature of the North Cape Current on the sections 3 and 29 in the 50-200 m layer during the first half of the year with a relative amount of Greenland halibut females at the IV stage of gonad maturity during October.

Furthermore, an attempt to elucidate a correlation between density of Greenland halibut aggregations during October, November and December in the spawning grounds (Kopytov area) with a degree of gonad maturity for a period previous to spawning has been also undertaken. The comparison indicated a direct statistical correlation between a level of prespawning Greenland halibut concentrations during October and November, and a relative amount of specimens with gonads at the IV stage of maturity. The amount of the specimens with the gonads at this stage of maturity in the spawning grounds was correlated with the level of Greenland halibut concentrations during October (r=0.80, p=0.01). This correlation is broken only during those years when the data are not qualitative (Fig. 6). A close correlation was found between a relative amount of Greenland halibut at the stage IV of gonad maturity with a level of concentrations in November (r=0.78, p=0.01) and December (r=0.65, p=0.05).

Thus, a high heat content of water masses in the feeding areas of Greenland halibut promoted an accelerated development of reproductive products which resulted in the active spawning migration of fish to the spawning grounds. In their turn, active migrations promoted a greater accumulation of specimens at the IV stage of gonad maturity in the Kopytov area during October, and as a consequence, conditions are formed to stabilize Greenland halibut concentrations. In addition, we came to the conclusion that the water temperature, characterized by the conditions in the feeding areas, may be a precondition to forecast the level of Greenland halibut concentrations.

This forecast during an October period for vessels of a trawler and medium trawler type - 1000 hp. uses a correlation between the variations of water temperature of the middle branch of the Norwegian Current on the section along $74^{o}30'$N in the 200-500 m layer during June, and the mean water

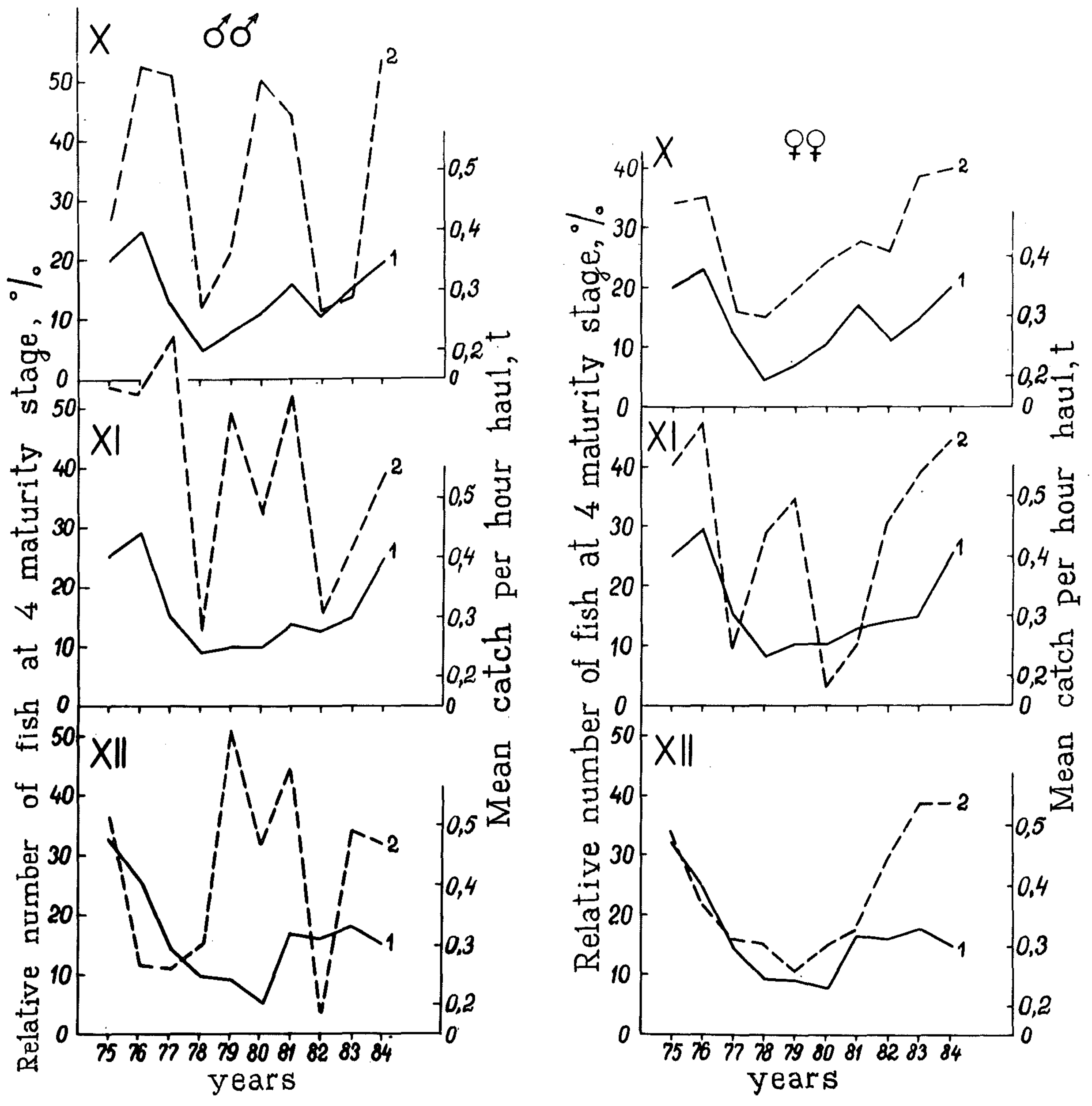

Fig. 6. Correlation between the number of individuals at stage IV of gonad maturation and density of Greenland halibut concentrations in the spawning area in October, November and December. 1 - mean catch per trawling hour, tonnes (t); 2 - a relative number of Greenland halibut specimens at stage IV of gonad maturation, %.

temperature of the North Cape Current on the sections 3 and 29 in the 50-200 m layer during the first half of a year with the level of concentrations during October. This correlation is characterized by the regression:

$$Y_1 = 0.728\ X_1 + 0.534\ X_2 - 0.546 \qquad (1)$$

(coefficient of multiple correlation to be equal to R=0.85 ± 0.06, n=10).

where Y_1 - the productivity of fishery in October, tonnes per trawling hour;

X_1 - water temperature of the middle branch of the Norwegian Current on the section along 74°30'N in the 200-500 m layer in June;

X_2 - mean water temperature of the North Cape Current on the sections 3 and 29 in the 50-200 m layer in the first half of the year.

The productivity of Greenland halibut fishery during November may be forecasted according to the water temperature of the middle branch of the Norwegian Current in the 200-500 m layer during June using the following equation:

$$Y_2 = 1.233\,X_1 + 0.109 \qquad (2)$$

where Y_2 - productivity of Greenland halibut fishery in November, tonnes per trawling hour;

X_1 - water temperature of the middle branch of the Norwegian Current on the section along 74°30'N in the 200-500 m layer in June.

Testing of the equations (1) and (2) on considered observations indicated their reliability. For example, a productivity of Greenland halibut fishery during October, estimated by the equation of correlation (1), is well correlated with an actual productivity (Fig. 7).

These relationships were observed for those years when the abundance of a commercial part of Greenland halibut stock was at the low level. By including those years into a number of observations, during which the abundance is greater than or equal to mean levels (i.e. if the entire period of observations from 1965 to 1984 is considered on the whole), then the correlation coefficients are reduced, and a sign of correlation is reversed. This may be explained by both that

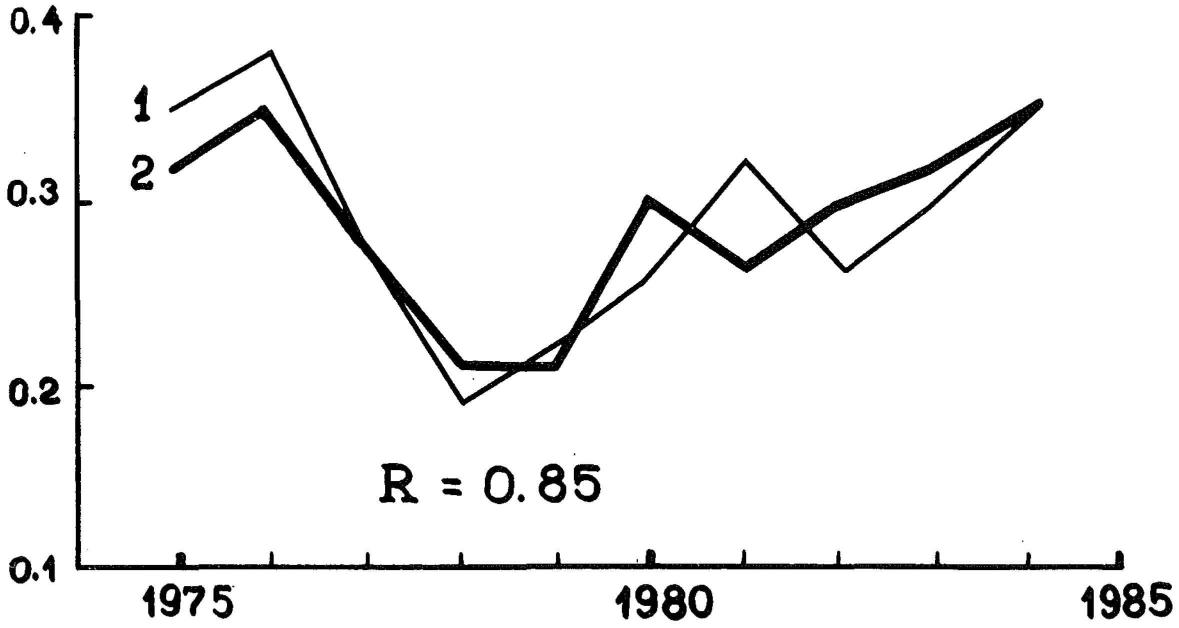

Fig. 7. Actual (1) and calculated (2) productivity of Greenland halibut fishery in October.

1) the trophic and spawning parts of the area are reduced during a considerable reduction of the abundance of a commercial part of the stock,
2) vital space, with the optimum conditions, becomes enough for the fish so the reduction of water temperature is no longer a factor which promoted the concentration of fish on a continental slope.

Thus, from the above analysis, it is clear that during the years with a low abundance of a commercial Greenland halibut stocks, such factors as feeding conditions, rate and timing of gonad maturation (which affect the timing of the mass approaches of fish to the spawning grounds), and also the water temperature in feeding areas (which influenced directly the metabolic and physiological processing in fishes) have a bearing on the formation and density of prespawning and spawning concentrations.

A linear stochastic correlation between the density of Greenland halibut concentrations during October and the density of concentrations during November and December (r=0.91 and 0.80, respectively) was obtained. A value of a productivity of the fishery during October predetermines the fishery productivity for a fishing season (r=0.91). The relationship is real and stable.

The productivity of Greenland halibut fishery during November, forecasted according to a factor of temperature, may be specified using the following equation:

$$Y_1 = 1.086\ Y_2 - 0.011\ (r=0.91 \pm 0.04, \text{ at } n=10)$$

where Y_2 - productivity of fishery in October, tonnes per trawling hour;

Y_1 - productivity of Greenland halibut fishery in November, tonnes per trawling hour.

Testing of this equation on the considered observations indicated their reliability.

Thus, as a result of our investigations, the close relationship between the density of prespawning and spawning concentrations of Greenland halibut, the physiological condition of fish, and the hydrological conditions in feeding areas were elucidated. This is of great importance for improving the method of forecasting.

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Proceedings of the third Soviet-Norwegian Symposium, Murmansk, 26-28 May 1986
Edited by H. Loeng. Institute of Marine Research, Bergen, 1987.

RECRUITMENT AND DISTRIBUTION OF NORTH-EAST ARCTIC SAITHE IN RELATION TO CHANGES IN THE ENVIRONMENT

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ABSTRACT

The stocks of North-East Arctic saithe and Arctic cod have responded in a similar way to the period of cold climate in the Barents Sea 1976 - 1982. Since a relationship with the climate has been established for Arctic cod, a relationship with the climate also for North-East Arctic saithe is indicated. Time series of recruitment, landings, and catch per unit of effort were compared with historic data on the climate. The results showed little evidence of relationships. A concurrence of poor recruitment in all North-East Atlantic saithe stocks 1974-1977 coincided with a period of extreme low salinities in the Faroe-Shetland Channel, indicating that the recruitment may suffer in years with reduced inflow of Atlantic water. Although little other evidence of a relationship with the climate is found, the lack of a close stock-recruitment relationship reveals that environmental factors affect the recruitment of the North-East Arctic saithe, but the nature of these factors are mostly unknown. The feeding area and therefore probably also the availability of food appears to be more stable for saithe than for cod. It is suggested that this may be the evolutionary basis for the relatively small variation in year class abundance for saithe compared to cod.

