ARCTIC
VOL. 48, NO. 3 (SEPTEMBER 1995) P. 267–278

Pelagic Fish and the Ecological Impact of the Modern Fishing Industry in the Barents Sea

HARALD GJØSÆTER[1]

(*Received 26 August 1993; accepted in revised form 24 January 1994*)

ABSTRACT. The Barents Sea/Norwegian Sea ecosystem is inhabited by two large pelagic fish stocks, the Norwegian spring spawning herring and the Barents Sea capelin. The herring stock feeds in the high-production polar front area in the western Norwegian Sea, and spawns at the Norwegian coast. The larvae are transported into the Barents Sea, where they spend the first two to four years of life. The capelin stock spends its whole life in the Barents Sea, spawning along the southern coasts and feeding in the nutrient-rich areas in the northern parts of the sea.

The herring stock was brought almost to extinction during the 1960s by the combined effect of overfishing and environmental conditions. This stock is now recovering. Much fishing effort was shifted to capelin when the herring fishery was stopped, and the capelin supported large fisheries in the 1970s. In the mid 1980s, the capelin stock size suddenly declined to a very low level. The factors involved were recruitment failure, low individual growth rates, high natural mortality, and, in the last phase, high fishing mortality. The recruitment failure was most likely caused by predation by some abundant year classes of herring in 1983–85. The low growth rate was probably caused by the scarcity of prey organisms, while the high mortality rate of the adult capelin stock was an effect of predation from abundant year classes of cod during the same period.

After having recovered in the period 1989–91, the capelin stock once more collapsed during 1992–93. The reasons were the same as for the collapse in the 1980s, except that fishing had no effect on the most recent collapse.

Key words: Barents Sea, ecology, fisheries, capelin, herring, polar cod

RÉSUMÉ. L'écosystème formé par la mer de Barents et la mer de Norvège est peuplé par deux importants stocks de poissons pélagiques, le hareng norvégien qui se reproduit au printemps et le capelan de la mer de Barents. Le stock de hareng se nourrit dans la zone hautement productive du front polaire dans l'ouest de la mer de Norvège, et fraie sur la côte norvégienne. Les larves sont transportées dans la mer de Barents, où elles passent de deux à quatre ans au début de leur vie. Le stock de capelan passe toute sa vie dans la mer de Barents, frayant le long des côtes méridionales et se nourrissant dans les zones riches en éléments nutritifs situées dans les parties septentrionales de la mer.

Au cours des années 1960, le stock de hareng a presque été décimé en raison de l'effet combiné de la surpêche et des conditions environnementales. Ce stock est maintenant en train de se renouveler. Lorsqu'on a cessé de pêcher le hareng, la pêche au capelan a connu un essor considérable et, dans les années 70, ce poisson a soutenu une importante industrie de pêche. Au milieu des années 80, la taille du stock de capelan a décliné subitement pour atteindre un très bas niveau. Les facteurs en cause étaient le manque de renouvellement, un faible taux de croissance individuelle, une mortalité naturelle élevée, et, durant la dernière phase, une haute mortalité due à la pêche. Le manque de renouvellement était probablement dû à la prédation exercée par certaines classes abondantes de harengs de 83 à 85. Le faible taux de croissance était probablement dû à la rareté des organismes-proies, tandis que le taux élevé de mortalité du stock de capelan adulte était une conséquence de la prédation causée par d'abondantes classes annuelles de morues durant cette même période.

Après avoir récupéré entre 1989 et 1991, le stock de capelan s'est de nouveau effondré au cours des années 92-93. Les raisons en étaient les mêmes que celles de l'effondrement des années 1980, sauf que la pêche n'était pas un facteur en cause.

Mots clés: mer de Barents, écologie, pêcheries, capelan, hareng, morue polaire

Traduit pour la revue *Arctic* par Nésida Loyer.

INTRODUCTION

The Barents Sea is a high-latitude, shallow continental shelf area. It is bounded in the north by the archipelagos of Svalbard and Franz Josef Land, in the east by Novaya Zemlya, and in the south by the coasts of northern Norway and Russia (Fig. 1). In the west, the boundary between the Barents Sea and the Norwegian Sea is usually drawn along the continental edge at about 10˚ to 15˚ E. Within these boundaries, the Barents Sea covers an area of 1 405 000 km^2 (Dragesund and Gjøsæter, 1988). More than 20% of the area is shallower than 100 m, but troughs deeper than 400 m enter the area from the west and northeast.

The Barents Sea is influenced by the high-salinity, high-

[1] Institute of Marine Research, P.O. Box 1870, N-5024 Bergen, Norway

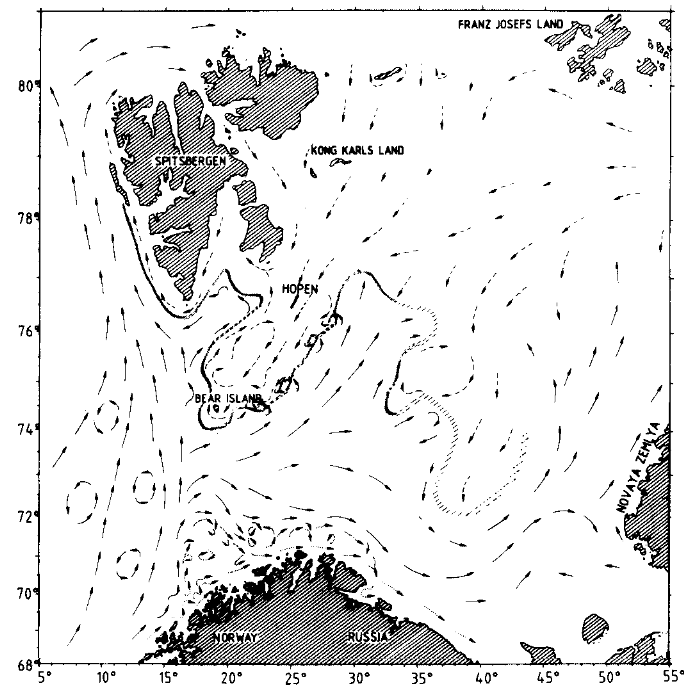

FIG. 1. Barents Sea with main current systems. —▶ = Atlantic currents, ····▶ = Coastal currents, ---▶ = Arctic currents. After Loeng (1991).

temperature Atlantic water and low-salinity, high-temperature Norwegian Coastal water flowing in from the southwest, and by low-salinity, low-temperature Arctic water flowing in from the north (Fig. 1) (Loeng, 1991). The water masses partly mix in the central and eastern parts of the Barents Sea, but in some areas, especially in the west, a front area (the polar front) is formed where the northeast-flowing Atlantic water and the southwest-flowing Arctic water meet.

The northern parts of the Barents Sea are covered with ice for part of the year. The ice coverage shows large variations from year to year (Loeng, 1991). Generally, the ice coverage is at its maximum during early spring, and at its minimum during September and October, when the entire Barents Sea may be ice-free.

The climate of the Barents Sea fluctuates to a large extent, with relatively warm periods of varying length alternating with cold periods. It is generally concluded that these climatic variations depend mainly on the activity and properties of the inflowing Atlantic water (Loeng, 1991).

From an ecological point of view, the Barents Sea is not isolated from the areas farther west and south. The Barents Sea serves as a nursery area for the offspring of several fish stocks spawning at the western and northwestern coast of Norway. This includes major species such as herring (*Clupea harengus* L.), cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.) and saithe (*Pollachius virens* L.). The Barents Sea is also visited by several species of whales on their feeding migrations, of which the minke whale (*Balaenoptera acutorostrata* Lacépede), the humpback whale (*Megaptera novaengliae*), white-sided dolphin (*Lagenorhynchus acutus*) and white-beaked dolphin (*Lagenorhynchus albirostris*) are the most important during summer and autumn. The adult stock of cod and haddock, which resides in the area in the feeding and wintering period, moves out of the area and farther south along the Norwegian coast to spawn in spring. The main species that spend the whole life cycle in the Barents Sea are the capelin (*Mallotus villosus* Müller) and the polar cod (*Boreogadus saida* Lepechin). A generalized food web above the primary producers in the Barents Sea/Norwegian Sea is shown in Figure 2.

In the Norwegian Sea, the zooplankton is grazed mainly by herring, but blue whiting (*Micromesistius poutassou* Risso) also plays an important role. In the Barents Sea the main plankton eater is the capelin, and to some extent the polar cod, but in years with young herring in this area this species may be the most important planktivorous fish in the Atlantic water. Several stocks of fish-eating fish, birds and mammals exploit the plankton feeders, which in addition are harvested by man. Finally, some of the predatory stocks are also harvested by man, mainly the various fish stocks, but also, to some extent, seals and whales.

