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Biodiversity and exploitation of the main fish stocks in the Norwegian – Barents Sea ecosystem

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Juvenile herring and capelin are the main stocks of plankton feeders in the Barents Sea, the cod is the dominant predator. Warm climate favours recruitment of herring and cod, but large stocks of juvenile herring hamper survival of the capelin fry. Since the early 1970s, the herring stock has been grossly overexploited, which could have led to an imbalance in the state of the predator-prey relationships in the Barents Sea. In the 1970s and early 80s, however, cod could feed on capelin which had excellent growth and recruitment conditions when the herring was absent. The consequences of the reduced herring stock were triggered in the mid 1980s, when excellent recruitment conditions for herring and cod occurred. Three abundant year classes of cod were recruited, but the herring stock was not sufficiently large to take full advantage of the favourable recruitment conditions. Given the lack of juvenile herring and a reduced capelin stock, the rapidly growing cod stock grazed down all other available prey species in the area, including its own progeny, and starved cod, seabirds and seals have in later years appeared on the north Norwegian coast. The capelin fishery collapsed, and the traditional coastal cod fisheries have been struck by the most serious crisis on record.

Keywords: Barents Sea; fish stocks; environment; collapse of stocks

Introduction

A severe crisis has developed in the Barents Sea's stocks of fish and fish eating species in recent years. The crisis became obvious in 1987 when many starving harp seals invaded the Norwegian coastal waters. In 1987 and subsequent years, thousands of under-fed seals have drowned in fishermen's gear, and flocks of starved seabirds have washed ashore on the coast of Finnmark. In 1986, the large Barents Sea capelin fishery collapsed and the North-East Arctic cod population, which is the largest stock of predator fish in the area suffered greatly from lack of food. In the late 1980s the cod stock nearly perished, and the traditional coastal cod fishery was struck by the most serious crisis on record.

The Norwegian spring spawning herring was the largest fish stock of Europe, but was grossly overexploited in the late 1960s. The Barents Sea capelin fishery replaced the herring fishery as the largest in Europe in the 1970s, and reached a record catch in 1977 of nearly 3 million tonnes. The capelin has been the major plankton feeding species in this area since the late 1960s, and the starvation of the stocks of marine carnivores in the 1980s therefore has been associated with the exploitation of the capelin stock. The North-East Atlantic region is an area of high productivity, but low biological diversity, meaning that the area is rich in fish, but the fish belong to few species. Such an ecosystem is attractive to fisheries, but has low stability and may be seriously affected by overexploitation of one key species in the system. There is evidence that overexploitation of the herring is the most likely explanation for the crisis. The present paper is a comprehensive review of the life history and exploitation of the main fish stocks concerned, in light of relevant knowledge of stock interrelationships and climatic conditions. The aim is to reconstruct the history and ecological processes behind the stock development of carnivores in the Barents Sea.

The environmental conditions

The physical conditions in the Norwegian Sea – Barents Sea region are governed by the inflow of Atlantic water through the Faroe-Shetland Channel (Fig. 1). Two main branches of the Atlantic Current create two separate ecosystems, one in the North Sea and one in the Norwegian Sea – Barents Sea. In the latter area, the interface between the inflow of warm Atlantic water and the cold Arctic water forms the physical basis for two highly productive areas, one in the Norwegian Sea along the Polar front, and one in the marginal ice zone of the Barents Sea. The rich production in the latter area is linked to the movement of the ice edge (Gjøsæter *et al.*, 1983).

The strength and properties of the inflowing Atlantic water vary periodically and determine the climate of the region. Increased inflow of Atlantic water increases the temperature in the upper water masses and favours recruitment of the main fish species (Manti and Fedorov, 1963; Saetersdal and Loeng, 1984). Mean temperature and salinity in the Barents Sea in the period 1964–1993 are shown in Fig. 2. A period of warm climate at the end of the 1960s was followed by 8 years of decreasing temperature and salinity during the 1970s, indicating low inflow of Atlantic water to the Barents Sea. The strength of inflowing Atlantic water shows an abrupt increase in the early 1980s, a decrease in the mid 80s and a new increase in the late 1980s.

The ecosystem

The rich plankton production in the Norwegian Sea has been harvested by two large stocks, the adult Norwegian spring-spawning herring *Clupea harengus*, and the adult blue whiting *Micromesistius poutassou*. The herring feeds in the upper water column, mainly on copepods, whereas the blue whiting is a semipelagic fish which usually feeds on larger planktonic organisms in the intermediate water masses. The capelin, *Mallotus villosus*, is the main plankton feeder in the Barents Sea, but in years with high inflow of Atlantic water and strong herring year classes, the juvenile herring plays an important part as prey species in the area. The polar cod, *Boreogadus saida*, feeds in the intermediate water of the northern and eastern Barents Sea, and has a similar relation to the capelin as the blue whiting to the herring in the Norwegian Sea.

Herring and capelin are the main food sources for a large variety of fish stocks, mammals and birds. The North-East Arctic cod, *Gadus morhua*, is the largest predator in the system and plays a decisive role in the balance of the predator-prey relationships. All the main stocks of fish and mammals are harvested by man.

Relevant features of the general biology of the fish stocks are illustrated in Fig. 3. Prior to the 1970s, the adult herring fed in the Polar front area of the Norwegian Sea during summer and autumn, but spawned on the Norwegian west coast in the early spring. In late autumn the herring gathered in a wintering area east of Iceland and started

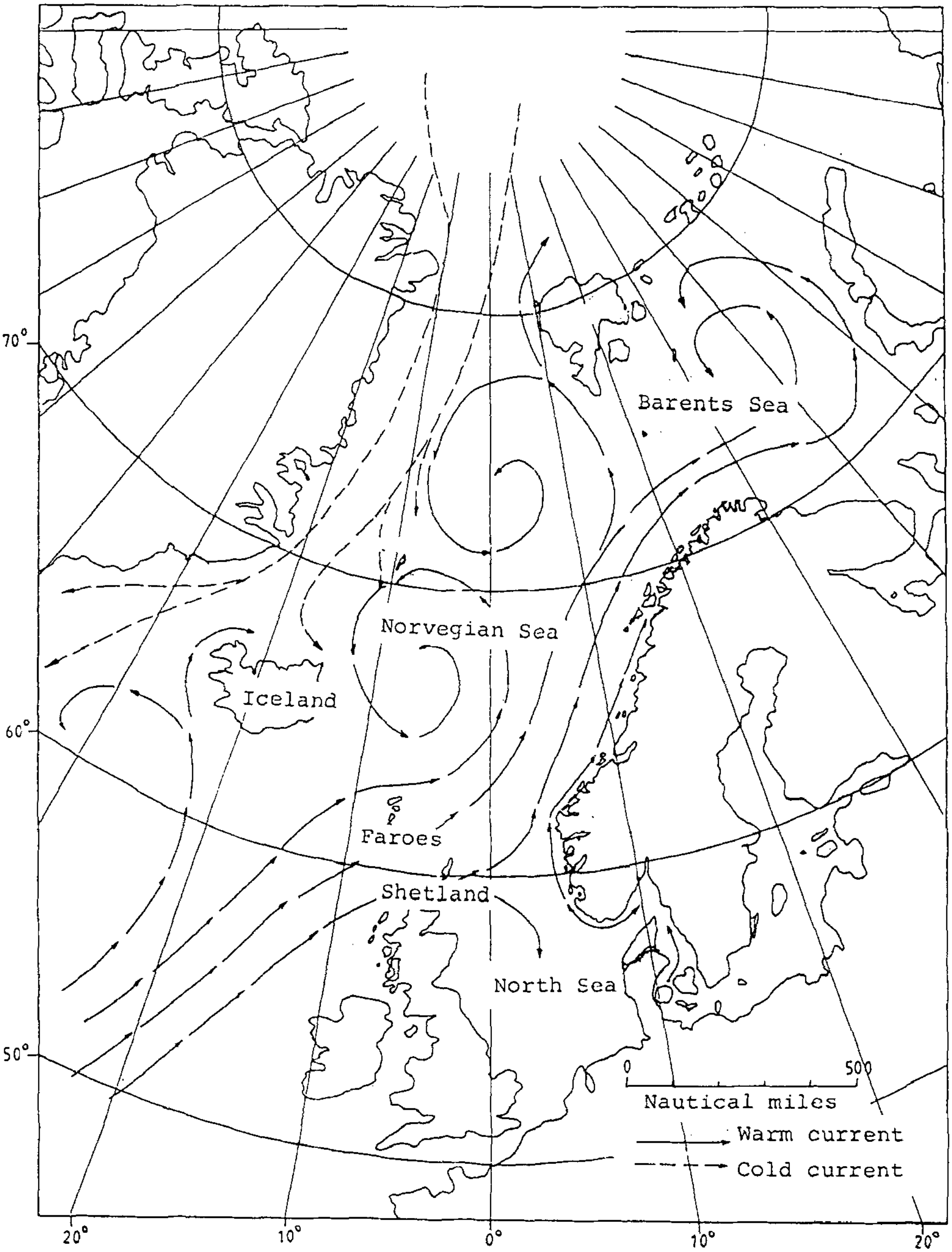

Figure 1. The circulation of the Norwegian Sea.