INTRODUCTION

The cold climatic regime in the Barents Sea from 1977 to 1982 coincided with a series of poor year classes of Arctic cod (ANON. 1986, SÆTERSDAL and LOENG 1984). Also for the North-East Arctic saithe recruitment was on the average poor, though the 1978 year class was abundant (ANON. 1985). In this period there was a westward shift in the distribution of cod (NAKKEN and RAKNES 1984). For saithe, there was a marked decline in the saithe fishery on the east coast of Finnmark, which may have been caused either by a westward migration or by reduced recruitment to that part of the coast. The recruitment was improved for cod from 1982 onwards, and there are strong indications that this has been the case also for saithe. The 1982 year class dominated the purse seine catches from Finnmark in 1985. In 1983 and 1984 substantial numbers of 0-group saithe were recorded in the Barents Sea and at Spitsbergen during the 0-group survey in August-September (ANON. 1983, 1984a). A similar distribution has previously been recorded only in 1967

(BENKO et al. 1967, HYLEN and JAKOBSEN 1971), and that year class of saithe was abundant also on the Norwegian coast. According to reports from fishermen living in northern Norway, the abundance of juvenile saithe has been increasing the last three years.

These observations indicate that the saithe has reacted to the changes in temperature during the last 10 years in a manner similar to cod and haddock. For the cod, SÆTERSDAL and LOENG (1984) showed that there is a relationship between the water temperature in the Barents Sea and the year class strength. It was decided to investigate if a similar relationship exists for saithe. Unfortunately, the historic data for North-East Arctic saithe are less extensive and probably also less reliable than for Arctic cod. Nevertheless, if temperature conditions significantly affect recruitment and distribution of saithe, this should in some way be reflected in recruitment estimates, landings, and catch rates.

MATERIAL AND METHODS

Hydrography

The saithe spawning takes place in Atlantic water which provides the environment during the early stages of life when the year class strength presumably is established.

The periodical changes in sea water temperature in the Barents Sea since 1900 have been described by SÆTERSDAL and LOENG (1984). The basis was observations along the Kola section where the temperature changes reflect fluctuations in the flow of warm Atlantic water into the Barents Sea. As far as fisheries are concerned, the flow of Atlantic water is undoubtedly the most influential environmental factor in this area as well as on a large part of the Norwegian coast. All references to temperature and climate in this paper, unless otherwise stated, are from SÆTERSDAL and LOENG (1984).

Recruitment Estimates

Estimates of year class strength for North-East Arctic saithe for the period 1959-1981 are available from Virtual Population Analysis (VPA). For the most recent year classes there are yet no reliable estimates. The full updated time series 1959-1981 is not published, but is available from the ICES data files. The most recent Saithe Working Group Report (ANON. 1985) gives the yearclass strength back to 1975.

Based on the numbers at age in the stock in 1960 and 1961 resulting from this VPA, estimates can also been obtained for the year classes 1946-1959 if assumptions are made about the fishing mortalities. The Norwegian saithe landings which were dominating in this period increased rapidly from 1946 to 1948, but thereafter the increase slowed down to an average annual rate of about 2% until 1960 (Fig. 1). The change in fishing mortality from 1948 to 1960 has therefore probably been relatively small, and the level generally low (about 0.2 in 1960). Ignoring possible changes in the fishing mortality, year class strength for 1946 to 1958 was estimated by comparing the stock numbers for the same age groups in 1960 and 1961 in the VPA.

While the errors introduced by the assumption of a stable fishing mortality are probably small, larger errors are likely to have been caused by the VPA. The size of the errors will generally increase backwards in time, both because

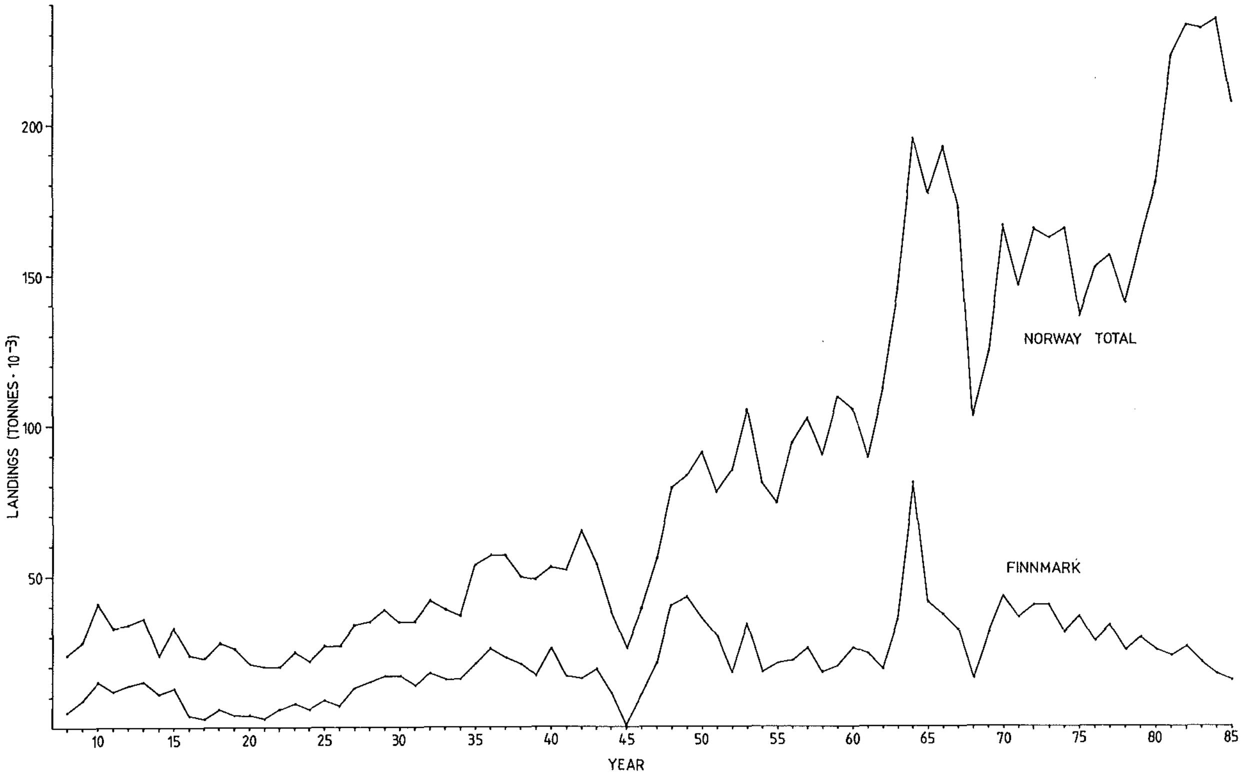

Fig. 1. Norwegian landings of saithe 1908-1985, total and in the county of Finnmark.

fewer years of sampling are included in the VPA for those age groups and because each year class is compared directly only with the previous one.

Prior to 1946, data on age and length distribution of saithe are very sparse, and reliable estimates of the recruitment could therefore not be obtained for earlier periods.

The changes in recruitment in recent years have to some degree been similar for Arctic cod and the North-East Arctic saithe, and it was decided to investigate if a relationship existed over a longer period. The cod data are available from the Arctic Fisheries Working Group Report 1985 (ANON. 1986) and the ICES data files.

There are apparently also common trends in recruitment of the different saithe stocks in the North-East Atlantic Ocean. The year class abundance of the North-East Arctic saithe 1960-1980 was compared with those of the North Sea, Faroe, and Icelandic saithe stocks (ANON. 1984b, 1985, ICES data files).

Catch Statistics

The official Norwegian fishery statistics give landings of saithe by county for each year from 1908. The catches are usually taken in the same area where they are landed, but trawl catches may be landed far from the catch locality. However, it is only after the rapid increase in trawling for saithe in the most recent years that this can give large discrepancies between landings and catches in the different coastal areas. If a westward shift in the distribution of saithe occurs, the effect would be expected to be greatest on the landings in the northeasternmost county, Finnmark. Fig. 1 shows the total Norwegian saithe landings and the landings in Finnmark 1908-1985. The ratios between landings in Finnmark and the total Norwegian saithe landings have also been calculated.

Catch per Unit of Effort

For saithe, the longest continuous data series of catch per unit of effort in the Barents Sea region is for English conventional trawlers in ICES Sub-area I for the years 1946-1978. For 1946-1972 data are given in ANON. (1974). Values for 1973-1978 and revised figures for the period 1966-1972 were submitted by Mr. B.W. Jones, Fisheries Laboratory, Lowestoft, England.

RESULTS

Recruitment

Table 1 shows the estimates of year class strength of North-East Arctic saithe for 1946-1958, the year class strength 1959-1981 taken directly from the VPA, and indications of the climatic regime in each year. There is no evidence of a close correspondence between year class strength of saithe and the climate. Of the seven most abundant year classes in the period 1959-1981, three were

Table 1. Year class strength (age 1) of North-East Arctic saithe 1946-1981 from VPA (1946-1958 back-calculated), and indications of the climatic regime in each year.

Year	Number (millions)	Climatic regime	Year	Number (millions)	Climatic regime
1946	157	Medium	1959	278	Warm
1947	69	Medium	1960	413	Warm
1948	144	Medium	1961	144	Warm
1949	122	Medium	1962	439	Warm
1950	200	Warm	1963	246	Cold
1951	312	Warm	1964	327	Medium
1952	237	Warm	1965	234	Cold
1953	238	Warm	1966	454	Cold
1954	179	Warm	1967	426	Cold
1955	131	Warm	1968	464	Cold
1956	194	Cold	1969	272	Cold
1957	127	Cold	1970	344	Warm
1958	140	Cold	1971	147	Warm
			1972	255	Warm
			1973	460	Warm
			1974	377	Warm
			1975	223	Warm
			1976	352	Warm
			1977	205	Cold
			1978	447	Cold
			1979	172	Cold
			1980	147	Cold
			1981	144	Cold

produced in warm years, and four in cold years. Exactly the same distribution between warm and cold years was found for the seven poorest year classes.

In the earlier period the year class strength was apparently on a lower level. However, this may be an artificial effect of the VPA. If only the relative sizes of the year classes 1946-1958 are considered, there seems to be a relationship with the climate. The four strongest year classes (1950-1953) coincide with a warm period, and two of the three most recent and therefore most reliably estimated of the poor year classes were produced in a cold climatic period.

Fig. 2 shows the year class strength of Arctic cod versus the year class strength of North-East Arctic saithe in the period 1959-1980. There is no linear correlation, and the only observation which may be of some significance, is that the most abundant year classes of saithe have been produced only in years with poor or medium year classes of cod, and vice versa. In other words, strong year classes of cod and saithe have not been produced in the same year.

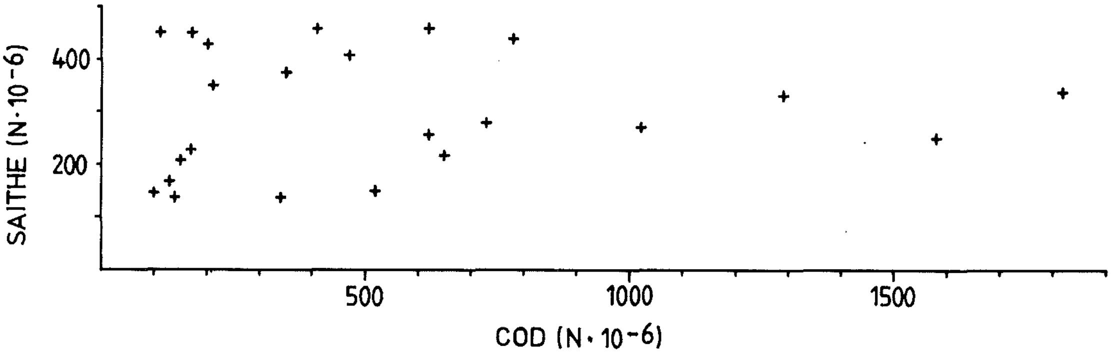

Fig. 2. Year class abundance of Arctic cod vs. year class abundance of North East Arctic saithe.