The aim of the present paper is to discuss the role of the pelagic fish stocks in the Barents Sea ecosystem and, in particular, the impact of the exploitation of pelagic fish stocks on the ecosystem.

Primary and Secondary Production

The Barents Sea is a highly productive area, with typical production rates of 165 g carbon per m^2 per year south of the polar front, and 115 g or lower, depending on the ice conditions, north of the polar front (Sakshaug et al., 1992). The primary production is highly variable, both within the area and between years. Even though the production per year is higher in the Atlantic water, the process of freezing and melting of ice in these northern areas prolongs the period of high production, and therefore makes this area an important feeding area for pelagic fish. While most of the production south of the polar front stems from a spring bloom, the production along the receding ice edge may be looked upon as a continuous bloom, following the ice edge northwards. Zooplankton grazes the phytoplankton bloom. Pelagic fish, capelin in particular, follow behind, grazing the zooplankton.

In the Norwegian Sea, there is also a highly productive region associated with the polar front. This area is located in the western parts of the Norwegian Sea, where the warm Atlantic water mixes with the southflowing cold arctic water of the East Greenland Current. In this area, the adult part of the Norwegian spring spawning herring stock had its main feeding area before the stock collapsed.

Planktivorous Fish

The plankton production in the Norwegian Sea is harvested by the adult herring, while the plankton production in the Barents Sea is harvested by capelin and juvenile herring (Hamre, 1991). There is little overlap between the feeding areas of juvenile herring and adult capelin in the Barents Sea;

the capelin mainly utilizes the region north of the 72° latitude, while the herring is confined to the more southern regions. There is, however, some overlap between juvenile herring and juvenile capelin. Two large stocks of semipelagic fish feed in the same areas; polar cod in the Barents Sea and blue whiting in the Norwegian Sea (Fig. 2).

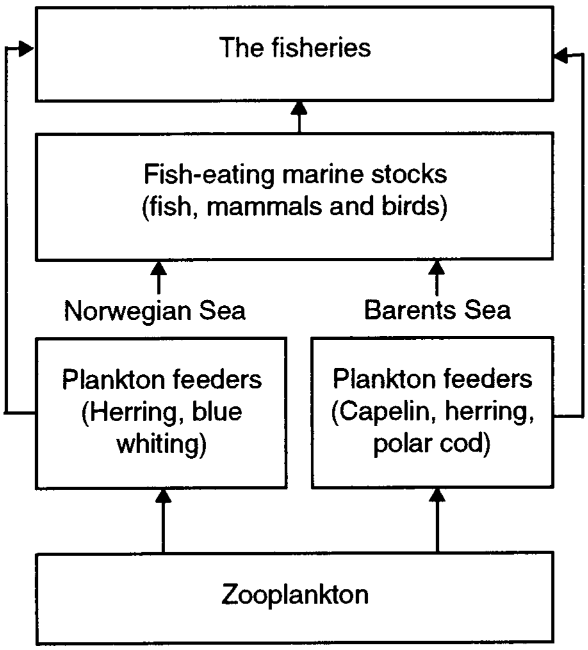

FIG. 2. Food web in the Norwegian Sea–Barents Sea. Redrawn from Hamre (1991).

Piscivorous Production

Planktivorous fish serve as the main food for various predatory fish, seals, whales and birds. In the Barents Sea, the Northeast Arctic cod stock is the main predator on the capelin and the herring. During summer, the larvae and juveniles of both herring and capelin are heavily predated by sea birds. The minke whale feed on capelin and herring during the summer-to-autumn period, while other whale stocks feed on these stocks more or less during the whole year. Seals take their share when capelin are located near the ice. Man harvests both the plankton-feeding and the fish-feeding stocks (Fig. 2).

THE PELAGIC FISH STOCKS IN THE BARENTS SEA

Capelin

Biology, Life History, and Migrations: The capelin is a small, schooling, pelagic, salmonid fish inhabiting subarctic and arctic regions. The Barents Sea is inhabited by one large oceanic stock, potentially one of the largest capelin stocks of the world. In addition, some small local stocks of capelin are found in the fjords of northern Norway.

The Barents Sea stock undertakes substantial migrations (Fig. 3). The spawning migration takes place during winter, and is an upstream movement towards the southern coast of the western Barents Sea, compensating the larval drift towards north and east. The spawning takes place at the coast of northern Norway and to a lesser extent at the Kola Peninsula during spring.

Most individuals spawn only once, at an age of three to five years. The mortality caused by predation is extensive both prior to, during and probably after spawning. Most individuals not eaten by predators will die of exhaustion or physical injuries soon after spawning. Females are injured to a lesser extent than the males during the spawning process, and are physiologically capable of surviving the spawning season to spawn a second time (Fridgeirsson, 1976; Forberg, 1982). Analysis of the sex ratio in scientific samples and in landings from the Barents Sea has not revealed any predominance of females among older fish, which is anticipated in case of a higher spawning survival among females and equal proportions of each sex spawning at a particular age. The short life expectancy after maturity also indicates a substantial mortality among mature fish.

The demersal eggs hatch after three to six weeks, depending on the temperature (Gjøsæter and Gjøsæter, 1986). The larvae are mainly found in the upper 50 m, and are transported by the currents towards the north and east (Figs. 1, 3). During autumn, they normally have a widespread distribution in the areas south of 76°N.

The young (immature and maturing) capelin take up a seasonal migrating pattern (Fig. 3). They overwinter south of the polar front, and move towards the coastal areas in the south to graze the spring bloom there. Then they migrate north and east during summer, following the receding ice-edge and the plankton bloom associated with it (Hassel et al., 1991). The northernmost distribution is reached at 79° – 80°N during September and October, when the stock is grazing heavily on the rich plankton production in these areas. In years with a warm climate, the stock will be found farther to the east than in years with a cold climate. The stock once again migrates southwards upon the cooling and freezing of these areas during late autumn and winter.

The individual growth is extremely variable, both between parts of the stock inhabiting different areas of the Barents Sea, and between different year classes (Table 1, Gjøsæter, 1985, 1986; Gjøsæter and Loeng, 1987; Skjoldal et al., 1992). Table 1 shows that the mean individual weight of two-year-olds in the period 1973 – 93 varied from 5.6 g to 15.3 g. The between-year growth variation, which is best studied by otolith analysis (Gjøsæter, 1986), is most probably caused by variable food conditions (Skjoldal et al., 1992) and temperature (Gjøsæter and Loeng, 1987).

The within-year growth variation between areas can also be large, and shows a similar pattern from year to year (Gjøsæter, 1986; Gjøsæter and Loeng, 1987). The growth is normally higher in the western areas (mainly the Bear Island, Spitsbergen, Hopen area) than in the more northern and eastern areas (Table 1).

Stock Abundance and Exploitation: The size of the Barents Sea capelin stock has varied considerably in the period 1973 –94 (Fig. 4). The collapse of the stock in the