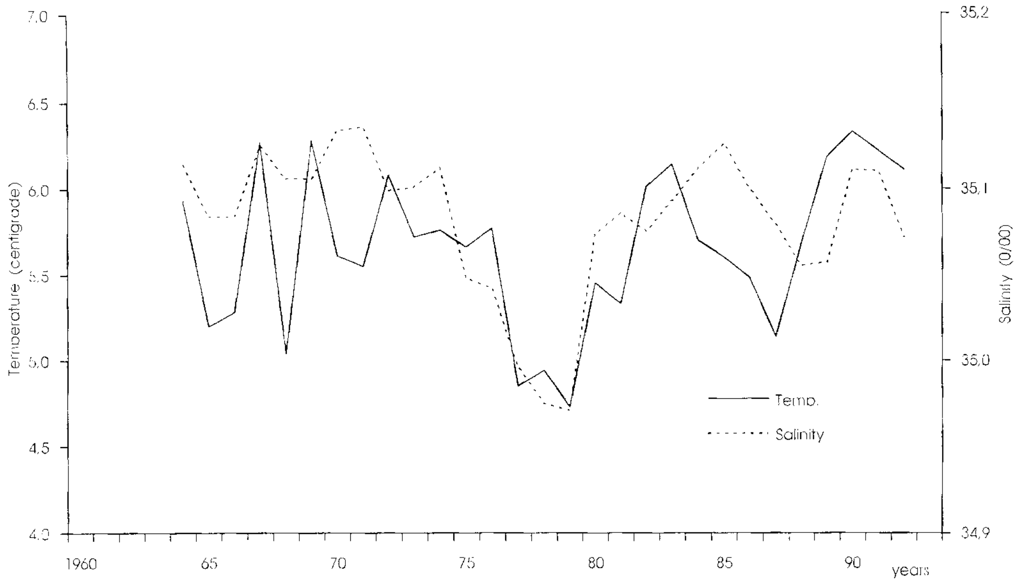

Figure 2. Mean annual temperature (solid line) and salinity (broken line) in the Barents Sea in 1964–1993 (Midttun and Loeng, 1986; Anon, 1993a).

the spawning migration towards the Norwegian coast around the New Year (Dragesund *et al.*, 1980). This migration transferred huge quantities of fish biomass from distant waters to the Norwegian coast and probably had a considerable effect on the marine life on the Norwegian shelf. The migrating herring shoals were followed by fish-predators: sea-mammals, birds and larger predatory fish and turned the Norwegian west coast into one of the richest fishing and hunting grounds in the world. Young herring (0–4 years old) are widespread on the Norwegian continental shelf and in the southern parts of the Barents Sea (Dragesund, 1970), and year classes are abundant when the inflow of Atlantic water is high. In the latter area the young herring distribution overlaps that of juvenile capelin and may affect recruitment to the capelin stock.

The adult herring stock collapsed in 1969, and the feeding migration to the Polar front was disrupted. The previous migration pattern has not yet been resumed, and the present distribution is as shown in Fig. 4. The adult herring as well as the juveniles are now feeding in Norwegian coastal waters, and the prespawners are wintering in Norwegian fjords. The spawning grounds have not changed to any appreciable extent (Hamre, 1990).

The capelin spends its whole life in the Barents Sea. During summer and autumn the catchable stock (2–4 years old) feeds in the marginal ice zone of the northern Barents Sea, and the maturing capelin migrates to the coast of Norway and the former USSR for spawning during winter and early spring. The spawning migration of capelin has the same positive effect on the Norwegian north coast fisheries as the herring had for the fisheries on the west coast. The capelin suffers mass mortality after spawning, and the life span of the fish therefore is relatively short, 3–5 years (Prokhorov, 1965). The larval and juvenile stages are distributed in the central and south-eastern Barents Sea, where they are subjected to predation by juvenile herring and cod.

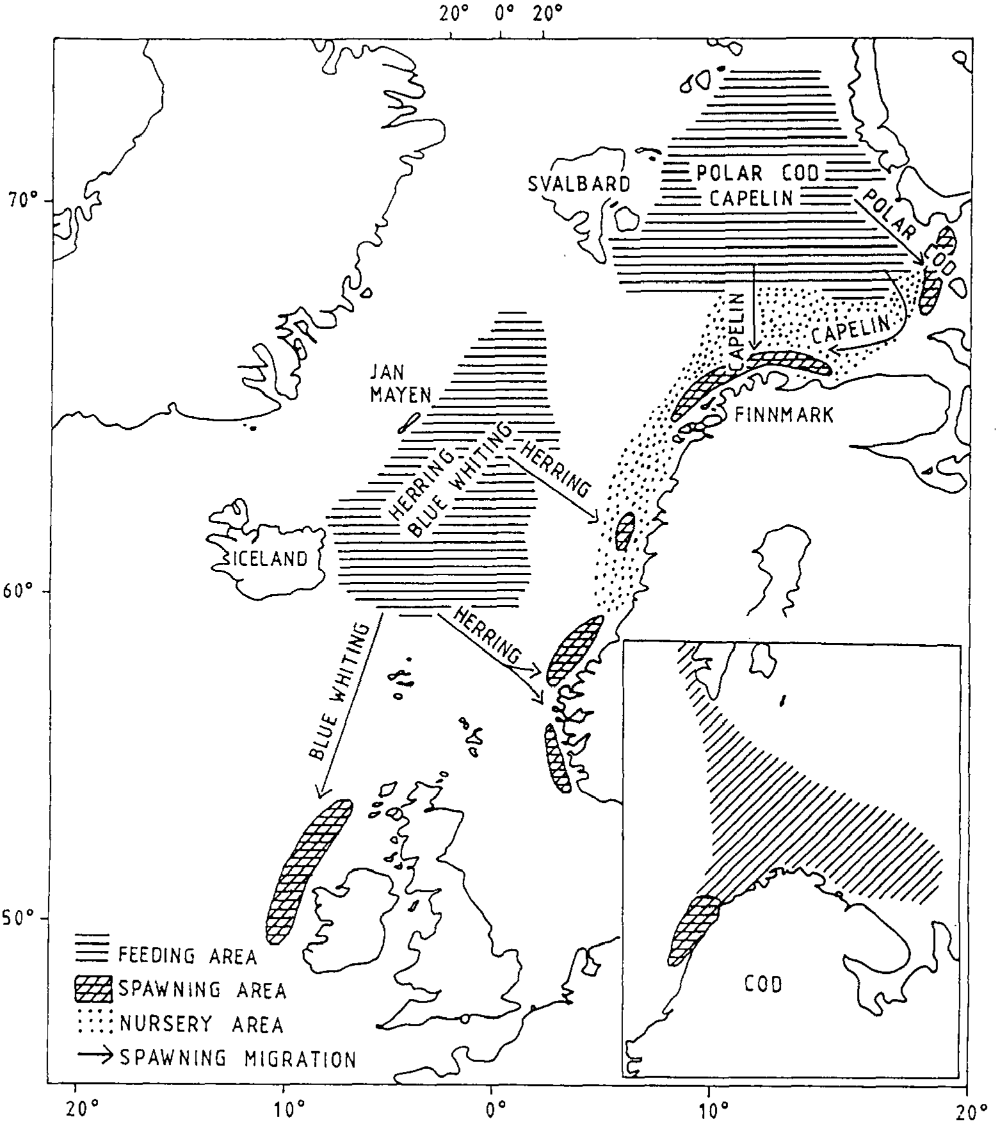

Figure 3. Distribution and migration of the most important fish stocks in the Norwegian-Barents Sea ecosystem.

The growth potential of the semipelagic stocks of blue whiting and polar cod is probably affected by the size of the pelagic stocks. However, the semipelagic stocks are of marginal importance as prey species in this ecosystem because they spawn in other areas.