Table 2 shows the year class strength 1959-1981 for the North-East Arctic, North Sea, Faroe, and Icelandic saithe stocks. Although the linear correlation between any two of the series is poor, a common feature is that all stocks had a period of good recruitment in 1966-1968 and a period with poor recruitment in 1974-1977.

Fishing

The landings of saithe in Finnmark were generally increasing from 1908 to 1940, approximately at the same rate as the total Norwegian saithe landings (Fig. 1). After the war, the total landings have continued to increase, whereas in Finnmark the landings show large fluctuations, but no clear trend until 1970. After 1970, landings in Finnmark have been declining. The general increase in saithe landings probably reflects improved efficiency in the fisheries. It is likely that deviations from the general pattern to some extent is caused by changes in the saithe stock, but it is equally possible that market mechanisms, weather conditions, and the availability of other fish stocks have influenced the fishing effort and accordingly the catches. It would therefore be only guesswork to try to infer something about the size of the saithe stock from the landings.

Table 2. Year class strength of the North-East Arctic, North Sea, Faroe, and Icelandic stocks of saithe 1960-1980. (For each stock, XXX=the seven strongest, XX=the seven medium, X=the seven poorest year classes in the period).

Year class	Stock of saithe			
	NE Arctic	North Sea	Faroe	Iceland
1960	XXX	X	XX	XXX
1961	X	X	X	XX
1962	XXX	XX	XX	XXX
1963	XX	X	XX	XXX
1964	XX	XX	XXX	XXX
1965	X	X	XX	XXX
1966	XXX	XXX	XXX	XXX
1967	XXX	XXX	XXX	XXX
1968	XXX	XXX	XXX	XX
1969	XX	XX	XXX	XX
1970	XX	XX	XX	X
1971	X	XX	XX	X
1972	XX	XXX	X	X
1973	XXX	XXX	XX	XX
1974	XX	XX	X	X
1975	X	X	X	XX
1976	XX	X	X	XX
1977	X	X	X	X
1978	XXX	XXX	XXX	X
1979	X	XX	X	X
1980	X	XXX	XXX	XX

A low ratio between landings in Finnmark and total Norwegian landings may be an indication of a westward shift in the distribution of the saithe stock. It is not known to what degree factors that are not stock-related can affect this ratio, but there is a possibility that they to some extent cancel out. Table 3 gives the ratios for the whole period 1908-1985 together with indications of the climatic regime. The ratios for 1940-1945 can safely be assumed to have been affected by the war. In the years after 1976, the ratios have been declining. This is to a large extent a result of the rapid increase in Norwegian saithe catches from the North Sea following the introduction of national economical zones. In both periods 1908-1939 and 1946-1976, the ratios are on the average slightly higher in warm than in cold periods. However, this difference is clearly not significant because the average ratios for the years of medium climate are by far the highest in 1908-1939 and the lowest in 1946-1976.

The time series of English catch per unit of effort in Sub-area I is given in Table 4. The high level immediately after the war is in all likelihood due to the increased stock size which must have resulted from the low level of exploitation during the war. Apart from this, three periods are outstanding: 1961-1963 with low values, 1969-1972 with high values, and 1974-1978 with low values. All three periods include both cold and warm years, and the only indication of relationship with the climate is that the periods with low values start towards the end of warm periods, while the high values start towards the end of a cold period. Allowing for a time-lag of about five years the two

Table 3. Landings of saithe in Finnmark 1980-1985 in proportion to the total Norwegian saithe landings, and indications of the climatic regime in each year.

Year	Ratio Finnmark/ Total	Climatic regime	Year	Ratio Finnmark/ Total	Climatic regime
1908	.22	Medium	1946	.28	Medium
1909	.33	Cold	1947	.37	Medium
1910	.38	Cold	1948	.51	Medium
1911	.37	Cold	1949	.51	Medium
1912	.42	Cold	1950	.40	Warm
1913	.41	Cold	1951	.39	Warm
1914	.47	Cold	1952	.21	Warm
1915	.40	Cold	1953	.32	Warm
1916	.18	Cold	1954	.23	Warm
1917	.12	Cold	1955	.28	Warm
1918	.21	Medium	1956	.24	Cold
1919	.14	Medium	1957	.26	Cold
1920	.21	Medium	1958	.20	Cold
1921	.17	Medium	1959	.18	Warm
1922	.33	Medium	1960	.25	Warm
1923	.32	Cold	1961	.27	Warm
1924	.29	Cold	1962	.17	Warm
1925	.32	Cold	1963	.24	Cold
1926	.25	Cold	1964	.41	Medium
1927	.39	Cold	1965	.23	Cold
1928	.43	Cold	1966	.19	Cold
1929	.44	Cold	1967	.19	Cold
1930	.48	Warm	1968	.16	Cold
1931	.39	Warm	1969	.25	Cold
1932	.42	Warm	1970	.26	Warm
1933	.41	Warm	1971	.25	Warm
1934	.43	Warm	1972	.24	Warm
1935	.39	Warm	1973	.25	Warm
1936	.45	Warm	1974	.19	Warm
1937	.40	Extra warm	1975	.27	Warm
1938	.42	Extra warm	1976	.18	Warm
1939	.34	Extra warm	1977	.21	Cold
1940	.49	?	1978	.18	Cold
1941	.33	?	1979	.18	Cold
1942	.24	?	1980	.14	Cold
1943	.36	?	1981	.11	Cold
1944	.30	?	1982	.11	Cold
1945	.01	Medium	1983	.09	Warm
			1984	.07	Warm
			1985	.07	Warm

first periods correspond to periods of respectively low and high recruitment. Also the low values in the most recent period correspond to a period where the year class strength was reduced, but not to the extent indicated by the catch rates.

Table 4. Catch of saithe per unit of effort by English conventional trawlers in Sub-area I, 1946-1978.

Year	Catch per unit of effort (tons per million ton-hours)	Climatic regime
1946	29	Medium
1947	74	Medium
1948	93	Medium
1949	75	Medium
1950	62	Warm
1951	47	Warm
1952	39	Warm
1953	49	Warm
1954	30	Warm
1955	27	Warm
1956	35	Cold
1957	39	Cold
1958	36	Cold
1959	36	Warm
1960	35	Warm
1961	16	Warm
1962	14	Warm
1963	12	Cold
1964	45	Medium
1965	38	Cold
1966	46	Cold
1967	25	Cold
1968	36	Cold
1969	56	Cold
1970	100	Warm
1971	58	Warm
1972	55	Warm
1973	32	Warm
1974	8	Warm
1975	10	Warm
1976	10	Warm
1977	10	Cold
1978	7	Cold

DISCUSSION

Although there are undoubtedly some errors in the recruitment estimates, the time series of year class strength is still the one most likely to reveal a relationship with the climate. The fact that no correlation was found therefore strongly indicates that there is no relationship or, at the most, a weak one. Since such a relationship has been demonstrated for Arctic cod (SÆTERSDAL and LOENG 1984), the poor correlation between year classes of North-East Arctic saithe and Arctic cod was to be expected.

The Norwegian data on landings are reliable, and except for the most recent years they correspond closely to the catches in the different coastal areas. The problem is that they do not necessarily reflect changes in the stock size and the geographical distribution, because the fishing effort, in addition to being generally increasing, obviously also has fluctuated somewhat from year to year. However, if the climate strongly affects the catches in Finnmark, it would be a rare coincidence if variations in the effort had masked this effect over such a long period. The landings therefore also indicate a lack of relationship between North-East Arctic saithe and the climate.

The catch per unit of effort seems to have been more influenced by the stock size than by the climate. However, the English trawlers were fishing mainly for cod, and the catch rates for saithe may not be a very reliable index of the abundance.

The lack of a close stock-recruitment relationship for North-East Arctic saithe (Fig. 3) is evidence of a dependence on environmental factors for the recruitment. Since the different time series have failed to reveal a relationship with the climatic regime in the Barents Sea, it seems likely that other environmental factors are more important. The similarities in relative year class strength between the stocks of saithe may be an indication of a common environmental influence for the North-East Atlantic Ocean. GARROD and COLEBROOK (1978) suggested that there was a common climatic effect on fish stocks in the area, but SHEPHERD, POPE and COUSENS (1984) found little evidence for this. For saithe they implied that the frequent long-range migrations of the species could mask differences in recruitment between the stocks. However, migration can hardly explain the concurrence of a period of low recruitment in all stocks from 1974 to 1977. It may therefore be significant that this occurred during a period when the salinities in the Faroe-Shetland Channel were reduced to a level not observed since before 1920 (DOOLEY, MARTIN and ELLETT 1984). The event started after 1972 and the minimum was reached in 1976. The Faroe-Shetland Channel is the principal route for the passage of Atlantic water into the Norwegian Sea, and the reduced salinities reflect, among other things, a reduced inflow. During the period of consistently high recruitment to the saithe stocks 1966-1968, the salinities were normal. This could mean that recruitment of the saithe stocks

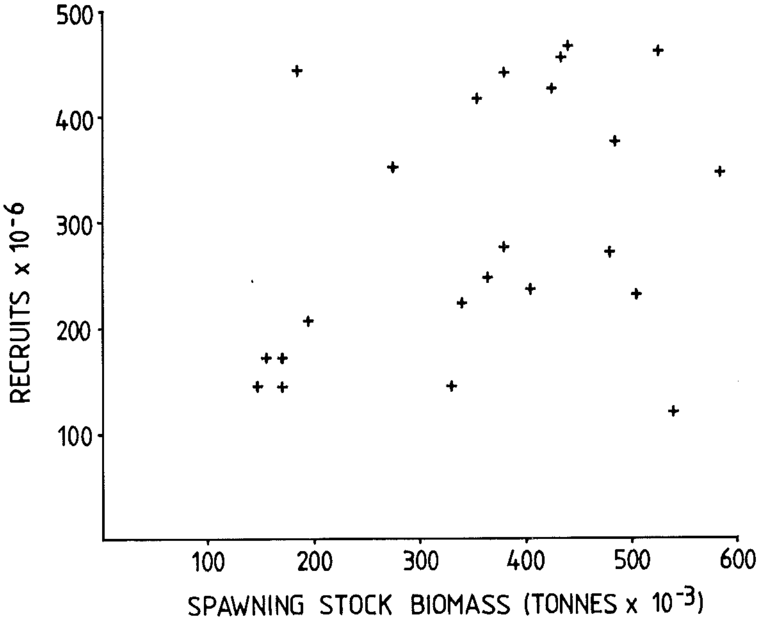

Fig. 3. North-East Arctic saithe. Spawning stock biomass vs. recruitment.

is reduced in years of extremely low inflow of Atlantic water, but that variations in inflow within the normal range is of minor importance. That fish stocks in many cases will react only to extreme changes of environmental conditions was suggested by SHEPHERD *et al.* (1984). Thus, the remaining variation in recruitment must be caused by other environmental factors. So far their nature is mostly unknown. However, there is evidence of one factor which seems to have a regulatory effect on the year class strength of saithe. EGIDIUS and ANDERSEN (1975) describe an epizootic of vibriosis on juvenile saithe along the Norwegian coast in 1974. Although the epizootics have not been regularly investigated, the disease which is caused by the bacterium *Vibrio anquillarum* seems to be especially lethal in years of high density of juvenile fish. This would tend to reduce the strong year classes and accordingly the variation in year class strength.

SÆTERSDAL and LOENG (1984) presented the hypothesis that the reproduction of cod through evolutionary processes is adjusted to the variations in the feeding area caused by climatic fluctuations. The feeding area of the North-East Arctic saithe is normally restricted to the coastal banks, and its extension appears to be clearly more stable than for cod. It is therefore possible that the saithe stock has a more stable supply of food. In this context it may also be significant that the saithe is feeding mostly on plankton. A stable supply of food from year to year is most efficiently utilized by a stable stock. This may be the evolutionary basis for the fact that the year class abundance for saithe is generally less variable than for cod.

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THE EFFECT OF AMBIENT TEMPERATURE ON THE SPAWNING MIGRATION OF CAPELIN

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ABSTRACT

The model presently in use for management of the Barents Sea capelin stock may be considerably improved by utilization of biological information from the spawning stock. The distributions of length and age for capelin during it's spawning migration exhibit considerable geographical variation. Previously, it was not possible to construct reliable length and age distributions based on direct measurements for the spawning stock. The present paper seeks to develop a method for estimating the geographical distribution of the spawning migration, once the initial distribution and the sea temperature is known. To do this, a theory for spawning migration is developed, and the east-west component of the migration pattern is estimated. Possible relationships between the estimated migration and the sea temperatures at onset of migration and sea temperatures at the end of migration are discussed.