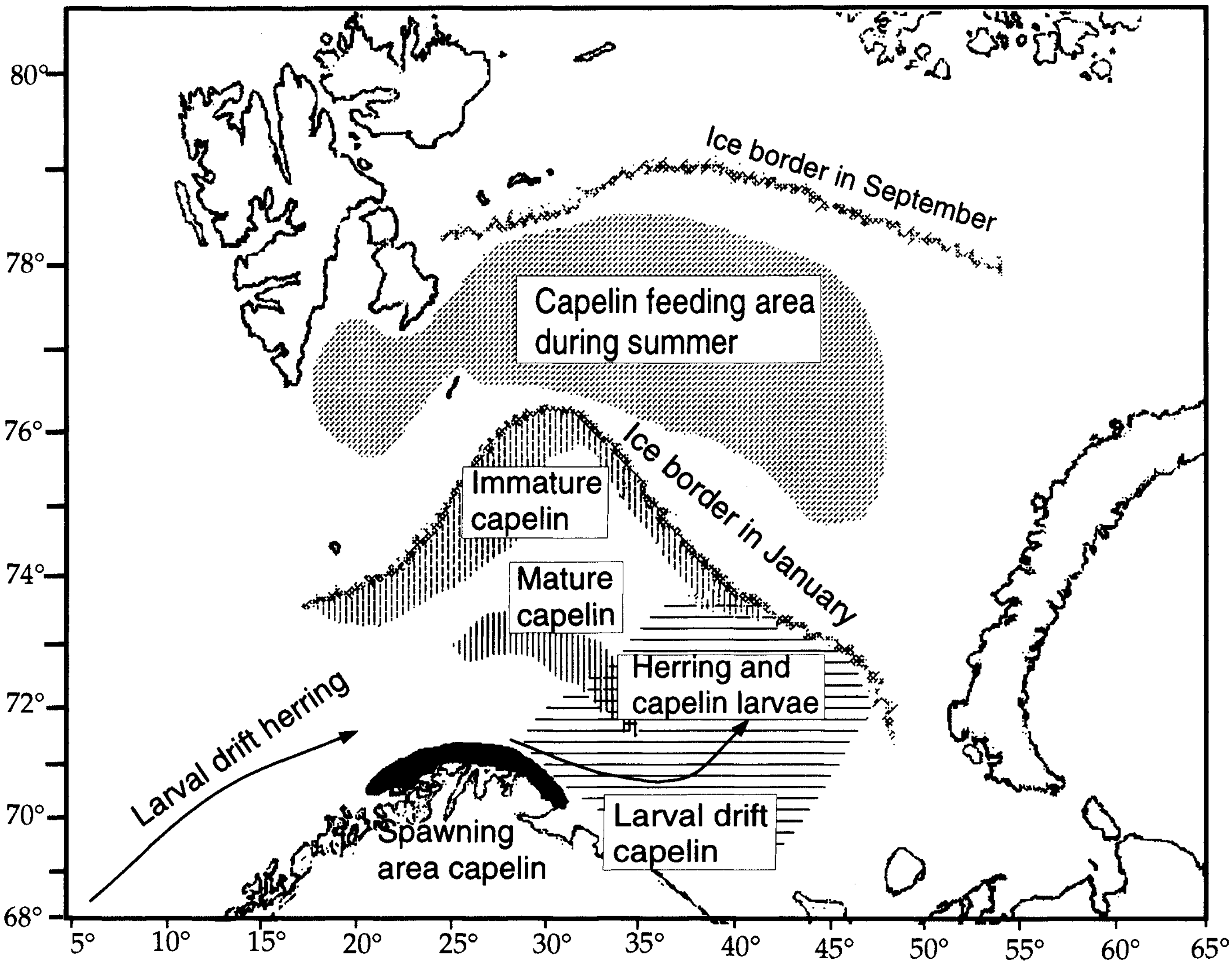

FIG. 3. Distribution and migrations of the Barents Sea capelin stock. Redrawn from Hamre (1991).

middle 1980s has naturally attracted most attention both from the scientific community, and from the fishing industry and management bodies. The various hypotheses proposed to explain the mechanisms underlaying the fall in stock size of capelin (and other stocks in the same area as well) will be discussed in a later section (Hamre, 1991; Hopkins and Nilssen, 1991; Tjelmeland and Bogstad, 1993).

The stock history of the capelin has been very well monitored since 1973, through joint efforts of the Institute of Marine Research in Bergen and the Polar Institute of Fisheries and Oceanography in Murmansk. Before this period, the state of the stock was known only indirectly from the success of the directed fishery, which dates back to the late 1950s, and from the catch of young cod following the ripe capelin to the spawning areas.

The capelin stock has been exploited as prespawners off the coast of Norway and the Kola Peninsula since the early 1950s (Table 2). The fishing effort increased, and so did the catches, until the fishery failed totally in 1962–64. The stock size and the catches then increased gradually during the late 1960s. The catches during the period 1970–75 reached 1.3 to 1.4 million tonnes, and peaked in the late 1970s with catches at almost 3 million tonnes.

The acoustic stock size measurements (Fig. 4) show an increase of the stock from 1973 to 1975. This was due to the recruitment of the three large but slow-growing year classes 1971–73. Slow growth implies late maturation, and the very large stock size in 1974 to 1976 can thus be explained by a combined effect of good recruitment and accumulation of age-groups in the immature stock caused by low (spawning) mortality (Hamre, 1991). On the other hand, the sudden fall in stock size from 1975 to 1977 is explained by the bulk of this accumulated stock spawning (and dying), without new strong year classes to replace it.

A new peak in stock size was experienced in 1980. Contrary to the peak in 1975, this was caused by a very high individual growth rate of year classes of intermediate sizes. Once more the peak was followed by a one- or two-year decrease in stock size due to a high portion of the stock maturing and spawning in the winter 1980–81 (Fig. 4). The

TABLE 1. Individual mean weights (g) of two-year-old capelin.

Year	Mean weight (g)		
	Total area[1]	West[2]	East
1973	5.6	8.1	7.6
1974	5.6	7.8	6.5
1975	6.8	11.0	7.4
1976	8.2	10.1	7.9
1977	8.1	9.4	8.1
1978	6.7	7.1	7.0
1979	7.4	7.5	7.9
1980	9.4	9.9	8.8
1981	9.4	11.9	8.9
1982	9.0	11.7	7.3
1983	9.5	11.8	6.9
1984	7.4	9.6	6.1
1985	8.2	9.5	7.7
1986	11.7	13.2	10.9
1987	12.3	14.7	12.7
1988	12.3	14.9	11.9
1989	12.4	17.8	11.0
1990	15.3	17.6	12.6
1991	8.7	12.2	8.1
1992	8.6	11.6	8.5
1993	9.0	9.7	8.6
1994	11.2	9.9	8.7

[1] Data from Dommasnes and Røttingen, 1985 (1973–83), and unpublished cruise reports (1984–94).

[2] "West" and "East" pertain to the areas nos. 6 and 7 in a multispecies model for the Barents Sea (Tjelmeland and Bogstad, 1993). The two areas do not comprise the total stock, and the mean weights in these areas can therefore not be directly compared to those from the total area.

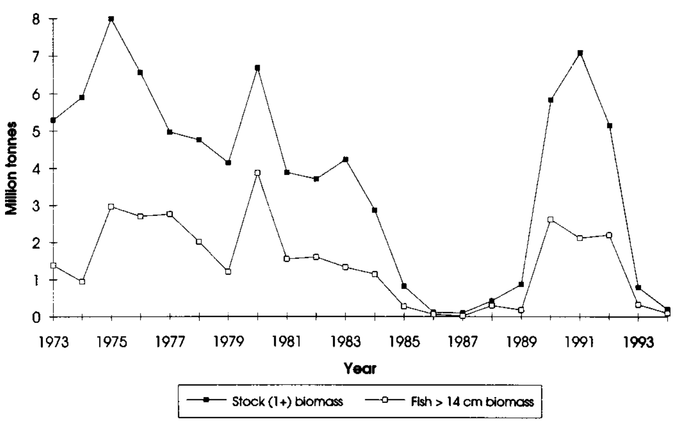

FIG. 4. Stock history of Barents Sea capelin stock 1973–94. Biomass of fish 1 year old and older, and biomass of fish larger than 14 cm (maturing stock).

level of 4 million tonnes was maintained until 1983. From 1984 to 1986 the stock was reduced to less than 100 000 tonnes. The following processes were involved: 1) a total failure of recruitment of the year classes 1984 and 1985, in spite of a "normal" larval abundance these years (Fig. 5; Alvheim 1985; Fossum, 1992); 2) a very low individual growth rate (Gjøsæter, 1986; Skjoldal et al., 1992); and 3) a substantial mortality of both immature and maturing stock (International Council for the Exploration of the Sea [ICES], 1987), mainly caused by predation from cod (Mehl, 1991). A

TABLE 2. Catches (thousand tonnes) and fishing mortality coefficients (F) for herring, capelin and polar cod.

Year	Herring		Capelin		Polar Cod	
	Catch	F[1]	Catch	F[2]	Catch	F[3]
1951	1278	0.09	9			
1952	1254	0.10	9			
1953	1090	0.09	18			
1954	1644	0.12	30			
1955	1359	0.09	41			
1956	1659	0.11	66			
1957	1319	0.09	70			
1958	986	0.08	91			
1959	1111	0.10	78			
1960	1101	0.10	92			
1961	830	0.08	217			
1962	848	0.08	0			
1963	984	0.10	28			
1964	1281	0.17	19			
1965	1547	0.29	224			
1966	1955	0.86	389		1	
1967	1677	1.34	409		4	
1968	712	1.91	537		2	0.01
1969	67	0.56	680		135	0.18
1970	62	0.98	1314		243	0.19
1971	21	1.23	1392		348	0.48
1972	13	1.87	1592		167	0.47
1973	7	1.29	1336	0.13	82	0.54
1974	7	0.67	1149	0.07	124	
1975	13	0.09	1440	0.07	63	
1976	10	0.04	2587	0.18	12	
1977	22	0.05	2987	0.33	8	
1978	19	0.05	1915	0.08	5	
1979	12	0.02	1783	0.29	+	
1980	18	0.03	1648	0.16	+	
1981	13	0.04	1986	0.31	24	
1982	16	0.02	1760	0.41	90	
1983	23	0.03	2358	0.67	37	
1984	53	0.10	1478	0.34	6	
1985	169	0.38	868	0.49	11	
1986	225	0.75	123	0.00	1	
1987	127	0.30	0	0.00	+	
1988	135	0.25	0	0.00	0	
1989	103	0.06	0	0.00	0	
1990	86	0.14	0	0.00	0	
1991	84	0.06	933	0.10	0	
1992	104	0.07	1123	0.06	0	
1993	232	0.17	586	0.00		
1994			0	0.00		

[1] Mean value for age groups 5–10 (ICES, 1995).