The spawning grounds of Arctic cod are strategically situated on the central Norwegian coast between the spawning grounds of the herring and the capelin. The cod feeds in the southern and central part of the Barents Sea and in the Svalbard area, and matures at an age of 5 to 8 years. The juveniles have a more north-eastern distribution than the adults, but the distribution is mostly limited to the area south and west of the marginal ice zone. The adult capelin therefore is mostly available as food for cod during the capelin's spawning migration in winter and spring, whereas the cod may feed on juvenile herring and capelin throughout the year (Ponomarenko and Ponomarenko, 1975; Mehl, 1989).

Little is known about the distribution, feeding behaviour and the magnitude of the predation caused by mammals and birds, but the whales and seals are no doubt of importance for the ecobalance of the region.

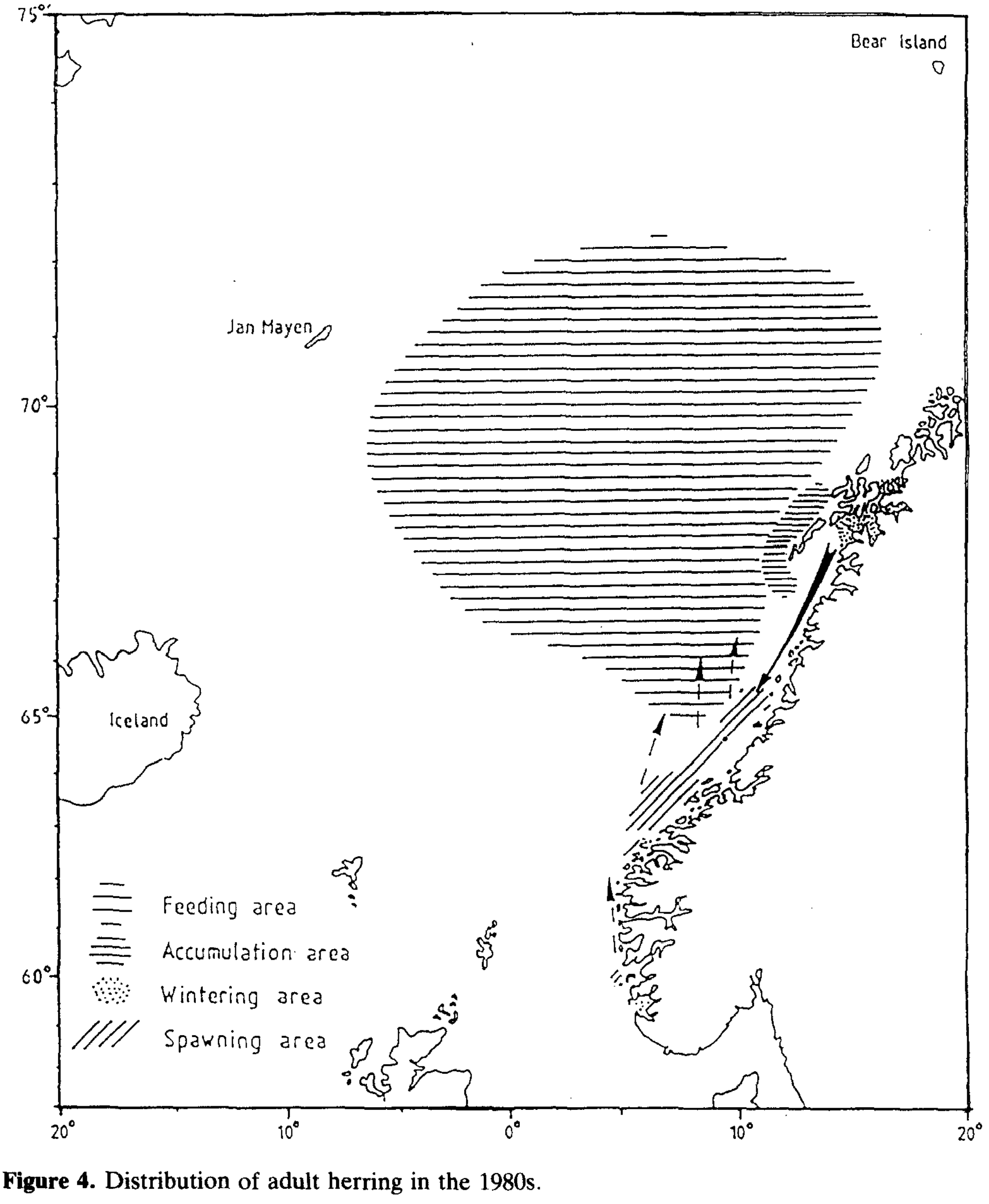

Figure 4. Distribution of adult herring in the 1980s.

Stock abundance and exploitation

Herring

The herring has been caught in Norway since ancient times, and has deeply affected the social life and activities of people living on the Norwegian coast. The history of the herring fisheries can be traced back hundreds of years, but data for stock assessment are only available since the 1950s. Back-calculated stock estimates based on catch in number by age (Gulland, 1965) i.e. VPA-based (virtual population analysis) estimates of the state of stock and the catches from 1950 onwards are summarized in Fig. 5. The adult herring stock was estimated to be 7 to 10 million tonnes in the 1950s, but declined to a level of some 3 million tonnes in the early 1960s. This was mainly due to poor recruitment in the period 1951–58. Two strong year classes were recruited in 1959–60, but the stock was depleted in the late 1960s due to increased exploitation caused by the introduction of the power block to the purse seining technique (Dragesund *et al.*, 1980). A fraction of the 1969 year class survived and gave rise to a new spawning stock of herring from 1973 onwards. In the mid 1970s the spawning stock was estimated to be 100 000 tonnes, and increased slowly to some 500 000 tonnes in 1983. In 1983–85 three relatively strong year classes were recruited as 0–group in the Barents Sea. These year classes (especially 1984–85) suffered heavy predation from an increasing stock of juvenile cod. The 1983 year class matured in 1988, and the spawning stock increased to some 2 million tonnes (Mehl, 1989).

The recruitment is variable, and very strong year classes in relation to parent stock have occurred in 1950, 1959–60, 1963 and 1983. A new period of favourable recruitment conditions started in 1989 (Fig. 5), and the subsequent herring year classes are relative

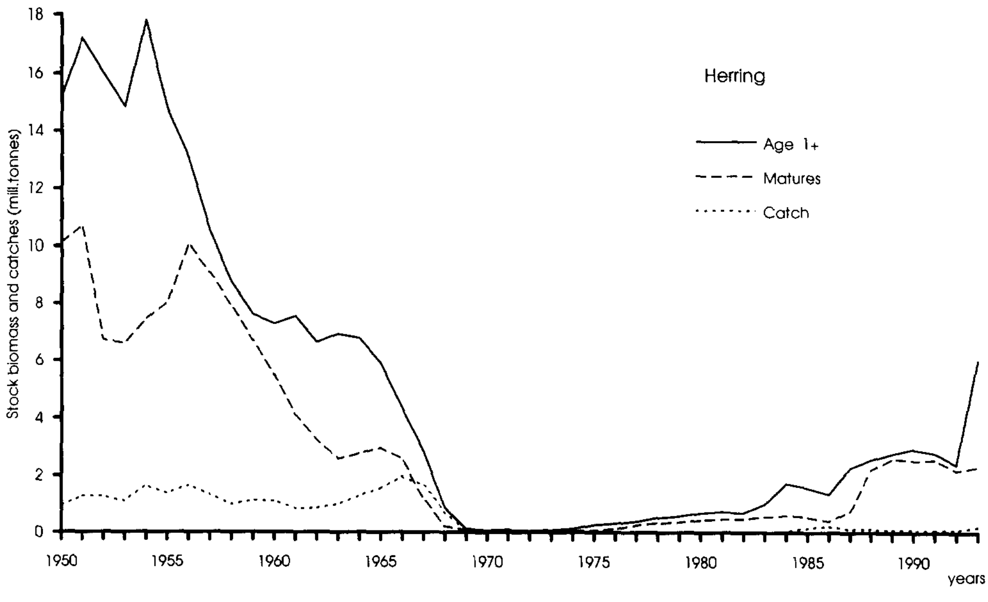

Figure 5. Estimated stock biomass of 1 year old and older herring (solid line), spawning stock biomass (broken line) and catches (dotted line) in the years 1950–1993.

abundant. The fishery has been regulated by catch quotas since the early 1970s. Although the fishing mortality has been low, the fishery has delayed the rebuilding of the stock, and the herring is considered to be recruitment overexploited (Hamre, 1990; Anon, 1993b).