INTRODUCTION

The most important part of the mathematical model presently in use for management of the Barents Sea capelin stock is the submodel for dividing the total population as measured in the autumn, into

1) a maturing part that will spawn the next spring, and
2) an immature part that will not take part in the spawning migration (TJELMELAND 1985).

This model is constructed by comparing the modeled immatures next autumn to the measured autumn stock (HAMRE and TJELMELAND 1982). By performing a similar procedure comparing the modeled mature stock to the measured spawning stock, an independent check of the model could be made. Also, calculations involving only half a year simulation should be preferred to calculations involving one year simulation.

Although having been tried (HAMRE and TJELMELAND 1982) such a use of data from the spawning stock is difficult because it is not possible to construct reliable distributions. The reason for this is that both the distributions for age and length may be very different in the western and eastern part of the spawning migration. A method for weighting these distributions properly, in order to obtain a distribution for the spawning stock based on biological samples from the spawning stock, does not exist.

The present paper is an attempt to construct such a method. The maturing part of the stock, as measured in the autumn, is transformed into an eastern and a western spawning stock component using a new theory for the spawning migration. An average migration pattern for the years 1980-1985 is estimated by comparing the mean length differences between modeled and measured stock in the eastern and western spawning area, respectively. One parameter for an annual east-west deviation from the migration pattern is then estimated year for year. This deviation parameter was found to correlate with the hydrographic conditions. This makes it possible to forecast the geographical distribution of the spawning migration for the following spring once the geographical distribution in the autumn and the temperatures are known.

The implications of this method for management are greater than just a safer basis upon which to construct models for the maturing of capelin. Also, a quantification of the east-west parts of the spawning migration is important in order to quantify the overlap between capelin and cod. Furthermore, an important feature is the possible correction of the recruitment relation which can be made. A western spawning gives rise to larvae having different surviving and growth conditions than an eastern spawning.

MATERIALS AND METHODS

OZHIGIN and LUKA (1985) treated the geographical distribution of spawning extensively, and demonstrated that during warm years, capelin tend to have a more easterly spawning than for cold years. However, in the present paper the scope will be widened to also include a quantification. In order to do so, a verbal theory for migration that can serve as a basis for quantification must first be constructed.

The spawning stock will be defined as the stock consisting of fish having a maturing stage at or above a certain level, as measured in the autumn. The new maturity scale based on microscope investigations of eggs will be used (FORBERG and TJELMELAND 1985, FORBERG 1982). Thus, the spawning stock in this paper will be an ambiguous concept, dependent on which stage is used. The use of the new maturity scale leads to the restriction that only females may be used. Also, only 3 year old fish during the autumn will be studied in order to simplify the investigations. This age group, which will be 4 years in the spring, constitute the major part of the spawning stock. Consequently, this age group gives the most comprehensive data base. Thus, for this paper, the geographical distribution of mature 4 year old females was studied, and the dependence on the temperature regime is discussed.

Throughout this paper, the geographical distribution of capelin will be based on the area division shown in Fig. 1. Table 1 shows the mean lengths of maturing 3 year old capelin in September. In constructing the table, the computer program presented at the Soviet-Norwegian symposium in 1984 is used (GJØSÆTER 1985). The area division (Fig. 1) is also the same as used in the previous symposium. The method of field sampling is described by DOMMASNES and RØTTINGEN (1985) and GJØSÆTER (1985).

With only one exception (stage IIIc, 1983), the mean lengths are always greater in area 7 than in area 8 for fish within the same maturity stage. There is thus no one-to-one correspondence between length and maturity, even for fish within the same age group. Environmental factors are most

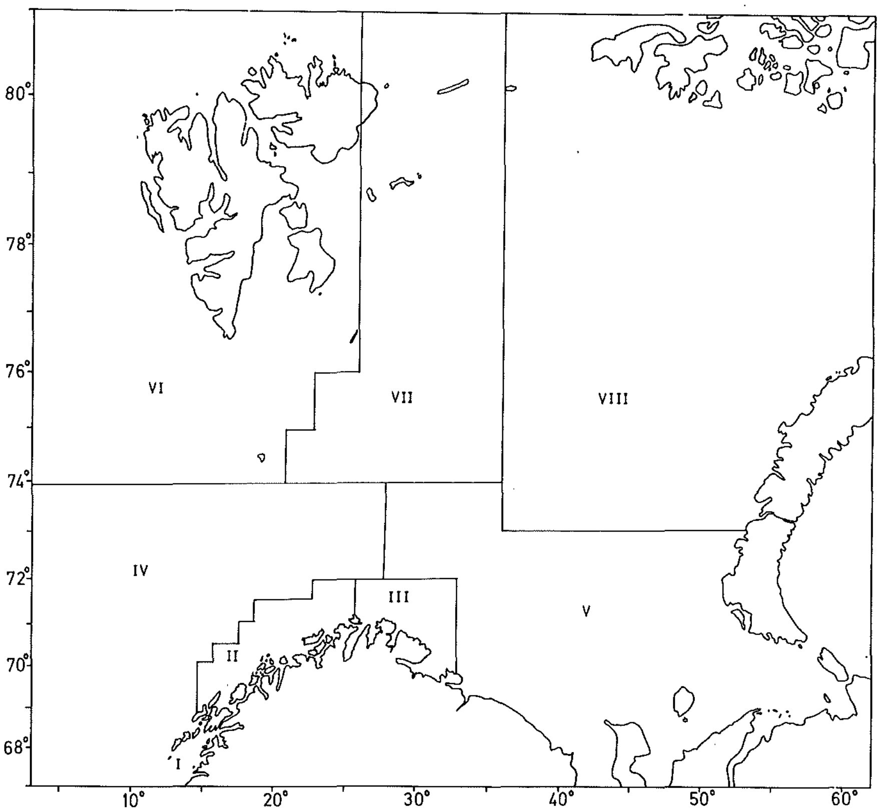

Fig. 1. Map of the Barents Sea showing the geographical division referred to in the text.

probably governing the relative speed between length growth and maturation. With the exception of 1980, the mean lengths are also greater in area 6 than in area 7. Thus there is an increase in length from east to west for all maturity stages.

Table 2 shows the mean length from biological samples of the spawning stock. Only fish of maturing stage 3 or greater (old stage, GJØSÆTER 1985) were used in order to avoid accidental catches of immature fish. Data from research vessels as well as from commercial catches were used. The sampling from commercial catches was described by GJØSÆTER (1985). Fig. 2 shows the geographical distributions of the samples used. With the exception of 1984, March samples from areas 2 and 3 have been used. For 1985, two samples from area 4 were also added to the samples from area 2. For 1984, February samples were used due to insufficient sampling during March.

During 1981, 1983, and 1984, the fish were longer in the western area 2 than in the eastern area 3. The mean length differences were, however, much smaller than would be expected from the differences in mean length between areas in the autumn. In 1982 the fish were longer in the eastern area. These figures are not consistent with the simple theory of migration which assumes that fish being found in the eastern parts of the sea during the autumn will spawn in the eastern parts of spawning area and vice versa.

DISCUSSION

A theory for the spawning migration of capelin

In order to explain these data, the following migration theory is suggested:

Table 1. Number (N, 10^6 ind.) and mean length (l, cm) of maturing 3 year old female capelin.

1980	Area V		Area VI		Area VII		Area VIII	
	N	l	N	l	N	l	N	l
IIb	4305	15.32	801	15.06	30906	16.19	34873	15.37
IIIa	3588	15.40	567	15.21	28061	16.30	29456	15.49
IIIb	2501	15.58	285	15.39	23887	16.48	16807	15.71
IIIc	1251	15.77	16	15.75	15226	16.75	5825	15.88
1981	Area V		Area VI		Area VII		Area VIII	
	N	l	N	l	N	l	N	l
IIb	477	15.21	499	17.89	14305	15.79	6766	15.60
IIIa	405	15.27	499	17.89	12505	15.96	6037	15.66
IIIb	234	15.60	499	17.89	9153	16.21	3807	15.84
IIIc	36	16.50	325	18.06	5314	16.41	501	16.00
1982	Area V		Area VI		Area VII		Area VIII	
	N	l	N	l	N	l	N	l
IIb	7339	15.60	3029	17.41	11590	16.42	12848	15.71
IIIa	6815	15.62	3029	17.41	11222	16.49	12088	15.73
IIIb	2983	15.82	3029	17.41	10642	16.56	7145	15.88
IIIc	517	15.90	2661	17.61	6311	16.79	1359	16.25
1983	Area V		Area VI		Area VII		Area VIII	
	N	l	N	l	N	l	N	l
IIb	635	16.02	373	16.08	8431	15.69	3194	15.04
IIIa	578	16.03	373	16.08	7576	15.81	3012	15.07
IIIb	55	16.59	175	16.82	6318	15.92	1838	15.15
IIIc	0		136	16.86	2344	16.06	518	16.16
1984	Area V		Area VI		Area VII		Area VIII	
	N	l	N	l	N	l	N	l
IIb	0		2108	16.09	3964	15.95	7090	15.29
IIIa	0		1967	16.29	3743	16.07	6242	15.29
IIIb	0		1568	16.49	2875	16.40	3493	15.61
IIIc	0		715	16.91	1785	16.73	1285	15.57

Table 2. Mean length (l, cm) and number of specimen (N, 10^6 ind.) of mature 4 year old female capelin. Data from March samples.

Year	Area 2		Area 3	
	l	N	l	N
1981	16.34	424	16.29	658
1982	16.49	305	16.72	612
1983	16.62	299	15.93	220
1984	16.28	425	15.74	191
1985	15.92	152	16.20	187

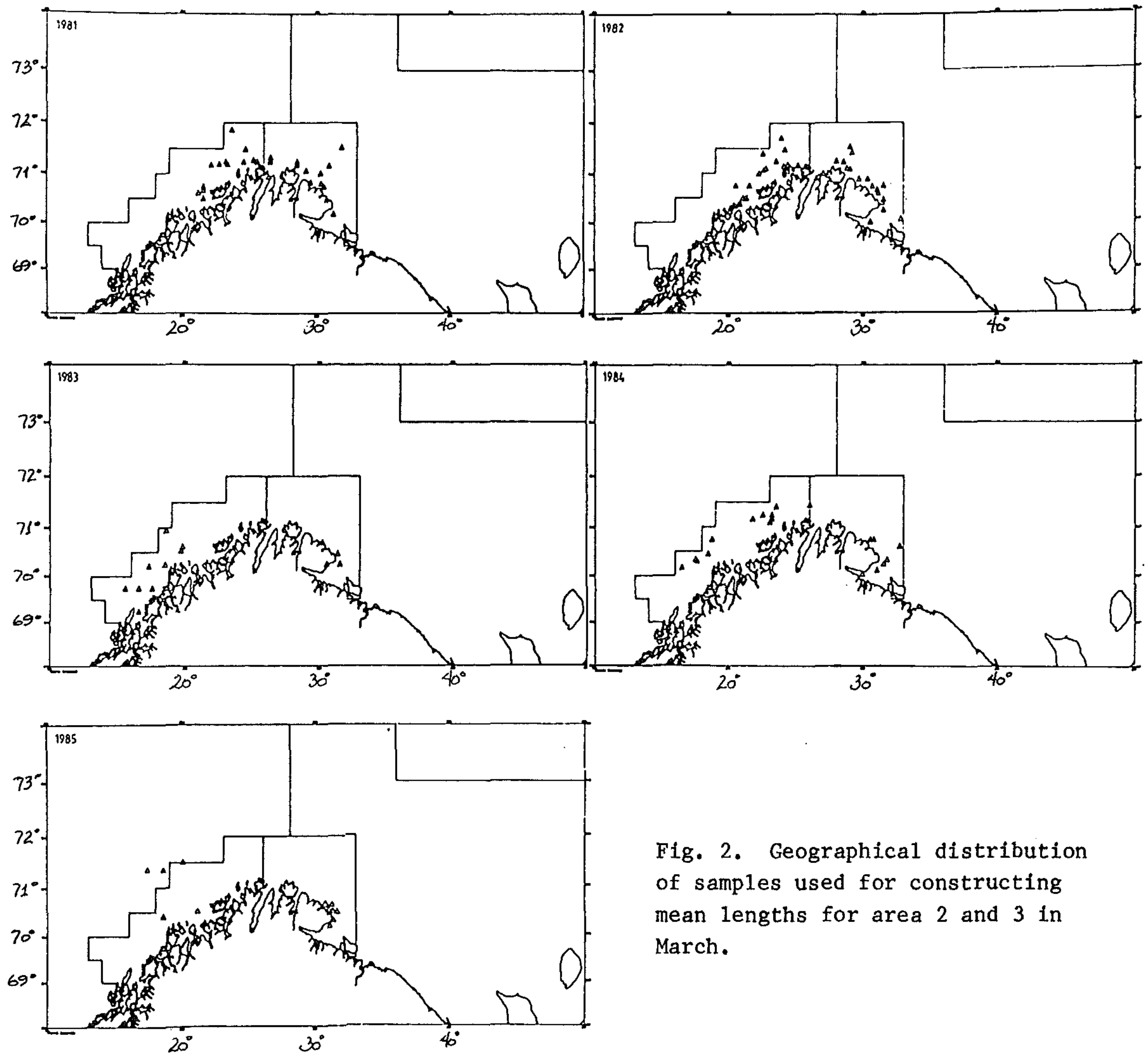

Fig. 2. Geographical distribution of samples used for constructing mean lengths for area 2 and 3 in March.