[2] Mean value for age groups 2–4 in the autumn fishery (ICES, 1995).

[3] Mean value for recruited age groups (Monstad and Gjøsæter, 1987).

possible impact of fishing will be discussed later.

The fishery levelled off at about 1.8 million tonnes after the peak in 1977, regulated by catch quotas. In the period 1983 to 1986 the fishing was rapidly reduced, and was banned from 1987 to 1990 (Table 2).

From 1988, the stock size increased rapidly, to reach 6–7 million tonnes in 1990–91. The increase was made possible by a very strong year class in 1989, but was mainly caused by a record individual growth in 1990. In addition, the mortality among all age groups decreased considerably after 1987.

In 1991–93, the situation resembled that in the early 1980s: herring and cod once more were seen to be producing strong year classes. So was the capelin (Fig. 5), but investigations

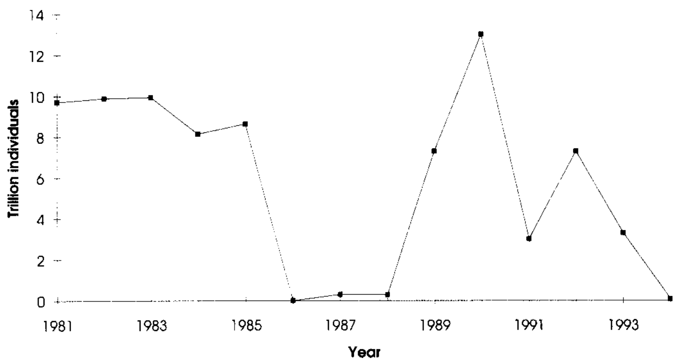

FIG. 5. Recruitment to the capelin stock. Number of larvae in June, based on catches in a Gulf III high-speed plankton sampler. Data for 1981–92 from Fossum (1992), data from 1993–94 from unpublished cruise reports, Institute of Marine Research, Bergen.

carried out in the autumn of 1992 and 1993 (Institute of Marine Research, survey data) showed that the capelin larvae produced in those years had been almost totally exterminated. Their disappearance was most likely due to heavy predation on the capelin larvae by young herring during the summer (Huse and Toresen, 1994). In 1994, the larval production of capelin was low (Fig. 5), probably mainly because of reduced spawning stock size (Fig. 4). Moreover, the mortality of the older age groups has increased dramatically because of increased predation by cod. Consequently, by autumn 1994 the capelin stock was back at the low level of 1986–87 (Fig. 4).

The Norwegian Spring Spawning Herring

Biology, Life History, and Migrations: The herring plays a major role in the Barents Sea ecosystem, although this area only functions as a nursery area for this stock. From the spawning areas along the coast of western Norway, the offspring are brought with the north-flowing currents into the southern Barents Sea (Fig. 6). At that time, the herring reach a length where they take up schooling, and are no longer passively drifting with the currents. The nursery area of the herring is therefore limited to the areas south of 74˚N. After two to four years, the herring move out of the area, to join the adult stock living in the Norwegian Sea.

The drift of herring larvae into the Barents Sea is, however, not a regular phenomenon. In many cases, all the larvae will enter the fjords along the coast. Large numbers of herring in the Barents Sea are associated with strong inflow of Atlantic water and strong year classes.

Stock Abundance and Exploitation: The Norwegian spring spawning herring stock was the largest fish stock in European waters until the collapse in the 1960s (Fig. 7). The rapid decrease in stock size was partly caused by weak recruiting year classes. The fishery, which exploited both immature and mature herring, undoubtedly played a key role as well: the fishing mortality coefficient (F, a quantity describing the proportion of the stock removed by the fishing) rose to more than 1.0 in the years 1967–73, when the stock was brought almost to extinction (Table 2; Hamre, 1991). From 1975 onwards, the stock slowly began to recover. The first relatively strong year classes appeared in 1983–85, and for the first time since 1959–60, herring larvae entered the Barents Sea. The year classes 1984 and 1985 disappeared, and the 1983 year class left the Barents Sea in spring 1986. The spawning stock of herring has gradually increased since 1975: first very slowly, then faster from 1988 as the 1983 year class started to recruit. As the result of the larger spawning stock, the year classes from 1988 onwards have gradually become better than average for the period after the stock collapse, but the stock is still at a very low level compared to the historic levels (Fig. 7).

The catches of herring were negligible in the 1970s, but increased somewhat in the 1980s (Table 2). Regulation has aimed at a fishing mortality level below 0.05, a level high enough to keep a small fleet going and fill a consumption market, but low enough not to hamper the rebuilding of the stock to any noticeable degree.

Polar Cod

Biology, Life History, and Migrations: The polar cod is a small, arctic, semipelagic, schooling, gadoid fish. There is one stock (or possibly two) inhabiting the eastern and northern cold-water areas of the Barents Sea. The polar cod is often found in near-bottom layers (Monstad and Gjøsæter, 1987), but is best categorized among the pelagic fishes in an ecological context, because it takes practically all its food from the pelagic part of the ecosystem (Ajiad and Gjøsæter, 1990).

The biology of this species has not been very much studied in this area. It is of minor importance in the fisheries, and parts of its life cycle are spent in ice-covered areas inaccessible to investigations.

During autumn, the polar cod is found more or less over the whole Barents sea, but mainly in the northern and eastern areas. In late autumn a spawning migration towards the very southeastern areas of the Barents Sea takes place, and spawning occurs under the ice in these areas during winter or early spring. Judging from the distribution of larvae observed during summer, spawning also takes place to the east of Spitsbergen. It is not clear whether these two spawning areas imply that there are two separate stocks in the Barents Sea (Gjøsæter, 1973). The polar cod rarely attains an age of more than five or six years, and probably spawns only once or twice.

Stock Abundance and Exploitation: The stock history is poorly known (Fig. 8). Information on stock size consists partly of virtual population analysis (VPA) calculations based on Norwegian and Russian catches in the 1960s and 1970s (Monstad and Gjøsæter, 1987), and partly of acoustic measurements from 1986 onwards. These acoustic estimates must be regarded as indicative only, as they are a by-product of the surveys for capelin, and therefore the total distribution area of the polar cod stock may not be covered each year. The acoustic properties of the polar cod are also not well known.

The stock size rose steeply up to 1970, supported by good recruitment from the year classes 1965 to 1967. A number of poor year classes followed, and the stock declined to a very