Capelin

Prior to 1960s, the capelin was regarded as an important stock as food for cod, but not as a large potential resource for exploitation. The capelin was fished on a small scale as prespawners off Finnmark since the 1950s. The catch increased in 1959–61, but a sudden collapse of the fishery occurred in 1962. From 1965 onwards the catch increased substantially and reached a record catch of 2.9 million tonnes in 1977 (Fig. 6). These large catches also include immature capelin which has been fished in the feeding area during summer and autumn since 1968. Since 1978, the fishery has been regulated by separate catch quotas for the autumn and winter fishery. From autumn 1986 onwards the capelin fishery was banned, but the fishery was reopened in 1991 (Anon, 1993b; Hamre, 1985).

No stock abundance estimate of capelin is available prior to the late 1950s. Olsen (1965) estimated the relative stock abundance in the years 1959–64. He found that the stock increased by 4 times in the period 1959–61, but declined below the 1959 level in 1962–64. This rise and fall in stock size was correlated to variable recruitment, the year classes 1960–61 being extremely poor compared with the previous ones (Olsen, 1968). From 1965 onwards, the recruitment increased considerably, and the 1967 year class was reported to be very strong (Dragesund *et al.*, 1971).

Acoustic estimates of stock abundance are available since 1972 (Fig. 6). The estimates

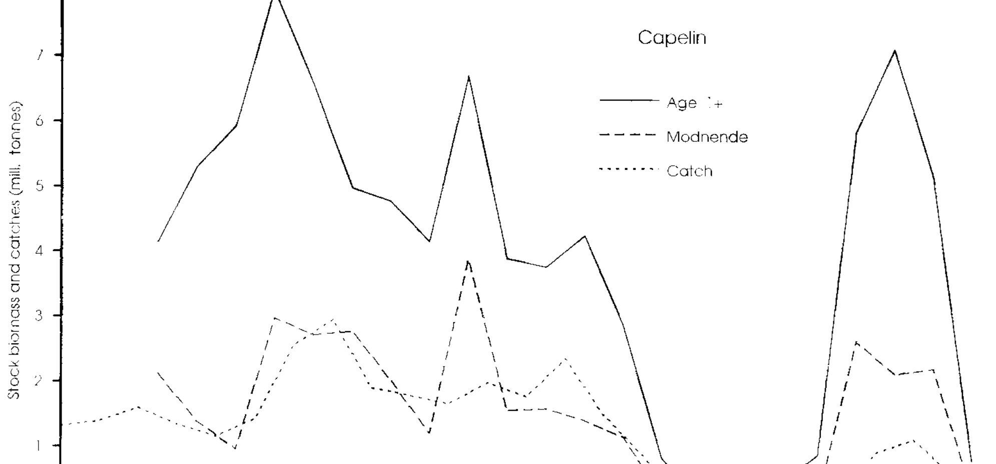

Figure 6. Estimated stock biomass of 1 year old and older capelin (solid line), maturing stock biomass in September (broken line) and catches (dotted line) in the years 1972–93.

(solid line) were obtained in September and cover the age groups 1 years old and older (Dommasnes and Røttingen, 1985; Anon, 1993b). The maturing of the capelin is correlated to the size, the capelin above 14 cm in September is expected to mature and spawn in the subsequent winter (Hamre and Tjelmeland, 1982). The latter estimate adjusted by the natural mortality and the catch in October–April is taken as the stock biomass of spawners (modnende) in the subsequent year (broken line).

The capelin stock continued to increase in the first half of the 1970s and reached a maximum in 1975 of about 8 million tonnes. In this period two strong year classes were recruited (1971–1972). These year classes were distributed far north and east in the Barents Sea, where the conditions for growth are poor (Gjøsæter and Loeng, 1987). Since the capelin suffers mass mortality after spawning, the reduced growth rate delays the maturation and increases the survival of the immatures. The extraordinary high stock abundance in 1975 thus was a result of high recruitment and the accumulation of older age groups in the immature stock due to delayed maturation and reduced spawning mortality. The 1971–72 year classes matured and spawned in 1976–1977, and the stock declined to a level of 5 million tonnes in the autumn 1977. This decline in stock size was determined mainly by spawning mortality and was little influenced by the fishery. In the late 1970s the individual growth increased and the stock biomass went up accordingly. A large portion of the stock matured and spawned in the subsequent winters, and the stock declined to some 4 million tonnes in 1982–84. This decline in stock size was also caused by increased spawning mortality mainly and was little influenced by the fishery (Hamre, 1985).

The natural mortality of immature capelin (M) has been estimated to 0.61 in 1974–78, 0.86 in the 1979–83 and 1.68 in 1984–85 (Anon, 1987). The dramatic increase in M in latter years is caused by predation associated with an increase in the stock of young cod from 1983 onwards (Mehl, 1989). In 1984 and 1985 the recruitment also failed, probably due to increased predation or food competition between capelin larvae and the juvenile herring, and the capelin stock collapsed in 1986. The evidence thus suggests that the capelin fishery contributed to some extent to the stock decline in the 1980s, but recruitment failure was the main reason for the stock collapse in 1986 and in 1962 as well.

The year classes after 1983 are weak, except the 1990, 1991, and the 1989 year class, which was extraordinary abundant in relation to the parent stock (Fig. 9). In 1989 the individual growth of capelin increased to the highest level recorded, and the stock biomass rose from less than 1 million tonnes in 1989 to 6 million tonnes in 1990. A similar abrupt fall in the stock size has taken place in recent years, and this has not been influenced by the fishery (Fig. 6). The stock has suffered from recruitment failure since 1991, and a pronounced increase in M since 1992. This coincides with the occurrence of abundant year classes of herring and cod (Anon, 1993b, Anon, 1994).

Blue whiting

The catch of blue whiting increased sharply in the late 1970s, from an insignificant catch prior to 1976 to above 1 million tonnes in 1980. These large catches were taken from an accumulated stock estimated to be about 5 million tonnes in 1981. The annual catches declined to some 0.5 million tonnes in the mid 1980s, but have shown a slight increase in recent years (Monstad, 1989). The role of the blue whiting as prey for the carnivores of this ecosystem is considered to be small because the fish spawns in other areas.

Polar cod

The catch of polar cod rose from an insignificant catch prior to 1969 to about 350 000 tonnes in 1971. The corresponding stock size was estimated at 2 million tonnes. Thereafter, the stock and the catch decreased to a very low level in the late 1970s (Monstad and Gjøsæter, 1987). The polar cod may be of importance as food supply for seals, but has limited availability to stocks distributed south of the marginal ice zone.

Cod

VPA-based estimates of the state of the stock from 1950 onwards and yearly catches are illustrated in Fig. 7. In the middle of the 1950s, a very strong 1950 year class was recruited, and the stock increased to about 5 million tonnes. In the subsequent years the stock declined to 2 million tonnes by 1964. This reduction was mainly due to increased exploitation. In later years the variation in stock size reflects to a large extent the variation in year class strength. Strong year classes were recruited in the early 1970s and the stock increased to 3 million tonnes in 1975, but in the cold period after 1975 the recruitment was poor, and the exploitation high, and the stock declined to 1 million tonnes in 1983. From 1982 onwards several abundant year classes were recruited, but the stock biomass did not develop as expected. Shortage of suitable food since 1985 caused a dramatic fall in the individual growth rate (Fig. 8), and information on cod food in subsequent years indicate high mortality due to cannibalism (Mehl, 1989). This resulted in a dramatic fall in stock number from 1986 to 1988 (Anon 1988). Although the exploitation of all age-groups above 3 years has been high since the early 1960s, the fall in stock size was thus a result of food shortage more than an effect of the high

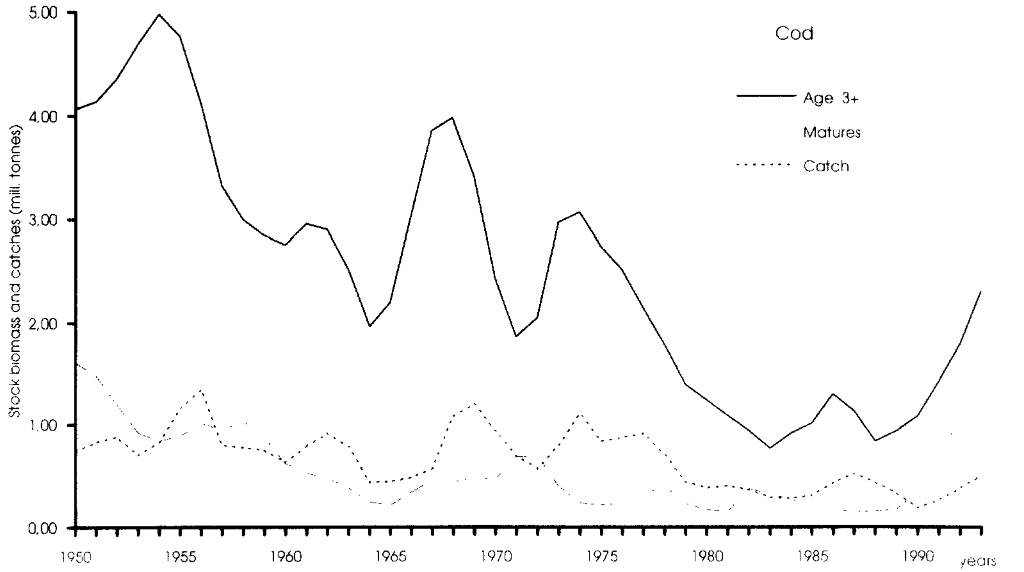

Figure 7. Estimated stock biomass of 3 years old and older cod (solid line), the spawning stock biomass (broken line) and catches (dotted line) in the years 1950–1993.