> Fish at the most mature stages during the autumn will start their spawning migration earlier than fish at lower maturity stages.

And in conjunction with this:

> The spawning migration is temperature dependent. Higher temperatures in the sea leads to migration routes which are further west.

We know from hydrographical observations (LOENG 1984) that the Barents Sea is cooled down during the winter period, and reaches the coldest temperature about April. The decrease in temperature during this period is about one degree, comparable to the temperature difference between areas. Loeng's results are, in this respect, considered generally valid. This means that during the whole period of spawning migration, the isotherms move westwards. Fish having a late start for spawning remain in colder water masses, and will eventually seek more western migration routes.

The theory above together with the fact that the sea is being cooled during the migration period implies that the fish will be of greater length in the eastern part of the spawning stock.

The length differences observed in the spawning stock between area 2 and 3 and the observation that longer fish tend to have a more westerly starting point support the above theory. Which factor is the most important is most probably linked to the oceanographic conditions each year.

The estimation procedure

Two maturity stages are defined. All fish in stage M1 and higher will start the spawning migration early. All fish in stage M2 up to, but not including M1, will start the spawning migration late. A definition of "early" and "late" in terms of dates is immaterial here.

For each of the areas 5-8 and stages M1 and M2, a number P_j^i is defined. The upper index i takes the values 1 and 2 and designates the maturity stage. The lower index j takes the values 5-8 and designates origin area.

P_j^i yields the fraction of the fish migrating to area 3, $1-P_j^i$ yields the fraction of fish migrating to area 2. There exists 8 such numbers, the upper index designating the stage, the lower index designating area. Three simplifying assumptions have been made:

The most mature fish in area 5 will spawn in area 3, $P_5^1 = 1.0$.

The most mature fish in area 8 will spawn in area 3, $P_8^1 = 1.0$.

The least mature fish in area 6 will spawn in area 2, $P_6^2 = 0.0$.

The collection of P's will be called the migration pattern.

The components of the stock spawning in area 2 from each of the areas 5-8 were pooled together, and the mean length, L_2 calculated. The same was done for fish spawning in area 3. The mean length of the biological samples, l_2, obtained for March was calculated. The goal function for the estimation is now defined as:

$$\sum_{\text{years}} ((L_2-L_3)-(l_2-l_3))^2$$

Thus, in order to estimate the migration pattern, the expression above is to be minimized.

Unknown factors

Maturity

We do not know specifically which maturity stage corresponds to fish that mature early, and which stage corresponds to fish maturing at all. The analysis is therefore carried out for two different cases:

a) early migrating fish will be found in stage IIIa+ and late migrating fish will be found in stage IIb, and

b) fish which migrate early will be found in stage IIIb+ and those which migrate late will be found in stage IIIa.

These stages are likely candidates for spring spawning (FORBERG and TJELMELAND, 1985).

Growth

By using length differences for comparison instead of absolute lengths, the uncertainty in the overall length growth during the period between the autumn and spring observations is removed. Still, the growth may have been different for fish in different geographical areas. Table 3 shows the otolith growth zone for the spring period for the fish that were used. The growth is more or less the same for fish found in area 2 and fish found in area 3. A slightly higher growth has, however, occurred for fish migrating to area 3 in 1985 and 1983. This difference in growth is corrected for by assuming a proportionality between the growth of otolith and the growth of length. The relationship of growth between length and otolith may not be the same for rapidly maturing fish as that of immature or slowly maturing fish. During the spawning migration, it is conceivable that excess energy is converted to spawning products rather than to growth in length. In this case the ratio of growth between length and otolith may be higher than average. Due to this consideration, the analysis has been performed for two cases. These are for full growth correction for 1983 and 1985, and half growth correction for 1983 and 1985.

Table 3. Spring otolith growth zone (mm) for 4 year old female capelin. Data from March samples.

Year	Area 2	Area 3
1981	0.047	0.044
1982	0.028	0.030
1983	0.024	0.038
1984	0.027	0.027
1985	0.038	0.063

During the autumn, there may be some growth between the time of measurement and the time of deposit of the winter ring. Table 4 shows the mean total otolith radius measured in the autumn and the mean total otolith radius measured during the spring. With correction for the spring otolith growth, it is seen that there was a non-negligible "rest autumn growth" during 1982 and 1985. With the method used in this paper, this can not be corrected for. If the rest autumn growth is much different for the different areas, our results become biased.

Table 4. Mean total otolith radii (mm).

	Autumn	Spring
1980-1981	0.897	0.947
1981-1982	0.907	0.978
1982-1983	0.909	0.948
1983-1984	0.916	0.946
1984-1985	0.904	0.970

ESTIMATION OF MIGRATION

Estimation of migration pattern for the years 1980-1985

Using the above outlined procedure, the migration pattern for the years 1980-1985 is estimated. The results are given in the text table below. Most later migrating fish (M2) from area 8 end in area 3. Most early migrating fish (M1) from area 7 end in area 3, most later migrating fish from area 7 end in area 2.

Migration pattern P_j^i 1980-1985

Full correction for 1983 and 1985 spring growth

	j	5	6	7	8
M1=IIIa	i=1	1.00	0.00	0.70	1.00
M2=IIb	i=2	0.94	0.00	0.01	0.73

M1=IIIa	i=1	1.00	0.02	0.79	1.00
M2=IIb	i=2	0.96	0.00	0.02	1.00

Half correction for 1983 and 1985 spring growth

	j	5	6	7	8
M1=IIIa	i=1	1.00	0.24	0.75	1.00
M2=IIb	i=2	1.00	0.00	0.13	0.74

M1=IIIa	i=1	1.00	0.00	0.73	1.00
M2=IIb	i=2	1.00	0.00	0.00	0.87

M2 is in both cases lower than M1 for area 7, in accordance with the migration theory.

Definition of the deviation from the migration pattern

The year-to-year deviation from the general migration pattern obtained above will be defined by a single parameter, D. This is added to P. The reasoning for this is that, if shifts in the ambient temperature cause a deviation from the general migration pattern, this deviation will be in the same direction for all areas, i.e. a cooling of the sea will lead to a more westerly spawning migration from all areas. By defining one single deviation parameter, the general trends for the impact of temperature on migration can be revealed. The influence of temperature may have a different magnitude for each area, but is not revealed by this procedure.

Confidence intervals

The variable

$$t = \frac{(L_2-L_3) - (l_2-l_3)}{\sqrt{\frac{1}{M} + \frac{1}{N}} \cdot s}$$

where M = Number of fish measured in area 2

N = Number of fish measured in area 3

$s^2 = [\sum_{i}^{M} (l_{2_i} - l_2)^2 + \sum_{i}^{N} (l_{3_i} - l_3)^2]$

l_i is the individual length for the i-th fish

will have a t-distribution. This is used to construct 95% confidence intervals. In using this procedure, the number of measured fish is fixed. This simplification does not alter the confidence intervals very much, since the t-values corresponding to the confidence limits will not vary much when the number of observations is high. In all cases, there were so many observations that the asymptotical limit of a normal distribution nearly approximated.

Estimating deviation

Both combinations of estimating maturity stages (M_1 and M_2) give the same general result (Fig. 3).

During the period of autumn through spring, 1981/82, and 1982/83, the migration was more easterly than for that period of 1980/81. During this period for 1983/84, there was an abrupt shift to a westerly migration which reversed towards the average pattern during this period for 1984/85.

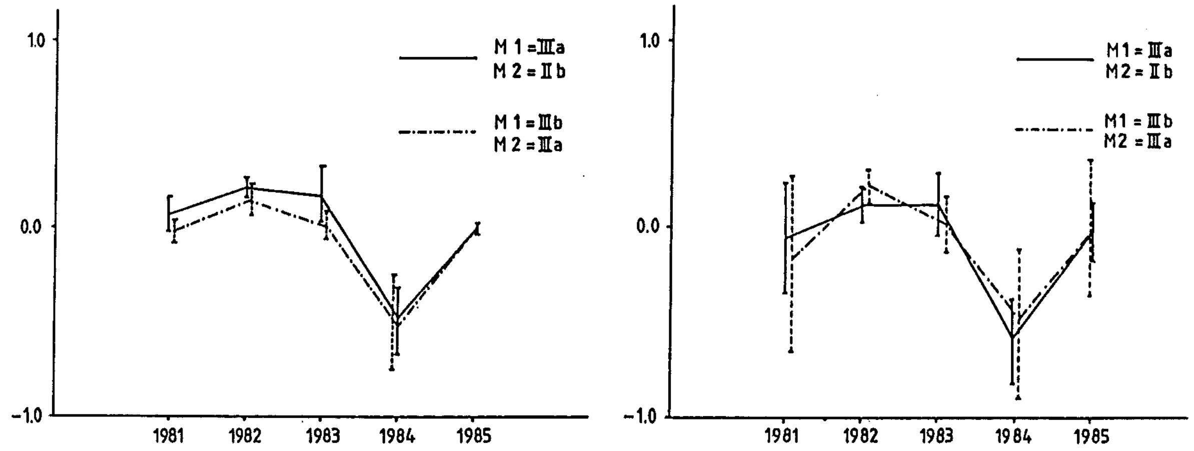

Fig. 3. Estimated migration deviation from the general migration pattern in Table 4. Left figure: Full correction of spring growth. Right figure: Half correction of spring growth.

These results have been obtained by relaxing the constraint of full migration to area 3 for the earliest migrating capelin from area 5 and 8, and full migration to area 2 of the latest migrating capelin from area 6. Estimates of migration with these constraints still in operation show nearly the same results with the exception of 1984, where the westwards migration has about half the value of the unconstrained case.

In some cases, the absolute value of migration (sum of P and D) is greater than one. However, the computer program forces all migration to lie in the range 0.0 - 1.0.

TEMPERATURE CHANGES 1980-1985

As an index for the temperature regime during the period, the temperature in

80-120 m depth in two locations near the coast, centered in area 2 and area 3 are (somewhat arbitrarily) chosen for the spring period, while the mean temperatures for the capelin distribution in areas 7 and 8 have been chosen for the autumn period. The latter figures are calculated by GJØSÆTER and LOENG (1987). The changes in temperature regime are given in Fig. 4.

There seems to be a general trend of increased temperatures during the spring. However, the most pronounced feature is the elevated temperatures for the eastern area during 1982 and 1983, which give rise to a vanishing, or negative, east-west gradient.

There also appears to be a general trend of increased temperatures during the autumn period. This is with the exception for 1984, when a cooling may begin. However, the trend is different for areas 7 and 8. The small decrease in temperature from 1980 to 1981 in area 8 gives rise to an increasing east-west gradient which later decreases until 1983. The east-west gradient again increases in 1984.