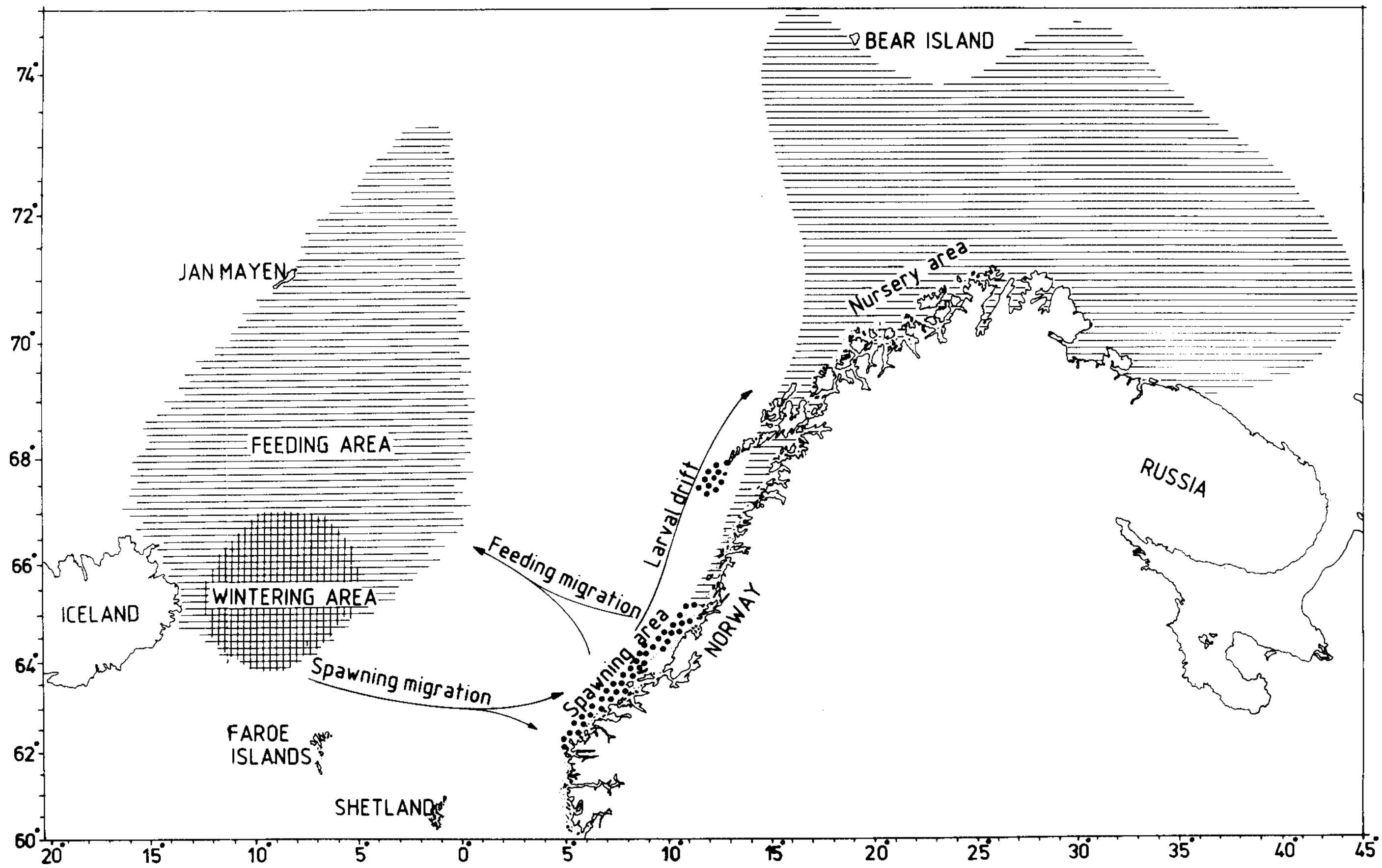

FIG. 6. Distribution and migrations of the Norwegian spring spawning herring. Redrawn from Hamre (1991).

small size in the middle 1970s. The stock size up to 1986 is not known. In that year, a stock of 500 000 tonnes was measured acoustically, and in 1987, 630 000 tonnes (Fig. 8). Both in 1985 and in 1986 very strong year classes were recruited to the stock. In the next three years, a much lower stock was recorded. Poor consistency between the number of fish in the various year classes measured acoustically indicates that the measurements in 1988 and 1990 may be underestimates. In 1992 and 1993, the stock size was estimated at nearly one million tons, and the recruitment was above average.

Both the former USSR and Norway started regular polar cod fisheries in 1969 (Table 2). The Norwegian fleet was active until 1973, when poor conditions made the fishermen lose interest in this fishery. The USSR fleet again took bigger catches in 1981–83, but the landings have been negligible since then.

THE FISHING INDUSTRY'S EFFECT ON THE ECOSYSTEM

When the fishery on the Norwegian spring spawning herring was stopped around 1970, the Norwegian fleet of purse seiners turned to other stocks, primarily North Sea herring and mackerel, Barents Sea capelin, and polar cod. At that time, the fleet was modernized with acoustic fish-finding instruments, power blocks and seines made of synthetic fibres, making both the fish finding and the catching operations much more effective than previously. The landings from the pelagic stocks in the North Sea rose sharply following the increased effort, but these stocks were apparently overexploited, and the catches soon were reduced.

Consequently, more and more effort was shifted to the Barents Sea stocks (Table 2). In this area, there were no regulations on the pelagic fisheries before 1978, and the development of the capelin fishery mirrors the availability of capelin and the fishing effort. From 1978 onwards, the fishery was regulated by catch quotas set by the former Soviet-Norwegian Mixed Fishery Commission. In most years the regulations followed the scientific advice given, except for the last years before the ban, when the scientists wanted heavier restrictions and a stop in the fishery already in 1986.

As mentioned earlier, the Norwegian fishing for polar cod came to an end in 1975, and there has been little interest in reopening this fishery on an industrial level since (Table 2).

The Ecological Impact of the Fishing Industry

Herring: In a comprehensive review of the herring fishery, Dragesund et al. (1980:69) conclude that "the collapse of the stock in the 1970s was mainly due to overexploitation." For centuries, "herring periods," when herring was abundant,

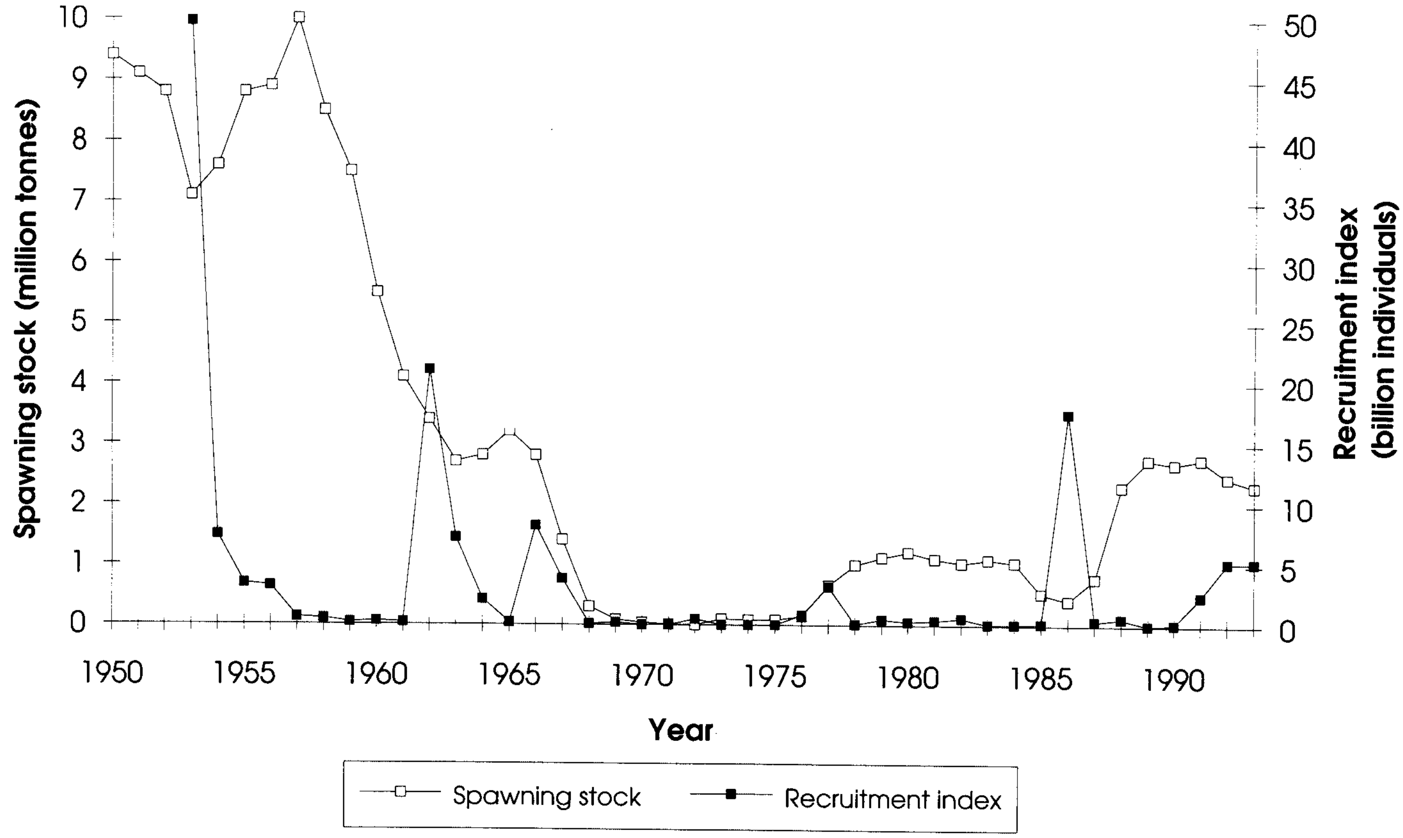

FIG. 7. Stock history of Norwegian spring spawning herring 1950–93. Spawning stock biomass and recruitment at age three, based on VPA. Data from ICES (1995).

have shifted with more or less regular periods without herring on the Norwegian coast. This also happened long before the fisheries reached a level where they could possibly have any effect on the stock size. Adverse oceanographical conditions may have played a crucial role in impeding the recruitment in the 1950s–60s. Nevertheless, the massive mortality caused by fishing in practically all age groups in this period makes the conclusion cited above a very plausible one.