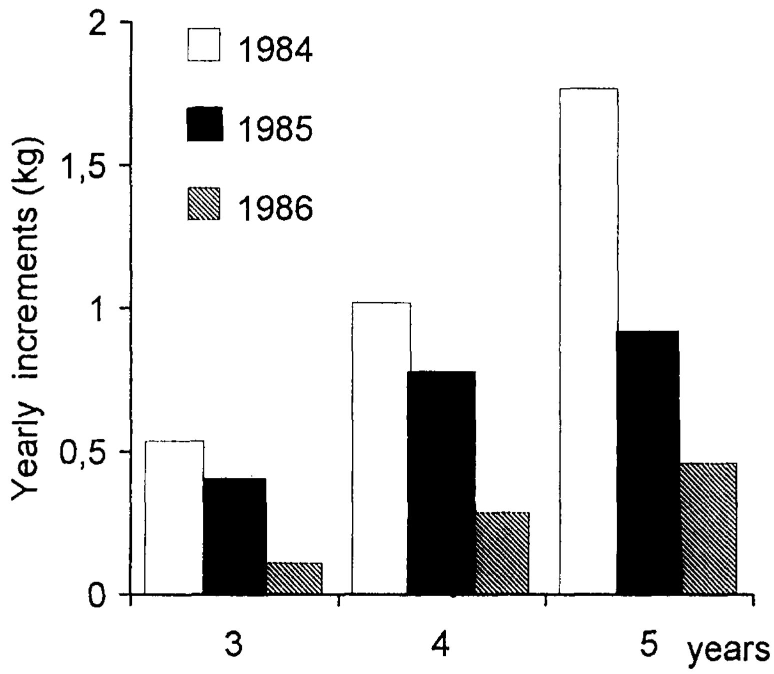

Figure 8. Yearly weight increment of cod by age in 1984–1986.

exploitation rate. The year classes recruited after 1989 are abundant and the stock biomass has increased to nearly 3 million tonnes (Anon, 1994).

Mammals

Mammals are important predators on plankton feeders and fish-feeding fishes in the Barents Sea, but data on stock sizes and feeding behaviour are inadequate to assess how much they consume. However, the commercially most important stock of whale, *Balaenoptera acutorostrata*, may have decreased in the relevant period and, there is no evidence for any substantial increase in the stocks of seals (Anon, 1989). The effect of the mammals on the abrupt decline in the prey species in the 1980s is considered to be small.

Recruitment mechanism

Information on the variation in the climate and the age structure of the stocks of cod and herring is available since the beginning of this century. This indicates that periods with a warm climate favour recruitment of cod and herring, whereas a cold climate is associated with low recruitment. Extraordinary strong year classes of cod and herring occurred around 1904, 1918, 1937, 1950, 1959 and 1963. In the warm period of the early 1970s, several abundant year classes of cod were recruited, but the herring failed to recruit due to the depletion of the spawning stock (Marti and Fedorov, 1963; Saetersdal and Loeng, 1984; Hamre, 1990).

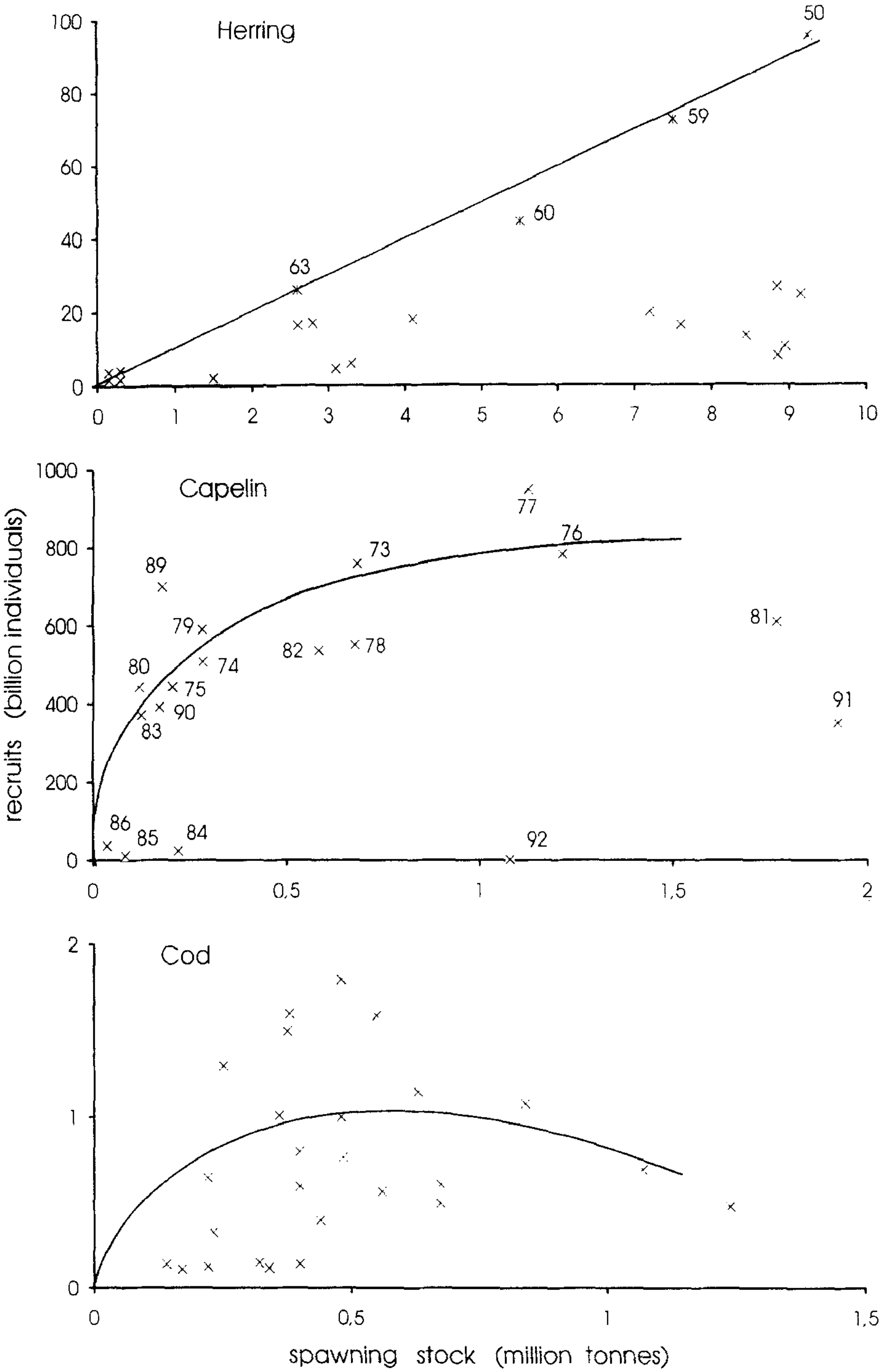

Figure 9. Stock versus recruitment plots of herring, capelin and cod. Recruits of herring and capelin are estimated as 1 year old, cod as 3 years old. The numbers indicate year classes (50 = 1950 year class).

Plots of recruitment versus spawning stock of herring and cod for the years 1950–1980 are shown in Fig. 9. The recruitment figures were back-calculated by VPA; increased mortality on juvenile herring in warm periods, when juvenile cod is abundant, is not accounted fro by VPA. Both the peak herring year classes, and those recruited immediately after the peaks, are likely to be underestimates. The latter may originally have been strong but may have, as in 1984–85, served as food resource for a growing stock of young cod.