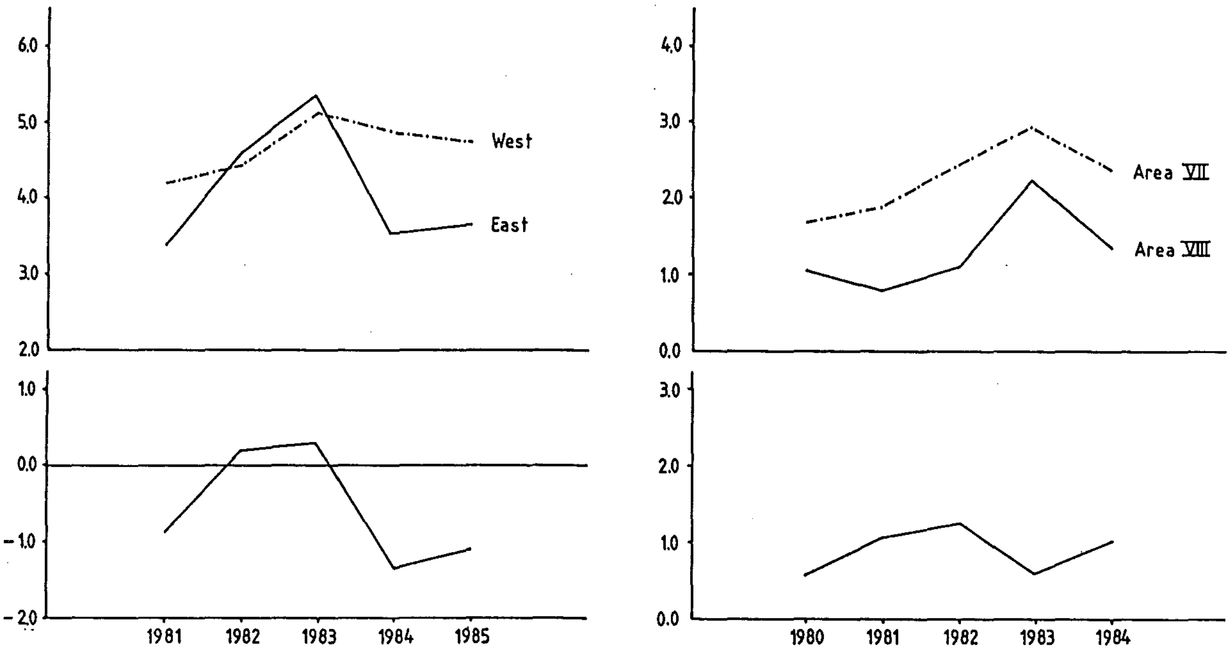

Fig. 4. Temperature indices for spring period (left) and autumn period (right). West-east gradient (spring) and east-west gradient (autumn) in bottom figure.

CONNECTION BETWEEN MIGRATION AND SEA TEMPERATURE

Temperatures in the spring period

The temporary shift in migration towards the west during 1982 and 1983 (spring) coincides with the heating of the coastal waters in 1982 and 1983. However, the temperature drop in 1984 was smaller than the westwards migration movement. Also, the eastwards displacement of migration in 1985 cannot be explained by the temperature level. The correspondence between migration and the east-west temperature gradient is better, such that high temperatures in the eastern part of the coastal area promoted an eastern migration. However, the great eastwards displacement during 1985 was not fully accounted for in this case either.

Temperature in the autumn period

There is a marked tendency to an anti-correlation between sea temperature in the autumn and migration deviation. The highest temperature reached during 1983 for both area 7 and 8 seems to correspond with the western maximum of migration. However, there is better correspondence between migration deviation and temperature gradient in this case, but the correspondence is to a positive, not a negative, gradient. This means that the migration would tend to be easterly if the temperature was much greater for the western than for the eastern part of the capelin distribution during the autumn.

Link between migration and temperatures

The estimations of migration made in this paper, together with the observed development of temperature during the autumn as well as spring, suggest that temperature gradients may be as important as the overall temperature level in the determination of the geographical distribution of the spawning migration. The positive correlation between east-west migration and the autumn temperature gradient is consistent with a theory that the capelin seeks cold temperatures during their pre-spawning migration, i.e. before the gonads are fully developed and some time before spawning. The negative correlation between east-west migration and the spring temperature gradient is consistent with a theory that the capelin seek a warm or some optimal temperature during the month prior to spawning.

The data used were not sufficient to decide which of these factors is the most important. Also, the data show a covariation between the gradients in the autumn and in the spring: High gradients in the autumn have occurred at the same time low gradients in the spring were measured. Therefore, a longer time series of data, where the reverse situation also occurs, is needed in order to quantify the two effects with respect to each other.

It is important to note that, in this context, the east- and westwards migration does not necessarily correlate well with a high abundance of mature capelin in the eastern and western regions of the spawning area, respectively. Our presentation demonstrates that there is a covariation between migration and temperature, irrespective of the actual distribution of the capelin during autumn. The abundance of mature capelin at the eastern and western parts of the spawning area will then be the combination of the migration and the geographical distribution during the onset of migration.

CONCLUSIONS

Although the link between temperature gradients and spawning migration has only been demonstrated for female 4 year old capelin (spring), there is reason to believe that the demonstrated method may be powerful in order to develop models of migration for the whole capelin stock.

A future development of the method would be to include more age groups and to allow the parameter of deviation to have different values in different areas. Also, we might use full distributions of length and distributions of age as comparative data. If so, however, problems concerning growth and the impact of the fishery will arise.

It is necessary to incorporate the geographical dimension and a submodel for migration into the present model for capelin in order to improve the base for future management of the capelin stock. Furthermore, in order to take full advantage of the extensive scientific work on Barents Sea capelin and related subjects, a more comprehensive model of capelin is needed. The present paper is a first attempt to explore some of the possibilities and problems which advance a model for management through the construction of models for migration.

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THE EFFECT OF OCEANOGRAPHIC CONDITIONS ON DISTRIBUTION AND POPULATION
DYNAMICS OF COMMERCIAL FISH STOCKS IN THE BARENTS SEA
Proceedings of the third Soviet-Norwegian Symposium, Murmansk, 26-28 May 1986
Edited by H. Loeng. Institute of Marine Research, Bergen, 1987.

DISTRIBUTION OF DEEP SEA SHRIMP (Pandalus borealis Krøyer) IN RELATION TO TEMPERATURE IN THE BARENTS SEA

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ABSTRACT

In the years 1980 to 1985 stratified random bottom trawl surveys were carried out on the shrimp fields in the Svalbard and Barents Sea regions. The objectives of the cruises were to study the structure of the shrimp stock and to estimate the abundance of shrimp. On each trawl station the bottom temperature was measured. Only the results from the surveys in the Barents Sea have throroughly been analysed with regard to temperature. In the investigated area the deep sea shrimp was abundant in areas with temperature between -1°C and 7°C. The deep sea shrimp appear to avoid cold water fronts of bottom water. The highest shrimp densities were found on the warm water side of the front.

INTRODUCTION

The deep sea shrimp (Pandalus borealis, Krøyer) is widely distributed in the boreal waters. The distribution is discontinuous circumboreal. Factors influencing the distribution patterns are depth, temperature, salinity and substratum. The most common temperature range for P. borealis is between 0°C and 5°C (e.g. HJORT and RUUD 1938, BRYAZGIN 1967, RASMUSSEN 1967). The deep sea shrimp has been reported found in waters with tempteratures of -1.6°C (GORBUNOW 1934, INGRAKAM 1981) and upwards to 12°C (BJØRK 1913). It has been reported that extended exposure to temperatures below -1°C is deleterious and may cause mass mortalities (HORSTED and SMIDT 1956, and INGRAKAM 1981). SMIDT (1978) observed that changes in the distribution of age classes in Disko Bay, West Greenland, were likely caused by intrusion of warm bottom water (7°-8°C). ABERCROMBIE and JOHNSON (1941) describe the effects of temperature shock on shrimps. They (op.cit.) observed that termal death at low temperatures was a slow process. At low lethal temperatures the period of depression may last for hours or days. The activity of shrimps increases as the temperature increases. At high lethal temperatures, between 10°C and 15°C, there may be no period of depression, and the shrimps may be subject to a sudden death.

MATERIAL AND METHODS

A stratified random sampling scheme was used on bottom trawl surveys with R/V "Michael Sars" in the years 1980 to 1985 in the Barents Sea. The main objective was to estimate the abundance and structure of the deep sea shrimp populations. Similar investigations were conducted in the Spitsbergen waters in the years 1982 to 1985. The results from both these investigations are published as reports to the ICES Shellfish Committee (TAVARES and ØYNES 1980, TEIGSMARK and ØYNES 1981, TEIGSMARK and ØYNES 1982, TEIGSMARK and ØYNES 1983, HYLEN, TVERANGER and ØYNES 1984, TVERANGER and ØYNES 1985). In this instance, only the results from the Barents Sea are presented.

The bottom temperature was measured at each trawl station in this program. However, during 1983 very few temperatures were measured because of some administrative and technical problems. Also from 1984 there are few temperature registrations available in time for this meeting because of an error in the computer system.

In the Barents Sea there are bottom temperatures from 93 trawl stations in 1981, 106 in 1982 and 116 in 1985. During 1984 the bottom temperature was measured, but only 14 can be found in the computer system. However, we know that the bottom temperature was above 0°C at each station (Loeng pers. comm.).

The investigations took place in the same area and during the same period of the year each year, namely April/May.

RESULTS AND DISCUSSION

Table 1 shows the number of trawl stations in each half degree temperature interval and the mean amount by weight of shrimps per 3 nautical miles (1 hour trawled). In 1981 the highest density of deep sea shrimps were in waters of temperature between -0.9°C and -0.5°C (233 kg per 3 nautical miles). In 1982 there were small differences in catch per hour in the different temperature intervals, and the maximum catch (199 kg per hour) were taken in an area with temperature between 2.1°C and 2.5°C. In the years 1984 and 1985 the bottom water was warmer on the shrimp fields than the years before.

Table 1. Number of trawl stations in different temperature regimes, and the mean amount by weight of shrimp in each haul of one hour duration (kg/h).

Temperature	YEAR 1981		1982		1984		1985	
	NO.	kg/h	NO.	kg/h	NO.	kg/h	NO.	kg/h
< - 1°C	3	27	2	63	0			
-0.9°C - -0.5°C	2	233	5	80	0			
-0.4°C - 0°C	9	142	5	117	0			
0.1°C - 0.5°C	14	137	9	141	3	289	9	166
0.6°C - 1.0°C	18	134	19	177	3	421	17	151
1.1°C - 1.5°C	18	157	30	116	2	149	26	148
1.6°C - 2.0°C	8	112	5	172	0		19	75
2.1°C - 2.5°C	5	87	8	199	4	197	20	42
2.6°C - 3.0°C	16	113	7	146	2	234	9	46
3.1°C - 3.5°C	0		13	93	0		5	42
3.6°C - 4.0°C	0		3	65	0		11	89

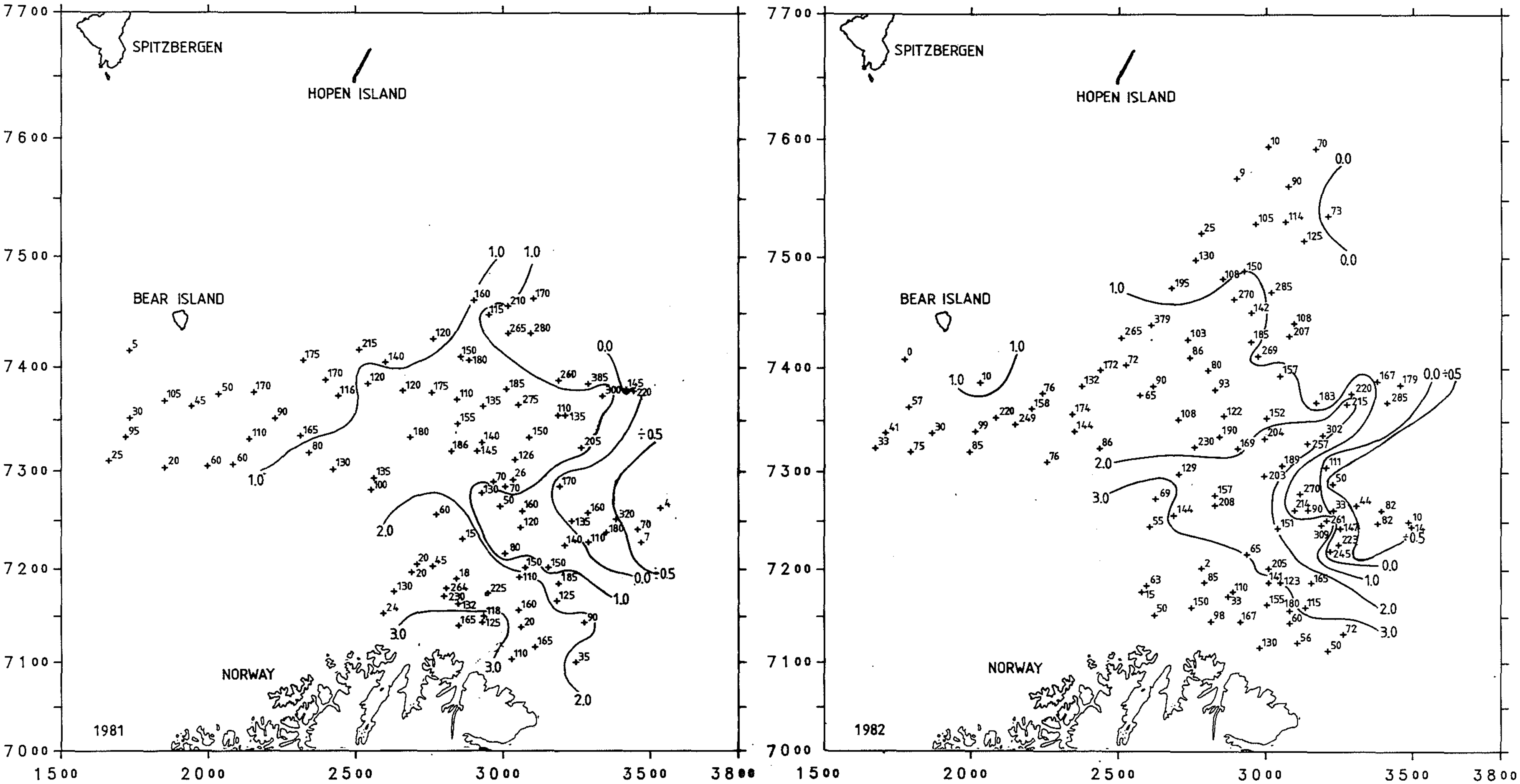

Fig. 1. Trawl stations with catch per 3 nautical miles and bottom isotherms ($^{\circ}$C) during the surveys in 1981 (left) and 1982 (right).