Capelin: Prior to 1968 the fishing was exclusively aimed at the prespawners approaching the coast to spawn in winter. From that year onwards, a fraction, in some cases half of the total catch, was fished during the summer-to-autumn period, in the feeding areas.

The winter fishing exploits the mature population exclusively, while the autumn fishery exploits a mixture of maturing and immature capelin. To protect the youngest age groups, a minimum landing size of 11 cm was enforced.

The Winter Fishery: In a stock which spawns only once, the main goal for the regulations of the fishery on the spawning stock, at least in a single-species context, should be to allow a sufficient number of fish to spawn to secure the recruitment. This may seem like an ideal scenario for regulating a fishery, but some crucial questions remain: How much will the predators (mainly cod), which are in direct competition with the fishing fleet, consume prior to the spawning? How large need the spawning stock be to produce enough offspring for sufficient recruitment even under poor survival conditions? Should the spawning stock be regarded as “lost,” or will predators or scavengers utilize also the dead and dying post-spawners?

Whatever the answers to these questions, the fact remains that the only possible effect of a winter fishery on the capelin stock is to hamper recruitment through reduction of the spawning stock and thus the larval production.

Can it be shown or demonstrated through circumstantial evidence that this has occurred? By comparing the historic stock sizes (Fig. 4) with the larval production (Fig. 5), it is seen that in 1984 and 1985, when both the total stock and the mature stock were drastically reduced, and there still was a substantial winter fishery taking place, the larval production was at the same level as in the previous years, and consequently sufficiently large to produce strong year classes under “normal” conditions. In 1986, however, a recruitment overfishing is likely to have taken place. Although fishing was limited to a quota of 120 000 tonnes, the spawning stock was at this time severely reduced, and the larval production was low. Figure 5 does not give a correct picture of the larval production in 1986, because some spawning took place unusually late in spring, and the offspring from this spawning were not recorded during the larval survey (Fossum, 1992). Surveys later in the autumn revealed that capelin larvae were distributed in small quantities over a limited area. It may be concluded that up to 1986, the winter fishing had had little effect on the stock collapse. In 1986, however, the fishery may have had a significant effect on larval production, and thereby on stock development, because survival of the larvae produced in 1986 was exceptionally good.

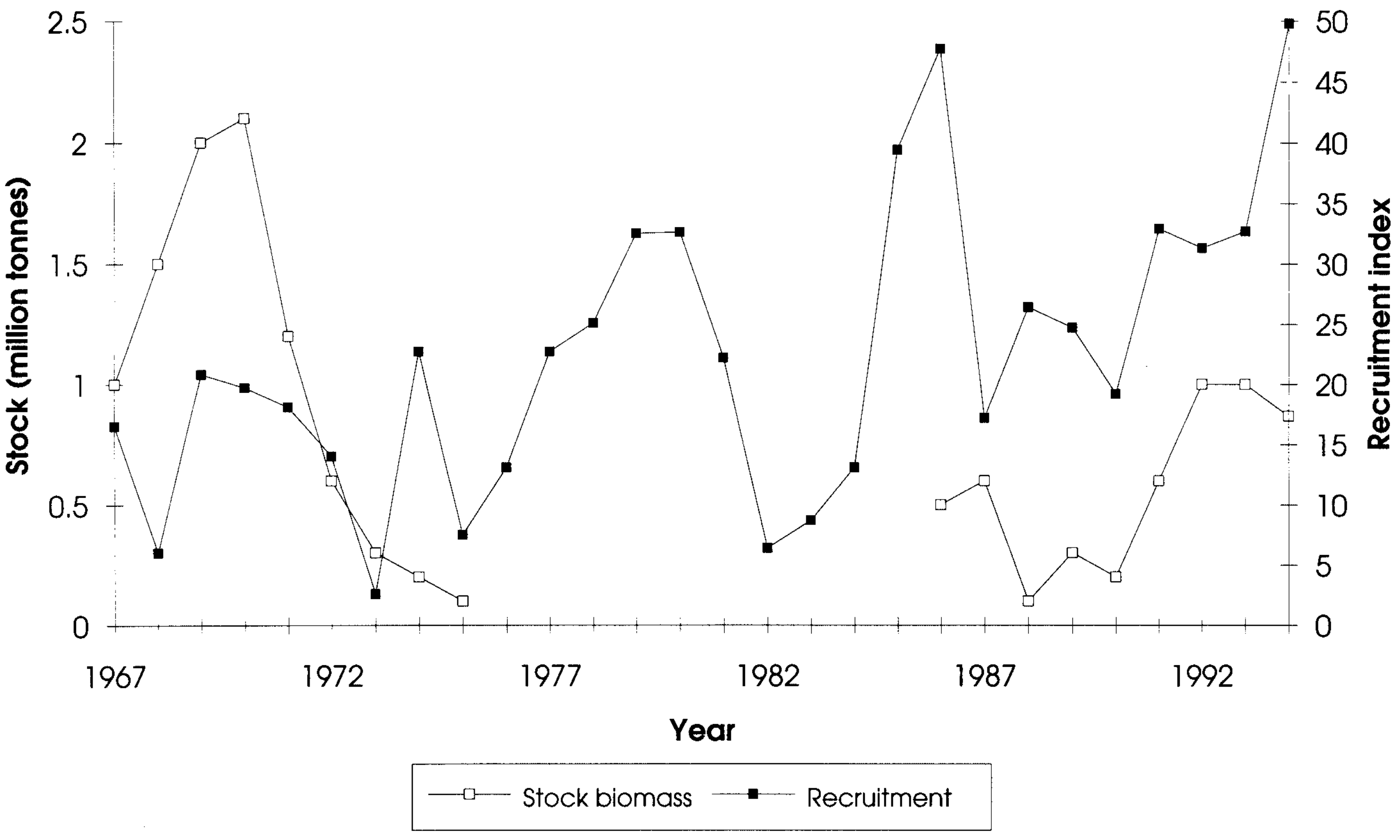

FIG. 8. Stock history of Polar cod 1967–94. Data on stock biomass for the years 1967–75 from Monstad and Gjøsæter (1987). Data on stock biomass 1986–94 from unpublished cruise reports, Institute of Marine Research, Bergen. Data on recruitment indices for the years 1967–93 from ICES (1994a), for 1994 from an unpublished cruise report, Institute of Marine Research, Bergen. The recruitment index is thousands of square nautical miles where polar cod larvae were found, weighted with mean number caught in the sampling trawl.

The Autumn Fishery: In contrast with the winter fishery, the autumn fishery, exploiting both adult and juvenile capelin, can have various effects on the stock. First, it can reduce the maturing part of the stock so much that the following winter, even without a winter fishery, the spawning stock will fall below the critical size needed to secure the recruitment. Second, the autumn fishery can reduce the number of juvenile fish to such an extent that the total production in the stock is reduced, or the spawning stock is reduced below a critical level 1.5 or 2.5 years ahead of time.

The first result will add to the possible effects of the winter fishery. Consequently, if the winter fishery has had no detrimental effects on the spawning stock in the period, neither has the autumn fishery preceding it. The catch of 250 000 tonnes of capelin in autumn 1985, however, undoubtedly contributed to reducing the spawning stock size below a critical level in 1986.

If the effects on the spawning stock can be ruled out, at least up to the autumn fishery in 1985, only the possible effects on the production of the immature and maturing stock remain. The weight of the two-year-old capelin is inversely related both to the number of individuals in the total stock (Fig. 9, N = 21, $p < 0.001$), and to the number of individuals of age 2 (N = 21, $p < 0.001$), indicating a density dependence—or rather, a stock size dependence—in growth. Consequently, a change in the number of fish will, within certain limits, be compensated by a change in the growth rate. This means that the capelin stock will be able to utilize the amount of food available, which is determined by the production at lower levels of the food web and other ecological factors, irrespective (within certain limits) of the number of individuals in the stock.