The stock/recruitment function of herring suggests that in periods with favourable recruitment conditions the strength of the year classes is proportional to the size of the spawning stock. The supply of juvenile herring as food for cod is thus proportional to the abundance of the adult herring stock, whereas the cod may recruit strong year classes on relatively low stock levels. This means that in a state of reduced stocks, for instance after a long period of cold climate and/or heavy exploitation, a latent imbalance state of the predator-prey relationship may develop, and will be triggered when a shift to a warm climate occurs. In the early 1980s, when the climate changed, the cod stock was large enough to recruit strong year classes. Conversely, the herring, which needs a large parent stock to produce abundant year classes, could not take full advantage of the improved recruitment conditions, and an abrupt shortage of cod prey occurred. These recruitment mechanisms thus explain the paradox that the crisis in the fisheries developed after a change in the climate which favours recruitment conditions for the most important species of the system.

The capelin recruitment versus spawning stock plots (Fig. 9) are closely related to a Beverton/Holt recruitment curve, except for the years 1984–85 and 1992 when the recruitment failed completely, probably due to the recruitment of abundant herring year classes.

Stocks and climate interrelationship

Climate – fish stocks

As already mentioned, the overlap in distribution of juvenile herring and 0–group capelin in the southern Barents Sea may affect survival of the capelin fry.

Year	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
I	9.7	9.9	9.9	8.2	8.6	–	0.3	0.3	7.3	13.0	3.0	7.3

The index (I) of larval capelin production (Alvheim, 1985; Anon, 1993b) showed no substantial decline in the larval production in 1984–85, and the failure of recruitment from these year classes as one year old (Fig. 9) therefore must be explained by mass mortality of 0–group fish. The stock of young cod was also abundant in these years, but the cod is usually feeding in sub-surface layers and not at the surface layer, where herring and capelin are distributed. The outstanding capelin year classes 1971 and 1972 show moreover that capelin survived the abundant 1970 year class of young cod when herring were absent. The evidence thus suggests that the strong herring year class 1983 was responsible for increased mortality of capelin fry in 1984–85.

The hypothesis that abundant herring year classes in general have fatal effects on the capelin fry is supported by the observed recruitment failure in recent years. This is also proved experimentally (Øyestad and Moksness, 1979) and is decisive for the fate of the capelin stock in warm periods. The hypothesis is supported also by studies of the annual changes of the occurrence of capelin in the stomachs of cod by Russian scientists made since the late 1940s (Ponomarenko and Yaragina, 1978). Their findings reflect the effect of the herring and also the effect of the climate on the capelin stock. The cod feeds mainly on maturing (3+) capelin, and presupposing that the herring affects the survival of 0–group capelin only, a time lag of some 3–5 years between the recruitment of an outstanding herring year class and a decline in the availability of capelin as food for cod could be expected. This decline should be pronounced, because the maturation of capelin prior to the decline is expected to increase (high growth rate due to a warm climate). The annual changes of the occurrence of capelin in the stomach of cod, in relation to the outstanding herring year classes 1950 and 1959 are shown in Fig. 10, and fit remarkably well with the expectations. The chances of capelin surviving a warm period are therefore very poor owing to increased mortality on the older age groups (increased spawning mortality and/or increased predation by cod) and mass mortality of capelin fry. This was the situation in the early 1950s and 1960s, and explains the decline in the availability of capelin in the subsequent years. In the warm period of the 1970s, when herring stocks were low, no abrupt shortage of prey species developed. Relieved of the predation pressure of the herring, the capelin recruited outstanding year classes in the early 1970s, which overpopulated the Barents Sea in the mid 1970s (Anon, 1975). This suggests that this ecosystem may be more stable without the herring than with a

Figure 10. Frequency of occurrence of capelin in the stomachs of cod in the years 1947–1976. The arrows indicate years of abundant herring year classes.

small herring stock present, as in the 1980s. In the 1980s the herring was sufficiently abundant to cause recruitment failure of capelin, but was too small to meet the predators' food demand and the abrupt food shortage developed. This hypothesis is of historic interest because a similar crisis in stocks and fisheries in Northern Norway occurred in the beginning of this century (Hjort, 1903). Prior to this the herring stock had been depleted for 30 years and was growing slowly. The crisis in stocks and fisheries at the end of the previous century may thus have developed under similar conditions as in the early 1980s (Hamre, 1988).

According to the literature, the rise and fall of the capelin stock in previous years seem to have been governed by similar stocks and climate conditions as in the 1980s. In the period 1959–61 vast numbers of capelin spawned on the western coast of Finnmark and Troms indicating a shift to a warm climate (the end of a cold period). These stocks produced extremely poor year classes (as in 1984–85) and the fishery collapsed in 1962–64, probably due to the occurrence of the outstanding 1959 herring year class (Møller and Olsen, 1962; Olsen, 1965; Olsen 1968; Dragesund *et al.*, 1971). According to Olsen (1968), the capelin also disappeared from the Finnmark coast in the period 1938–42 after recruitment of the outstanding herring year class 1937.

Another important coincidence related to the climate is concerned with the migration pattern and spawning behaviour of the capelin. In the warm periods 1959–61 and 1983–85, the capelin spawned at the most westerly spawning grounds in Finnmark and Troms, early in the season (Fig. 11). After two years of recruitment failure (1960–61, 1984–85) the capelin changed its migration pattern in 1962 and 1986 to an extreme easterly route, which was difficult to detect before the spawners approached the easterly spawning grounds in the Barents Sea very late in the season (Møller and Olsen, 1962; Anon, 1986). In these years the spawners avoided the main distribution area of the cod, and after hatching the capelin fry was distributed to the east of the distribution area of the herring. The 1962 year class matured as 3-years old in 1965 and constituted the beginning of the rebuilding of the capelin stock in the latter half of the 1960s. Olsen (1986) noted also that the relatively rich year classes 1962 and 1963 were both derived from late easterly spawning in relatively low temperatures and the spawning stocks producing these abundant year classes were very small. On the other hand the vast number of capelin, which in 1960 and 1961 were spawning already in February and March in relatively warm waters at the western coast of Finnmark and Troms produced very poor year classes. A similar description would have been used for the fate of the year classes 1984 and 1985 compared with the year class 1986. This year class could have played a similar role in the rebuilding of the capelin stock in the late 1980s as the 1962 year class in the 1960s, if the winter fishery in 1986 had been banned.

Fish stocks – mammals

The dependency on the plankton feeders by carnivores at higher trophic levels is most clearly demonstrated for sea birds and Arctic seals which were affected severely by the abrupt food shortage which occurred in 1986. The large scale invasion of harp seal to the Norwegian west coast in 1986–87 coincided with the depletion of the immature capelin stock. The immature capelin used to accumulate in front of the advancing ice edge during autumn and winter in previous years, and groups of seals have been