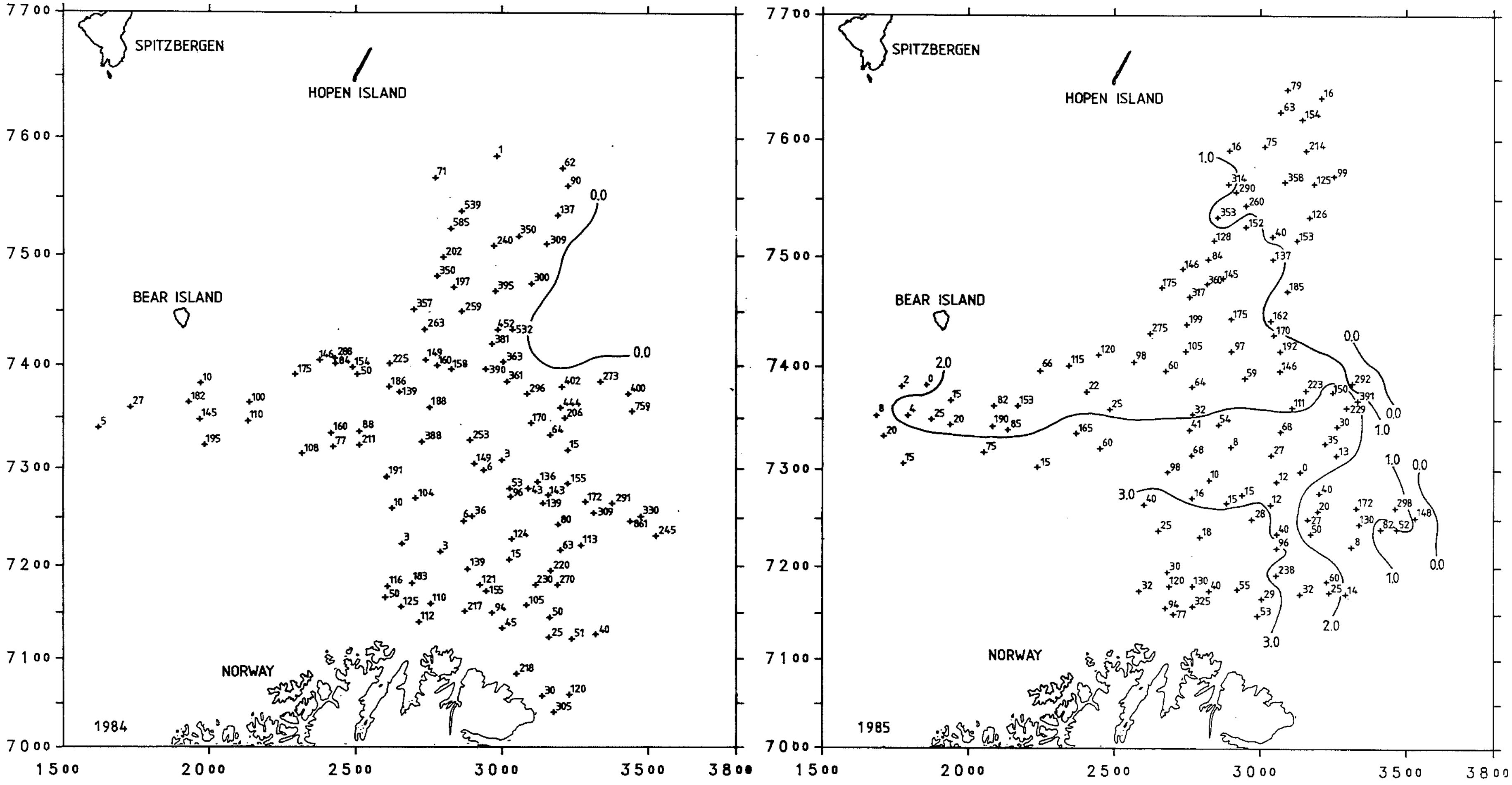

Fig. 2. Trawl stations with catch per 3 nautical miles and bottom isotherms (^{o}C) during the surveys in 1983 (left) and 1984 (right).

During these two years there were no temperatures below 0°C on the shrimp fields. The highest density of shrimps were found in the coldest water between 0 and 1°C. Figs 1 and 2 show the position of trawl stations and the catch per 3 nautical miles on each station. The bottom isotherms are indicated based on the temperature measurements taken at each station. In 1981 the eastern part of the shrimp fields was overflown by cold water (Fig. 1). The highest density of shrimps was at the border between the cold and warm bottom water. The same situation occurred during 1982 on the shrimp field at the Tiddly Bank between N72°00' to N73°00' and E32°00' to 36°00' (Fig. 1). During the years 1984 and 1985 there were no temperatures below 0°C. But for 1984 and 1985 the cold front was close to the eastern shrimp fields (Fig. 2).

CONCLUSIONS

It looks like the shrimp do not prefer any specific temperature interval between -0.5°C and 4°C but the deep sea shrimp seem to avoid fronts of cold bottom water. At temperatures below -0.5°C, the catches of shrimps decreased sharply. Other factors like depth, currents, and predation from fish are probably more decisive factors for the density of shrimps.

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THE EFFECT OF OCEANOGRAPHIC CONDITIONS ON DISTRIBUTION AND POPULATION
DYNAMICS OF COMMERCIAL FISH STOCKS IN THE BARENTS SEA
Proceedings of the third Soviet-Norwegian Symposium, Murmansk, 26-28 May 1986
Edited by H. Loeng. Institute of Marine Research, Bergen, 1987.

EFFECTS OF OCEANOGRAPHIC FACTORS ON POPULATIONAL STRUCTURE OF SHRIMP (Pandalus borealis Krøyer) IN THE BARENTS SEA AND SPITSBERGEN AREA

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ABSTRACT

An attempt to develop a pattern of interpopulation relationships for the shrimp (Pandalus borealis Krøyer) in the Barents Sea area was undertaken. This was based on long-term investigations of larval drift (1977-1985) and peculiarities of reproduction for the population (1972-1985). The locations of the main and intermediate mother populations as well as their role in the recruitment of exploited shrimp swarm by recruits from different sea areas were elucidated. Each of these populations, with its larvae included, provided the density estimates for a definite sea sector. The extent of their aggregation depended on the stability and velocity of current, and in which mother population it was found. The maximum range of larval drift approximated 500 miles. Relationships between the populations are mainly transportation of larvae from the mother- to intermediate populations and, further, to dependent ones. The latter are distinguished from that of donor-populations by a low reproductive potential, and these are aggregated in relatively cold water areas. The reproductive potential of dependent populations was found to be 1.5-3 times lower than the corresponding index of independent mother groupings.

INTRODUCTION

Oceanographic conditions exert great influence on the growth, development and distribution of shrimp Pandalus borealis (RASMUSSEN 1953, IVANOV 1972). However, relatively little is known about either the role of larval drift in the recruitment of populations in northern and eastern areas of the Barents Sea, or the effect of water temperature on shrimp self-reproduction.

MATERIAL AND METHODS

Material on the ecology of shrimp which inhabit the bottom, was collected in the Barents Sea and adjacent waters during different seasons for 1972-1985. Trawls were made with 19 mm mesh (inner mesh size) nets having a codend. More than 30.000 shrimp individuals were sexed (RASMUSSEN 1953). Absolute fecundity was determined by a direct counting of eyed eggs. Relative fecundity was the quotient of the absolute fecundity by the weight of ovigerous females. Reproductive potential (number of embryos per 1000 specimens in population) was determined by multiplying the mean relative abundance of ovigerous females from each area by their absolute fecundity (KUZNETSOV 1964). The relative abundance of ovigerous females and reproductive potential for a population were estimated for a period which was preceded by a hatch of larvae. Stages of embryonic development and maturity of reproductive products were also determined (HAYNES and WIGLEY, 1969). Survival of embryos for an incubation period was estimated in percentage in accordance with a relationship between the fecundity of the IV and I stages of embryonic development.

Investigations on larvae were carried out for locations in the northeastern Norwegian and southwestern Barents Seas during 1977-1983. Annually, during April-May and June-July, plankton were collected and hydrographic observations were carried out with an invariable grid of stations (LYSY 1984). Egg-net, ring-trawl with a 160 cm ring diameter, and a 3.3 m Isaacs-Kidd trawl were used for fishing gear.

The characteristics of the dynamic water regime were estimated according to the hydrographic observations of others (DVININA and LYSY, 1983). The names of currents were given according to TANTSIURA (1959). The names of the areas of the Norwegian and Barents Seas were used in accordance with the scheme of fishing areas (Trudy PINRO, 1957, v.10, p. 281).

RESULTS

The relationship between populational reproduction of shrimp and hydrographic conditions

The relative abundance of ovigerous females from populations in the Barents Sea and Spitsbergen area are not definitely distinguished. This is with exception to the area of the Novaya Zemlya Shallows where it is by 6-7 times lower than for the other areas investigated. Absolute and relative fecundity are 30-48% lower in the eastern part of the sea compared to other areas. The lowest reproductive potential (12 700) for the coastal populations of Murman was registered in the northern part of the Novaya Zemlya Shallows, while the highest (182 300) was within the Barents Sea.

Populations with a high reproductive potential are concentrated in relatively warm water areas, while low ones are located in the sections with water temperature being close to 0^{o}. The long-term mean water temperature at the bottom during May (when hatching of larvae takes place) was directly related to the reproductive potential of shrimp populations ($r=0.84$; BERENBOIM 1982).

Not only the reproductive potential and fecundity, but also the survival of embryos for an incubation period, are low in relatively cold water areas. In these areas, a relatively large amount of dead eggs are observed on pleopods. For some females, this may reach 60% of the whole number of eggs by the end of incubation.

An analysis of the gonad maturity was made in June 1979. In the relatively warm water area of the Kildin Bank (off the Murman coast) practically all the females which had hatched that year had reproductive products at stage III and were ready for a repeated spawning. In the relatively cold area of the Goose Bank, all the examined females from the similar age group had gonads at stage I, and were not ready for the next spawning. In the Demidov Bank and Spitsbergen areas, where long-term mean temperature has a value intermediate between the temperatures of the Murman coastal waters and Novaya Zemlya Shallows, females with gonads with a range of maturity stages were registered. Thus, through the year, females in the Kildin Bank were able to spawn twice, once at the Goose Bank area, and only part of females could take part in a repeated spawning in the other areas.

Therefore, in areas with the coldest water, the abundance of ovigerous females, their fecundity, survival of embryos during incubation, and probability of a repeated spawning, are low. In addition, the natural mortality of ovigerous females and occurrence of dead eggs are also relatively high there. These factors specify limited possibilities of reproduction for the populations due to their own reproductive habits. In anomalously cold years (1979-1980) practically all of the ovigerous females on the Goose Bank, either completely or partially, have lost eggs on pleopods long before the hatch of larvae. Therefore, for shrimp reproduction even at a high absolute abundance of populations in the areas with unfavourable conditions, the production of larvae of their own may be considered to be extremely low and would not make up for those losses due to natural mortality.