Have the catches taken during autumn reduced the number of fish in the stock beyond a level where growth compensation can maintain a maximal production? This question is probably impossible to answer with certainty, because there are so many environmental (abiotic and biotic) factors which also affect production. A decrease in weight-at-age is evident as the number of individuals in the stocks increases (Fig. 9), indicating a density-dependent growth variation. Gjøsæter (1986) could not, however, demonstrate density-dependent growth variation when comparing growth in various subareas to the observed fish density. The growth variation seen in Figure 9 is probably caused by a larger capelin stock exhausting its total food base, not necessarily by a real shift in fish density. It is, however, a fact that the individual mean weight of the age groups increased steadily up to 1990, partly compensating for a decrease in stock numbers (Fig. 9). As the age at maturity is inversely proportional with the size at age, this trend is parallelled by a decrease in the age at maturity. As pointed out by Hopkins and Nilssen (1991), there are certain limits to how far this compensation can go: the capelin

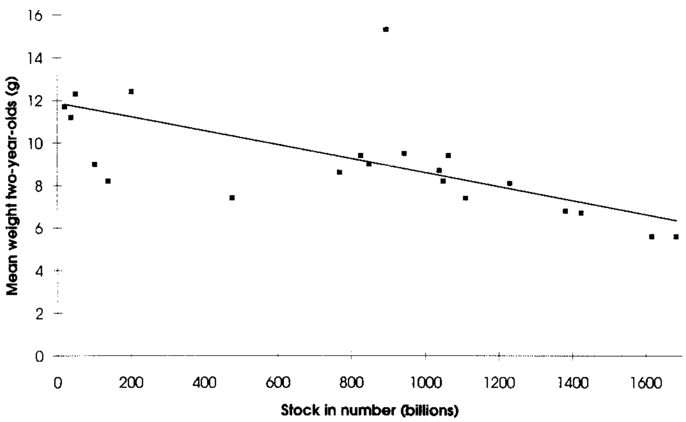

FIG. 9. Relationship between total number of individuals in the capelin stock and the mean weight of the two-year-olds. Data from ICES (1991), Dommasnes and Røttingen (1985), unpublished cruise reports, Institute of Marine Research, Bergen.

has a limited spawning period and it is highly unlikely that individuals will mature before they have had three growth seasons, regardless of growth rate. It cannot be ruled out that the reduction in number of individuals in the stock which took place during the early 1980s, accompanied by higher growth rates, had an adverse affect on the stock—not primarily by reducing the spawning stock beyond a warrantable size, but by making the spawning stock more and more dependent on a single year class.

The fishing mortality coefficients for age group 2–4 in the autumn fishery (Table 2), show that prior to 1977, the fishing removed a relatively small proportion of the individuals, in most cases far less than the natural mortality (M) estimated for the autumn period at that time (M = 0.05 month^{-1}). In the period 1977–81, the fishing mortality coefficient varied between 0.08 and 0.33, and increased to about 0.4 from 1982 onwards. The year 1983, when F equalled 0.67, is an exception.

A Scenario of the "Rise and Fall and Rise and Fall" of the Capelin Stock: As mentioned earlier, various hypotheses explaining the severe changes in the sizes of the pelagic stocks have been proposed. Hopkins and Nilssen (1991), argued that the capelin stock decline started as early as 1975, and that fishing was an important contributory factor during the whole period. They did not take into account the climatically-driven changes in recruitment, growth and geographical distribution of the cod, capelin and herring stocks. Hamre (1991) and Tjelmeland and Bogstad (1993), maintain that the decreasing stock size prior to 1982–83 can be explained by a natural response to changes in growth and maturation. Their view is that the collapse started in the early 1980s, and is best understood in light of changing environmental factors. This analysis is, in my opinion, preferable to that of Hopkins and Nilssen (1991). As was explained above, the history of the capelin stock up to the mid 1980s can be explained by factors other than exploitation. The fishery probably played a minor role, at least up to the autumn 1985 to winter 1986 fishing season. The new stock collapse in 1992–94 can also not be attributed to overexploitation, since the exploitation rate was low during this period. Following this logic, a scenario of the capelin stock history is outlined below.

The environmental effects involved can be outlined as follows: During the winter of 1982–83 there was an increase in the inflow of Atlantic water to the Barents Sea, carrying nutrient-rich water with large stocks of zooplankton. This change in oceanographic conditions provided a very good recruitment environment for the stocks of Norwegian spring spawning herring and Northeast Arctic cod. These favourable conditions for cod and herring persisted for three years, resulting in large stocks of young cod and herring in the Barents Sea. The herring is a potential predator of capelin larvae (Moxness and Øiestad, 1987), and there are reasons to believe that this predation may have caused the almost total recruitment failure of capelin in 1984–85. The strongest evidence supporting this hypothesis, apart from the direct observations of capelin larvae in the stomachs of young herring (Huse and Toresen, 1994), is that the larval production was seemingly normal these years, but the resulting year classes never recruited to the stock of one-year-olds and older fish, as measured by acoustic methods.

Observations of capelin larvae in the stomachs of 0-group cod show them to be another potential predator of capelin larvae. No quantitative investigations have so far been carried out to study the significance of this predation.

The inflow event ended in late winter 1983, and left the southwestern Barents Sea with a low abundance of the dominant copepod *Calanus finmarchicus*, because this copepod overwinters in the Norwegian Sea deeper than the depth at the entrance to the Barents Sea (Skjoldal et al., 1992). This resulted in a minimum in zooplankton biomass in the central Barents Sea in 1984, and consequently the growth rate of the capelin was low (Table 1). This decreased growth contributed to the decline of the capelin stock.

Another effect of the increased inflow and higher water temperature was a northeastern displacement of the capelin stock. The growth rate is always lower in the northeastern areas (Table 1), and this effect added to the effect described above.

The large stock of young cod caused an increasing demand for food, which could only to a minor degree be filled by the herring year classes 1984 and 1985 (Mehl, 1991). These two year classes almost disappeared, while the 1983 year class, which grew up together with the first strong cod year class was inaccessible to the cod because of a too small size difference and therefore survived. The young cod then turned to the capelin, and predated heavily upon the capelin stock whenever there was a geographical overlap. Tjelmeland and Bogstad (1993) estimated the natural mortality of the capelin to have increased from 0.04–0.09 per month in the period 1979–83, to 0.18–0.26 per month in the period 1985–87. An instantaneous mortality coefficient of 0.26 per month means that more than 96% of the individuals in the stock will die within one year.

Thus, the predation by cod added to the possible effects of the fishing in the period, and contributed to the capelin stock collapse in 1985–86.

The 1983 year class of herring left the Barents Sea in May 1986, and the small number of capelin larvae produced in 1986 and 1987 had excellent survival conditions. When the

1986 year class recruited to the spawning stock in 1989, one of the largest year classes of capelin ever recorded emerged. The growth conditions improved, and the mean weight of the two-year-olds peaked in 1990 (Table 1). The large 1989 year class had a much lower growth, probably caused mainly by density-dependent factors. The biomass of the capelin stock in 1991 was found to be among the largest recorded in the period 1972–91.

The cod stock experienced a severe shortage of food when the capelin stock collapsed. This resulted in a dramatic reduction in individual growth and increased mortality because of cannibalism (Mehl, 1991). The initially rich year classes of 1984 and 1985 never recruited to the fishable cod stock as expected, and the fishing on that stock had to be reduced.

More or less the same mechanisms were probably involved in the 1992–94 stock collapse. The natural mortality of capelin once more increased to the levels found in the period 1985–87. The recruitment of the year classes 1991 and 1992 failed completely, in spite of an average larval production these years (Fig. 5).

One of the lessons to be learned from the ecological events in the 1980s, and those in 1992–93, is that the capelin stock will be the loser when both cod and herring recruit strong year classes in the Barents Sea. From historical books and reports dealing with life in northern Norway back to the 16th century, it is known that the capelin disappeared at irregular intervals (Øiestad, 1992). From the recent history, it is known that such periods of capelin disappearance are associated with strong year classes of herring (1938–42, herring year class 1938; 1962–64, herring year classes 1959 and 1960; 1986–87, herring year class 1983 [Olsen, 1965; Hamre, 1991]; 1993–94, herring year classes 1990–92). Note that only prior to the period 1986–87 was there any notable fishing on the capelin stock.

CONCLUSIONS

The Barents Sea-Norwegian Sea is a highly productive ecosystem, able to maintain large stocks of pelagic fish to feed its predators, including man. The ecosystem has an inherent tendency to fluctuate between periods of strong recruitment of cod and herring with reduced size of the capelin stock, and periods of absence of herring in the Barents Sea, moderate recruitment to the cod stock, and a large capelin stock.

The fisheries for pelagic stocks may play, and have played, a major role in the ecosystem, by intensifying these inherent fluctuations. The fisheries clearly contributed to the collapse of the herring stock in the 1960s, and may also have played a role, albeit a minor one, in the collapse of the capelin stock two decades later.