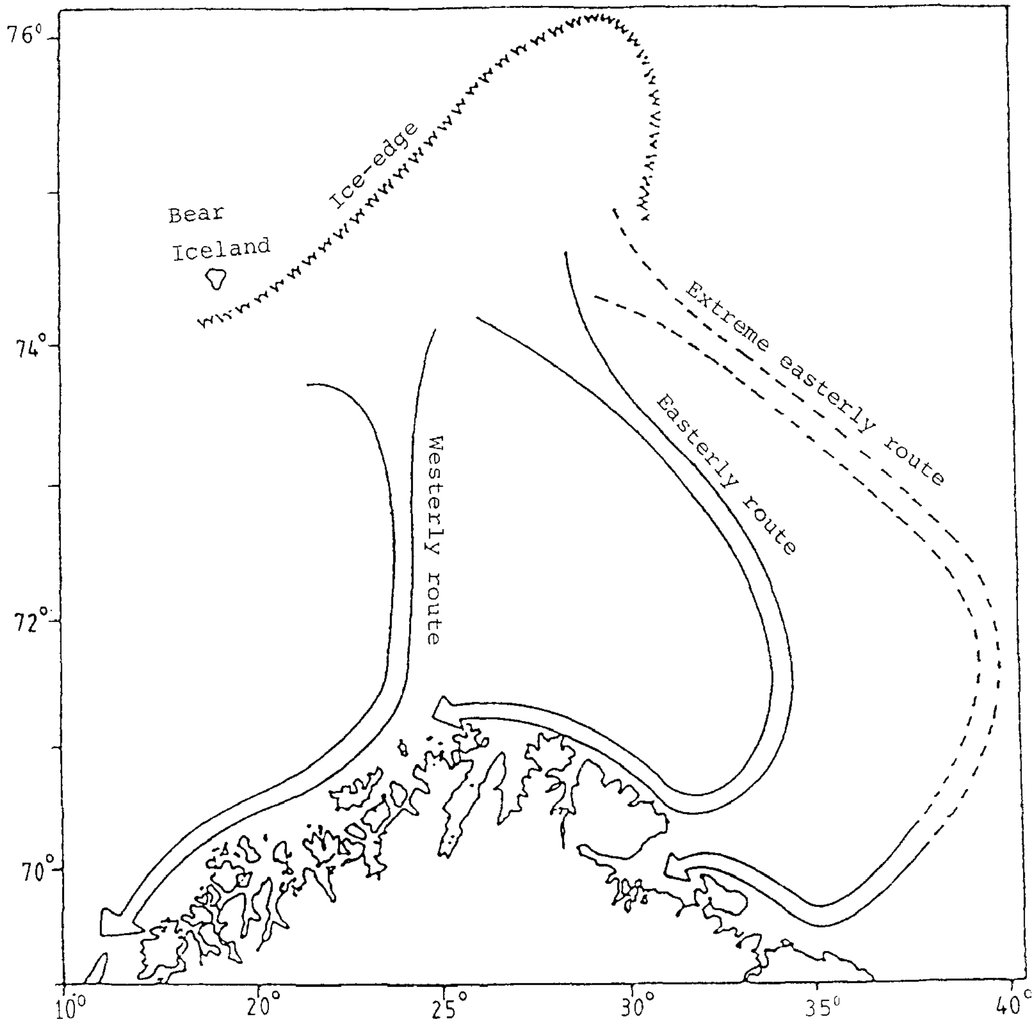

Figure 11. Typical spawning migration routes of capelin in January–March.

observed in this area during the winter surveys, especially in the localities east of Bear Island. No capelin and seals were recorded when this area was surveyed in January 1987 and although no sampling of these seals has been made, it is reasonable to assume that the majority of the harp seals which invaded the Norwegian west coast in 1986–87 originated from the Bear Island area (Wiig, 1988). It may be noted that no seal invasion occurred when the capelin disappeared in the early 1960s. In those years however the Barents Sea was inhabited by a large stock of juvenile herring, which may have fed the seals thus obviating their need to move to coastal areas.

Fish stocks – birds

The Norwegian Sea – Barents Sea region sustains a rich and diverse seabird fauna which also suffered greatly from lack of food after the collapse of the juvenile herring and capelin stocks. Almost all major bird-cliffs in Norway are situated north of the Arctic Circle close to the north-flowing Norwegian Coastal Current north of the spawning grounds of the herring and in the neighbourhood of main spawning localities of the capelin.

Seabirds feed on various stocks of small pelagic organisms. Atlantic puffin, *Fratercula arctica* and the common guillemot, *Uria aalge*, feed on capelin and 0–group herring. These birds therefore may serve as indicators on the state of their food resource, and are those that were most severely hit by the depletion of the plankton feeders (Vader *et al.*, 1990; Anker-Nilssen, 1990).

The Atlantic puffin is the most numerous seabird in the region and mainly feed their chicks on 0–group herring. After the collapse of the herring stock in the late 1960s, most of the puffin chicks starved to death due to lack of suitable food (Vader *et al.*, 1990). These birds however are long-lived, and can withstand periods of herring recruitment failure. Due to the puffin's long period of immaturity poor young production leads to declines in the adult puffin stock only after several years. In a colony in the main breeding area (Lofoten), the annual decrease in the number of breeding pairs was estimated to be about 10–15% since 1979; this decline slowed in 1988–89 due to recruitment into the colony of chicks fledged in 1983. Puffins have thus experienced a long-term recruitment failure due to shortage of 0–group herring, whereas there is no sign of food problems for the adults (Vader *et al.*, 1990).

A large number of common guillemots bred also in the Lofoten area. This bird has also produced few and often underweight young ones in many years and a steady decrease of some 5% annually of the breeding population has been recorded (Barrett and Vader, 1984). Poor nesting success due to lack of 0–group herring may partly be responsible for this decrease. After 1985, breeding numbers of common guillemot decreased steeply, by some 70–90% in Northern Norway and on Bear Island respectively. These common guillemot relied on capelin outside the breeding season, and the sharp decline in stock numbers reflects the collapse of the capelin stock. In the winter 1986–87 thousands of common guillemots washed ashore on the coast of Finnmark, probably starved to death by lack of suitable food. The shortage of food due to the collapse of the short-lived capelin stock however is of a much shorter duration than the depletion of the long-lived herring stock. This dramatic decline in common guillemot number has now eased, and a substantial increase in the stock of wintering birds was recorded in 1989 (Vader *et al.*, 1990).

Conclusions

In conclusion, the evidence indicates that the herring is the key prey species at fish level of the food chain in the Norwegian Sea – Barents Sea ecosystem, and the cod is the dominant predator. The capelin has an opportunistic life pattern, whose prospects of survival are governed by the state of the stocks of young herring and cod. The abundance of immature herring determines the survival of 0–group capelin, whereas the abundance of cod and death after spawning, determine the mortality of older capelin. The dynamics of the system are governed by the inflow of Atlantic water, which determines distribution, recruitment success and growth of the main species involved. Based on this knowledge, the following scenario for the events which led to the recent crisis in the Barents Sea's stocks and fisheries is suggested.

Towards the mid 1960s, relatively abundant stocks of herring and cod inhabited the Norwegian Sea – Barents Sea region. They were only moderately exploited, and the state of the stocks was determined more by natural fluctuations than by the fisheries. The Norwegian spring spawning herring and the North-East Arctic cod were the dominating stocks in the system, but the Barents Sea capelin was important as food for cod, especially when the herring had poor recruitment conditions.

In the mid 1960s the exploitation of herring increased dramatically as a result of new technology in the purse seine fishery. Within a few years the adult herring stock was exhausted, and the fishing grounds of Western Norway, where herring used to spawn and their progeny fed, became depleted. This situation forced the fishermen of Western Norway to relocate their efforts largely to the capelin fishery in the Barents Sea.

After a long period of cold climate in the 1950s, and heavy exploitation in the 1960s the stocks of herring and cod were much reduced in the 1970s. This favoured capelin survival. Outstanding capelin year classes were recruited in the early 1970s, and, despite large catches, the stock approached the maximum level the area could sustain. These year classes matured and spawned in 1976–77, and the stock biomass declined accordingly. The individual growth rate however was low (cold period), and at the end of the 1970s the stock consisted of several age groups of immature, relatively small fish.

A marked change to a warm climate took place in the late 1970s, and the individual growth rate of capelin rose to the highest level recorded. The biomass of the capelin stock increased accordingly, and a large part of the stock matured, spawned and died in the winter 1981. These processes reduced the stock in number substantially; the fishery had marginal effect on this development. In the period 1981–83 the immature stock was poor in number, but the growth in biomass was relatively high due to a high individual growth rate. From 1984 the stock suffered from recruitment failure due to the occurrence of the strong 1983 year class of herring, and the immature stock collapsed in 1986.

When the climate changed in the early 1980s, the stocks of herring and cod were very much reduced, but the spawning stock of cod was large enough to produce strong year classes. The herring, which needs large parent stocks to produce abundant year classes, was sufficiently abundant to reduce the survival of the capelin larvae significantly, but was too small to take full advantage of the improved recruitment conditions. Given the lack of juvenile herring and a reduced stock of capelin, the rapidly growing cod stock grazed down all the other available food fishes in the area, including its own progeny. From 1986 onwards the cod suffered from starvation and turned to cannibalism, the Arctic seals invaded the Norwegian coast in search of food and the sea birds died in thousands. In the period 1986–1988, the fish-eating stocks were dramatically reduced, and the balance of the predator-prey relationship was thus restored.

In later years the trend has changed. After a cold period in the mid 1980s, the climate changed in 1989 (Fig. 2). This coincided with a pronounced increase in the individual growth rate of capelin, as in the late 1970s, and the 1989 capelin year class is recorded as one of the largest on record (Fig. 9). This resulted in a rapid increase in the stock biomass. Since 1991 the stock has suffered from recruitment failure, probably due to an increasing stock of juvenile herring, and an abrupt fall in stock size has taken place.

The development in the recruitment of herring and cod is similar to that observed in the early 1980s. The cod and herring year classes have increased in strength during the years 1989–92, whereas the 1993 year classes are less abundant than the previous ones. This coincides with corresponding changes in the climate (Fig. 2), and the present state of climate and stocks is comparable to that in 1984–1985. The recent warm period seems to have terminated, and the prospects of herring recruitment in the coming years are poor. The juvenile stock of herring may therefore be dominated by the 1992 year class, which probably will leave the eastern part of the Barents Sea as 3 years old, i.e. in 1995, and thus improve the survival of capelin fry. Meanwhile the stock of young cod will become dependent on the herring as the main source of food. The stock of young cod is at present some 50% more abundant than the stock in 1985, whereas the juvenile herring is about 2.5 times more abundant than in 1985. The state of the herring stock however is still considered as overexploited (Fig. 5), and the question whether the present stock of juvenile herring in the Barents Sea is large enough to feed the predators and survive in sufficient numbers to rebuild the adult stock is difficult to predict.