Populations of shrimp in the Barents Sea may be considered as independent, half-independent, dependent or pseudopopulations (the elements of only one superpopulation) depended upon their different capabilities to self reproduction (BEKLEMISHEV 1960). Independent shrimp populations are concentrated mainly in the coastal area of the Barents and Norwegian Seas. Half-dependent populations are concentrated mainly in the Demidov Bank areas, the Central Plateau, and off West Spitsbergen. The ranges of shrimp populations in the open sea correspond to the zones of interaction between the Atlantic and Arctic water masses (BRYAZGIN 1970, BERENBOIM, LYSY and SEREBROV 1980), where favourable conditions are formed for the "settling" of larvae which drift in the streams of currents. Dependent populations are formed near by and on the slopes of coldwater banks (e.g. Goose Bank, the eastern slope of Bear Island, and the Central Elevation). Pseudopopulations are found in the areas where the long-term mean temperature of the near-bottom water layer is about -1^{0} during the period of seasonal temperature minimum. The location of pseudopopulations is a boundary of area for sterile eviction of species.

Thus, independent populations are concentrated in the warmest waters, while the dependent ones in coldwater sea areas (BERENBOIM 1982). Shrimp reproduction in the eastern and north-eastern Barents Sea areas occurs considerably less effectively than in the Murman coastal waters.

The availability of vast areas for sterile eviction which occupies the whole northeastern Barents Sea area and most of the part of the Kara Sea may be an indirect confirmation of the dependent character of shrimp populations near the northern boundaries of a reproductive part of the area (GORBUNOV 1932, RETOVSKY 1936, IVANOV 1972).

Drift of larvae and interpopulational relations

Investigations carried out during the first half of April for 1980-1982 in the Norwegian Shallows from Vestfjorden to 62°N, indicated a nearly complete missing of shrimp larvae in the Western Norway coastal waters south of the Lofoten Islands (LYSY 1984, 1985). This may indicate a relative isolation of shrimp groupings from the Western Norway fjords. Apparently in connection with this, for most of the fjords in the western coastal region of Norway, rapids are observed, and local larvae are not carried into the open sea and thus remain in the fjords. A lack of larvae to the south of the Lofoten Islands indicates that shrimp populations, which concentrate in the northeastern Norwegian Sea without receiving recruits from southwest, support their abundance due to their own reproductive capacities, i.e. are independent populations. Thus, mother populations of shrimp in the northeast of its area concentrate to the north of the Lofoten Islands.

A location of mother populations was determined by concentrations of larvae in the early stages of development which occurred in surface waters. A mass hatch of larvae (April-early May) concentrations (with a density over 50 spec./1000 m^3) occur annually in the same areas. These waters are the coastal waters of Norway from the Malang Bank to the North Cape, the southern part of the Tromsøflaket area, and off the western coast of the Kola Peninsula (Fig. 1). For separate years, larval concentrations were also observed by us to be further out to sea, i.e. on the North Cape and Finnmarken Banks, Murman Tongue, and the parts of the Norwegian Deep which is influenced by the North Cape and Murman Currents. The areas of mass concentration in surface waters during spring approximately correspond to the areas of the mother populations, as far as larvae rise to the surface immediately after a hatch (LYSY 1980).

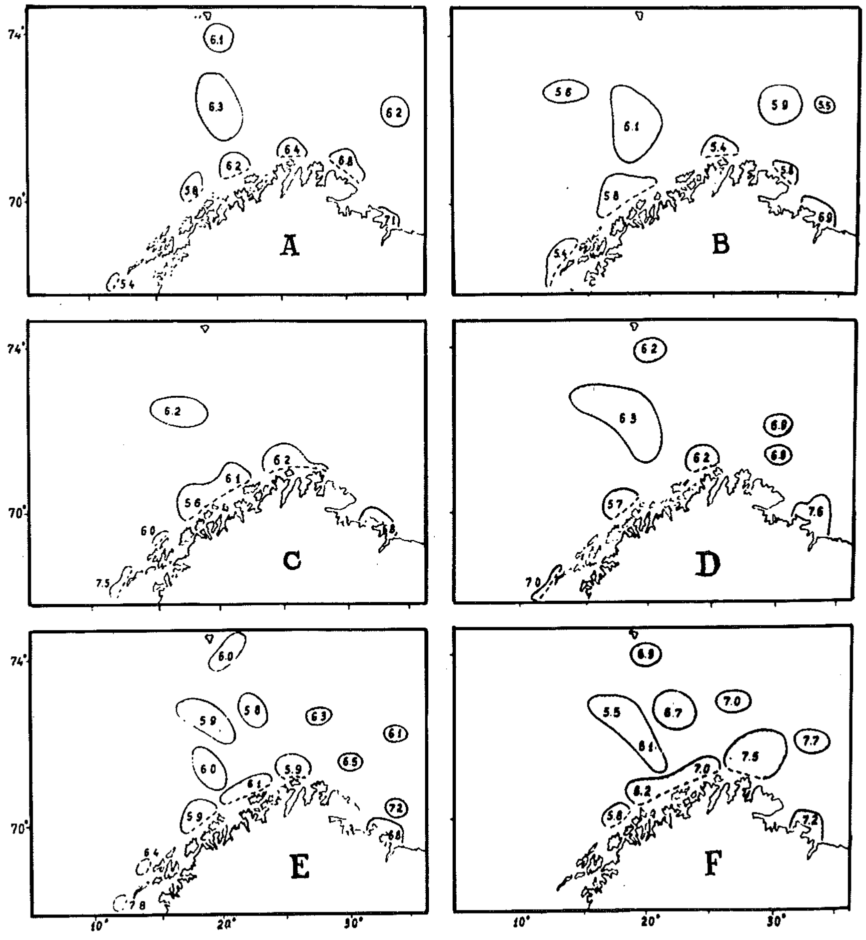

Fig. 1. Areas of larval concentrations *Pandalus borealis* with a density of over 50 individuals/1000 m^3 (encircled) during April-May 1977 (A), 1978 (B), 1979 (C), 1980 (D), 1981 (E), 1982 (F). The values indicate the mean lengths of larvae.

On the basis of data on mean age of larvae and dynamic regime of currents during spring, it was possible to follow a drift of larvae from the moment of hatching for a number of years, and also to determine the areas from which they had been transported. These regions were the Malangen, Fugløy and Sørøy Banks, the southern part of the Kopytov area, the Norwegian Deep and the Murman coastal areas. These correspond with where the main mother populations are found.

Intermediate mother populations are half-dependent, they recruite larvae from the main mother populations. These in turn, serve as mother populations for the most remote dependent populations and pseudopopulations. They are registered in the areas of the Finnmarken and Murman Banks, Murman Tongue and southern slope of the Bear Island Bank.

The larvae from the Kopytov area are mainly transported into the waters of the Spitsbergen and northern branch of the North Cape Currents. Their main mass is transported by approximately 150 nautical miles (nm) to the north and 100 nm to the northeast during 1.5-2 months of drift. A second possible range of drift for these larvae may be estimated on the basis of the mean long-term velocity of currents during summer. The Spitsbergen Current velocity from the Bear Island to Isfjord has a rate of about 4.7 nm• day^{-1}. By assuming that the period of larval life which is planktonic is equal to 4 months, we shall prove that during this time, the larvae may be transported by 500 nm to Kongsfjord at 79°N.

During July, the long-term mean velocity of the Northern branch of the North Cape Current is about 1 nm•day^{-1} at 74°30'N. This means that the larvae transported from the Kopytov area remained for two months before settling, and maybe transported 50-60 nm more to the northeast of the Bear Island. The total distance for their drift in this direction from their place of hatching will not exceed 150-170 nm. Most larvae which drift in the waters of the central branch of the North Cape Current surmount a distance of 250-270 nm with a mean velocity of 2-3 nm•day^{-1}.

The larvae hatched off the Northern Norway coasts drift in the waters of the main and coastal branches of the North Cape and Murman Currents. These are transported on the average by 300-320 nm from their place of hatching at a velocity of 3-4 nm•day^{-1} during 2.5-3 months of drift. Further east, a reduction of velocity to 2-3 nm• day^{-1} in the Murman and Novaya Zemlya Currents result in a total transport distance of larvae to maximum 400 nm. By considering probable "delays" for the transport of these larvae in quasi-stationary gyres, we suggest that, via the larvae, populations of the northern Norway coastal areas provide mostly half-dependent groupings west of 40°E.

Larvae mainly from intermediate mother populations of the Finnmarken Bank and Murman Tongue are transported by the waters of Murman and Novaya Zemlya Currents further to the east. A range of their drift constitutes not less than 300 nm at an average velocity of 2-3 nm• day^{-1}. This makes it possible for them to reach the Goose Bank and the northern part of the Novaya Zemlya Shallows.

Larvae of mother populations which are concentrated at the coasts of the Kola Peninsula (31-36°E), are also transported eastward. A range of transport for these larvae is not large in comparison, because it is limited by the low velocity (usually <2 nm•day^{-1}) of the coastal branch of the Murman Current (DVININA and LYSY 1983). Nevertheless, larvae from the coast of Murman may reach the Goose Bank area for a period of their planktonic existence.

The data presented make it possible to consider that mother populations of the Barents Sea shrimp have their "daughter" groupings concentrated in a limited area. Thus, a population of the Kopytov area mainly provides larvae to the north and northeast via waters of the Spitsbergen Current, and northern and central branches of the North Cape Current. These larvae directly recruit half-dependent groupings of shrimp from the South Cape Deep, southwestern coast of Spitsbergen, Western Deep and Hopen Island areas.

Most of the larvae of the Northern Norway population settle in the regions of the Central Plateau, Murman Bank, and Murman Shallows. The recruitment of shrimp groupings off the Novaya Zemlya takes place because of larvae from intermediate mother populations located in the Murman Tongue, Finnmarken, and Murman Banks. Mother populations of the Western Murman coastal waters play a specific role in recruitment of shrimp larvae of the Goose Bank. Essentially, this role is increased during the years when, due to the peculiarities of water circulation on the boundary between the Norwegian and Barents Seas, the main abundance of larvae from northern coast of Norway is transported to the northeast (1979) or remain in the gyres in the southwestern Barents Sea (1980, 1981).

Thus, relationships between shrimp populations in the Barents Sea region may be realized as the transport of larvae from the main mother populations to intermediate ones, and further, to dependent groupings. This also occurs directly between independent and dependent mother populations.

CONCLUSIONS

A close positive relationship between the long-term mean water temperature and a reproductive potential of shrimp populations in the Barents Sea was found. The abundance and fecundity of ovigerous females and survival of embryos during incubation, suggest the probability that repeated spawning is low for the areas where the water temperature is relatively cold. Furthermore for these populations, there is a high natural mortality rate for the embryos. These circumstances limit the possibility that self reproduction for populations will occur in the extremities of the northeastern part of this species habitat.

Results from the analysis of larvae drifting in the northeast of the Norwegian and southwest of the Barents Sea indicate the extent of all mother populations of shrimp to be north of the Lofoten Islands. So called intermediate mother populations were found in the northern coastal waters of Norway and Murman, and also in the southern Kopytov area. They are also found in the areas of the Murman, Finnmarken, the southern slope of the Bear Island Banks, the Central Plateau and the Murman Tongue.

A stock of shrimp, with reproductive recruits on the boundaries of the area adjacent to the Arctic area, occurs mainly by a transport of larvae in stages from the main to intermediate mother populations, and further to the dependent ones.

The zone of effective reproduction in the Barents Sea is in the warmest waters, e.g. in the coastal areas of northern Norway, Kola Peninsula, some areas of West Spitsbergen, and Kopytov area. The direction of the main larval drift from these areas depends on the intensity of the Norwegian, North Cape and Murman Currents, as well as on a continental flow.

In reality, the presented scheme of interpopulational relations of P.borealis suffers from annual variations which depend on hydrographic conditions. Therefore, it is reasonable, on the basis of bilateral agreement, to organize oceanographic monitoring of the watershed for the Norwegian and Barents Seas during March-July so that the influence of the intensity of currents, vortexes and other hydrographic factors on a drift of fish larvae, crustaceans and cephalopods, can be elucidated.

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