Perhaps the most important effect of the fisheries for pelagic stocks in this ecosystem is not the reduction of the pelagic stocks themselves, but the enlargement of the instability in the whole ecosystem. The reduced stock of herring in 1983 was too small to fully take advantage of the good recruitment conditions in 1983–85. The resulting herring year classes were therefore too small to feed the cod, and the capelin stock was more heavily predated. The cod stock suffered from food shortage, the growth declined and the mortality increased, because of both increased cannibalism and larger fishing mortality. The result was that all three stocks were more heavily reduced than would have been the case if a larger herring stock had been present. The crisis at the fish levels of the ecosystem had severe effects on the higher levels of the food web. Paradoxically enough, perhaps one of the main reasons for the dying seals and birds, and the economic ruin of many fishermen in the mid 1980s should be sought in the overexploitation of the herring stock 20 to 30 years earlier.

ACKNOWLEDGEMENTS

The author thanks Valantine Anthonypillai for preparing most of the figures, and Kenneth G. Foote for correcting the English text. I am also grateful for constructive comments from two reviewers.

REFERENCES

AJIAD, A.M., and GJØSÆTER, H. 1990. Diet of polar cod, *Boreogadus saida*, in the Barents Sea related to fish size and geographical distribution. International Council for the Exploration of the Sea, Council Meeting 1990/G:48. 9 p.

ALVHEIM, O. 1985. Investigations on capelin larvae off northern Norway and in the Barents Sea in 1981–84. In: Gjøsæter, H., ed. The proceedings of the Soviet-Norwegian symposium on the Barents Sea Capelin, Bergen, 14–17 August 1984. Bergen: Institute of Marine Research. 171–183.

DOMMASNES, A., and RØTTINGEN, I. 1985. Acoustic stock measurements of the Barents Sea capelin 1972–1984: A review. In: Gjøsæter, H., ed. The proceedings of the Soviet-Norwegian symposium on the Barents Sea capelin, Bergen, 14–17 August 1984. Bergen: Institute of Marine Research. 45–108.

DRAGESUND, O., and GJØSÆTER, J. 1988. The Barents Sea. In: Postma, H., and Zijlstra, J.J., eds. Ecosystems of the world 27: Continental shelves. Amsterdam: Elsevier. 339–361.

DRAGESUND, O., HAMRE, J., and ULLTANG, Ø.1980. Biology and population dynamics of the Norwegian spring-spawning herring. Rapports et Procès-verbaux de la Réunion du Conseil International pour l'Exploration de la Mer. 177:43–71.

FORBERG, K.G. 1982. A histological study of development of oocytes in capelin, *Mallotus villosus* (Müller). Journal of Fish Biology 20:143–154.

FOSSUM, P. 1992. The recovery of the Barents Sea capelin (*Mallotus villosus*) from a larval point of view. International Council for the Exploration of the Sea, Journal of Marine Science 49:237–243.

FRIDGEIRSSON, E. 1976. Observation on spawning behaviour and embryonic development of the Icelandic capelin. Rit Fiskideildar 5(4):1–24.

GJØSÆTER, H. 1985. Growth of the Barents Sea capelin of the year classes 1975 – 1981. In: Gjøsæter, H., ed. The proceedings of the Soviet-Norwegian symposium on the Barents Sea capelin, Bergen, 14 – 17 August 1984. Bergen: Institute of Marine Research. 193 – 212.

———. 1986. Growth of the Barents Sea capelin compared to stock size and geographical distribution. International Council for the Exploration of the Sea, Council Meeting 1986/H:38. 16 p.

GJØSÆTER, H., and GJØSÆTER, J. 1986. Observations on the embryonic development of capelin (*Mallotus villosus* Müller) from the Barents Sea. Fiskeridirektorates Skrifter, Serie Havundersøkelser 18:59 – 68.

GJØSÆTER, H., and LOENG, H. 1987. Growth of the Barents Sea capelin, *Mallotus villosus*, in relation to climate. Environmental Biology of Fishes 20(4):293 – 300.

GJØSÆTER, J. 1973. Preliminary results of Norwegian polar cod investigations 1970 – 1972. International Council for the Exploration of the Sea, Council Meeting 1973/F:8. 23 p.

HAMRE, J. 1991. Interrelation between environmental changes and fluctuating fish populations in the Barents Sea. In: Kawasaki, T., Tanaka, S., Toba, Y., and Tanaguchi, A., eds. Long-term variability of pelagic fish populations and their environment. Proceedings of the international symposium, Sendai, Japan, 14 – 18 November 1988. Oxford: Pergamon Press. 259 – 270.

HASSEL, A., SKJOLDAL, H.R., GJØSÆTER, H., LOENG, H., and OMLI, L. 1991. Impact of grazing from capelin (*Mallotus villosus*) on zooplankton: A case study in the northern Barents Sea in August 1985. In: Sakshaug, E., Hopkins, C.C.E., and Øritsland, N.A., eds. Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, 12 – 16 May 1990. Polar Research 10(2):371 – 388.

HOPKINS, C.C.E., and NILSSEN, E.M. 1991. The rise and fall of the Barents Sea capelin (*Mallotus villosus*): A multivariate scenario. In: Sakshaug, E., Hopkins, C.C.E., and Øritsland, N.A., eds. Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, 12 – 16 May 1990. Polar Research 10(2):535 – 546.

HUSE, G., and TORESEN, R. 1994. Predation by adolescent herring (*Clupea harengus* L.) on Barents Sea capelin (*Mallotus villosus* Müller) larvae. Paper presented at the Sixth Norwegian/Russian Symposium: "Precision and relevance of pre-recruit studies for fishery management related to fish stocks in the Barents Sea and adjacent waters." Bergen, Norway, 14 – 17 June 1994.

ICES (International Council for the Exploration of the Sea). 1987. Report of the Atlanto-scandian Herring and Capelin Working Group, Copenhagen, 27 – 31 October 1986. Council Meeting 1987/Assess:8. 57 p.

———. 1991. Report of the Atlanto-scandian Herring and Capelin Working Group, Copenhagen, 15 – 19 October 1990. Council Meeting 1991/Assess:6. 58 p.

———. 1994a. Preliminary report of the international 0-group fish survey in the Barents Sea and adjacent waters in August-September 1993. Council Meeting 1994/G:3. 38 p.

———. 1994b. Report of the Atlanto-scandian Herring and Capelin Working Group, Copenhagen, 18 – 22 October 1993. Council Meeting 1994/Assess:8. 78 p.

———. 1995. Report of the Atlanto-scandian Herring and Capelin Working Group, Copenhagen, 17 – 21 October 1994. Council Meeting 1995/Asses:9. 101 p.

LOENG, H. 1991. Features of the physical oceanographic conditions of the Barents Sea. In: Sakshaug, E., Hopkins, C.C.E., and Øritsland, N.A., eds. Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, 12–16 May 1990. Polar Research 10(1):5 – 18.

MEHL, S. 1991. The Northeast Arctic cod stock's place in the Barents Sea ecosystem in the 1980s: An overview. In: Sakshaug, E., Hopkins, C.C.E., and Øritsland, N.A., eds. Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, 12 – 16 May 1990. Polar Research 10(2):525 – 534.

MONSTAD, T., and GJØSÆTER, H. 1987. Observations on polar cod (*Boreogadus saida*) in the Barents Sea 1973 to 1986. International Council for the Exploration of the Sea, Council Meeting 1987/G:13. 24 p.

MOXNESS, E., and ØIESTAD, V. 1987. Interactions of Norwegian spring-spawning herring larvae (*Clupea harengus*) and Barents Sea capelin larvae (*Mallotus villosus*) in a mesocosm study. Journal du Conseil International pour l'Exploration de la Mer 44:32 – 42.

ØIESTAD, V. 1992. Er lodden til å stole på? Fiskets Gang Nr. 4-1992:22 – 23. In Norwegian.

OLSEN, S. 1965. Abundance estimates of Barents Sea capelin. Fiskeridirektoratets Skrifter, Serie Havundersøkelser 13(8):76 – 82.

SAKSHAUG, E., BJØRGE, A., GULLIKSEN, B., LOENG, H., and MEHLUM, F., eds. 1992. Økosystem Barentshavet. Norwegian Research Program for Marine Arctic Ecology - Pro Mare, Norges Allmenvitenskapelige Forskningsråd, Norges Fiskeriforskningsråd, Miljøverndepartementet. 304 p. In Norwegian.

SKJOLDAL, H.R., GJØSÆTER, H., and LOENG, H. 1992. The Barents Sea ecosystem in the 1980s: Ocean climate, plankton, and capelin growth. International Council for the Exploration of the Sea, Marine Science Symposia 195:278 – 290.

TJELMELAND, S., and BOGSTAD, B. 1993. The Barents Sea capelin stock collapse: A lesson to learn. In: Smith, S.J., Hunt, J.J., and Rivard, D., eds. Risk evaluation and biological reference points in fisheries management. Canadian Special Publication of Fisheries and Aquatic Sciences 120:127 – 139.