References

Alvheim, O. (1985) Investigations on capelin larvae off northern Norway and in the Barents Sea in 1981–84. *Proc. Soviet-Norwegian Symp. Barents Sea Capelin, Bergen-Norway, 14–17 August 1984*. Bergen: Institute of Marine Research.

Anker-Nilssen, T. (1990) Sjøfuglsituasjonen i Barentshavet. *Biolog nr. 1* (In Norwegian).

Anon (1975) Ressursoversikt for 1975. Fisken Hav., (Saernr. 1975). (In Norwegian).

Anon (1986) Årsberetning 1986. Feitsildfiskernes Salgslag. (In Norwegian).

Anon (1987) *Report of the Atlanto-Scandian Herring and Capelin Working Group, Copenhagen 27–31 October 1986*. ICES C.M. 1987/Assess:8.

Anon (1988) *Report of the Arctic Fisheries Working Group, Copenhagen 14–24 September 1987*. ICES C.M. 1988/Assess:5.

Anon (1989) Ressursoversikt for 1989. Fisken Hav., 1989 (Særnr. 1) (In Norwegian).

Anon (1993a) Miljørapport 1993. Fisken Hav., (Særnr. 1, 1993). (In Norwegian).

Anon (1993b) *Report of the Atlanto-Scandian Herring and Capelin Working Group, Copenhagen 19–23 October 1992*. ICES C.M. 1993/Assess:6.

Anon (1994) *Report of the Arctic Fisheries Working Group, Copenhagen 24 August–2 September 1993*. ICES C.M. 1994/Assess:2.

Barrett, R.T. and Vader, W. (1984) The status and conservation of breeding seabirds in Norway. *Status and conservation of the world's seabirds* (J.P. Croxall, P.G.H. Evans and R.W. Schreiber, eds) pp. 323–33. ICBP Techn. Publ. No. 2.

Dommasnes, A. and Røttingen, I. (1985) Acoustic Stock measurements of the Barents Sea capelin 1972–1984. A review. In *Proc. Soviet-Norwegian Symp. Barents Sea Capelin, Bergen-Norway, 14–17 August 1984* (H. Gjøsaeter, ed.) pp. 5–24. Bergen: Institute of Marine Research.

Dragesund, O. (1970) Distribution, abundance and mortality of young and adolescent Norwegian spring spawning herring (*Clupea harengus*, Linne) in relation to subsequent year class strength. *FiskDirSkr., Ser.HavUnders.*, **15**, 451–556.

Dragesund, O., Gjøsaeter, J. and Monstad, T. (1971) Preliminary results of the Norwegian capelin investigations during winter and spring 1971. *Coun. Meet. Int. Comm. Explor. Sea, 1971* (H:24): 1–14, 4.

Dragesund, O., Hamre, J. and Ulltang, Ø. (1980) Biology and population dynamics of the Norwegian spring spawning herring. *Rapp. P-v. Reun. Cons. Int. Explor. Mer.*, **177**, 43–71.

Gjøsæeter, H., Hassel, A., Loeng, H., Rey, F. and Skjolda, H.R. (1983) Preliminaere resultater fra tokt i Barentshavet med M/S "Lance" og F/F "G.O.Sars" i mai/juni 1983. Inst. of Mar. Research, Bergen Report F08310: 1–21. (In Norwegian).

Gjøsæter, H. and Loeng, H. (1987) Growth of the Barents Sea capelin, *Mallotus villosus*, in relation to climate. *Env. Biol. Fish* **20**, 293–300.

Gulland, J.A. (1965) Estimation of mortality rates. Annex to Arctic Fisheries Working Group Report (meeting in Hamburg, January 1965). ICES C.M. 1965, Doc.No. 3, 9 pp.

Hamre, J. (1985) Assessment and management of Barents Sea capelin. In *Proc. Soviet-Norwegian Symp. Barents Sea Capelin, Bergen-Norway, 14–17 August 1984.* (H. Gjøsæter, ed.) pp. 5–24. Bergen: Institute of Marine Research.

Hamre, J. (1988) Some aspects of the interrelation between the herring in the Norwegian Sea and the stocks of capelin and cod in the Barents Sea. ICES C.M. 1988/H:42: 1–15. (Mimeo).

Hamre, J. (1990) Life history and exploitation of the Norwegian spring-spawning herring. In *Proceedings of the Fourth Soviet-Norwegian Symposium, Bergen 12–16 June 1989.* (T. Monstad, ed.) pp. 5–39. Bergen: Institute of Marine Research.

Hamre, J. and Tjelmeland, S. (1982) Sustainable yield estimates of the Barents Sea capelin stock. ICES C.M. 1982/H:45: 1–24. (Mimeo).

Hjort, J. (1903) Årsberetning. Norg. Fisk., 1903. (In Norwegian).

Marty, J.J. and Fedorov, S.S. (1963) Features of the population dynamics of marine herring as seen from the Atlanto-Scandian stock. *Rapp.P.-v. Reun. Cons. Perm. Int. Explor. Mer.* **154**, 91–97.

Mehl, S. (1989) The Northeast Arctic cod stocks consumption of commercially exploited prey species in 1984–1986. *Rapp.P.-v. Reun. Cons. Int. Explor. Mer.* **188**, 185–209.

Midttun, L. and Loeng, H. (1986) Climatic variation in the Barents Sea. *Proceedings of the third Soviet-Norwegian Symp. The Effect of Oceanographic Conditions on Distribution and Population Dynamics of Commercial Fish Stocks in the Barents Sea, Murmansk, 26–28 May 1986.*

Monstad, T. (1989) Distribution and growth of blue whiting in the Northeast Atlantic 1980–1988. *Proceedings of the fourth Soviet-Norwegian Symp. Biology and fishery of the Norwegian spring spawning herring an blue whiting in the Northeast Atlantic. Bergen, 12–16 June 1989.*

Monstad, T. and Gjøsaeter, H. (1987) Observations on polar cod (*Boreogadus saida*) in the Barents Sea 1973 to 1986. ICES C.M. 1987/G:13.

Møller, D. and Olsen, S. (1962) Lodda og loddefisket. *Fiskets Gang* **48**, 27–36. (In Norwegian).

Olsen, S. (1965) Abundance estimates of Barents Sea capelin. *FiskDir. Skr. Ser. HavUnders.*, **13**, 76–82.

Olsen, S. (1968) Some results of the Norwegian capelin investigations 1960–1965. *Rapp. P.-v-Reun. Cons. Int. Explor. Mer.* **158**, 18–23.

Ponomarenko, V.P. and Ponomarenko, I.Y. (1975) Consumption of the Barents Sea capelin by cod and haddock. ICES C.M. 1975/F:10: 1–6. (Mimeo).

Ponomarenko, I.Y. and Yaragina, N.A. (1978) Year-to-year and seasonal fluctuations in the feeding of the Barents Sea cod on capelin in 1947–1976. ICES C.M. 1978/G:24: 1–19. (Mimeo).

Prokhorov, V.S. (1965) Ecology of the Barents Sea capelin. (*Mallotus villosus* (Müller)) and prospectives for its commercial utilization. *Fish. Res. Bd. Can. Trans. Ser.* **813**, 1–131. [Mimeo] (Translated from Russian).

Saetersdal, G. and Loeng, H. (1984) Ecological adaptation of reproduction in Arctic Cod. Pp. 13–35. *Proc. of the Soviet-Norwegian Symp. Reproduction and Recruitment of Arctic Cod.* Bergen: Institute of Marine Research.

Vader, W., Anker-Nilssen, T., Bakken, V., Barrett, R. and Strann, K.B. (1990). Regional and temporal differences in breeding success and population development of fish eating seabirds in Norway after collapses of herring and capelin stocks. *Trans. 19th IUGB Congress, Trondheim, 1989.*

Wiig, Ø. (1988) Selinvasjonen til Norskekysten. *Fiskets Gang*, **6**, 18–19. (In Norwegian).

Øyestad, V. and Moksness, E. (1979) Interaction between Atlanto-Scandian herring larvae (*Clupea harengus* L.) and capelin larvae (*Mallotus villosus*) in a concrete enclosure experiment. ICES D.M. 1979/F:52: 1–10. (Mimeo).