

## Causes of trends and fluctuations in the Arcto-Norwegian cod stock

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Published information is used to review trends and fluctuations in landings and stock characteristics/variables (abundance, growth, maturation, distribution, and migrations) in relation to changes in environmental and anthropogenic factors as well as interactions with other species. The stock declined from about 4-5 million tonnes in the 1950s to less than 1 million tonnes in the 1980s owing to exploitation. For more than 30 years the annual fishing mortality rate was well above any calculated safe level, so that the spawning stock was at times reduced to levels at which recruitment was impaired. Age of maturity fell as the stock declined. Recruitment is positively related to temperature. A temperature-regulated mechanism of interaction between cod larvae and their prey, and driven by variations in inflows of Atlantic waters to the area, determines larvae survival and probably also the abundance and size of the 0-group at age 5-6 months. Predation from birds and marine mammals as well as cannibalism are shown to cause considerable interannual variations in the mortality of juveniles and young cod, and thus variations in the number of fish recruiting to the fisheries at ages 3-5 years. Large short-term variations in the growth of cod caused by varying availability of prey (capelin) have been observed; growth is also positively related to the temperature within the distribution area of the stock.

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### Introduction

The stock of Arcto-Norwegian cod, or Northeast Arctic cod, as it is called in most ICES publications, is potentially the largest stock of true cod (*Gadus morhua* L.) in the world. Spawning areas, migration routes, and feeding areas are shown in Figure 1. Bergstad *et al.* (1987) and recently Sundby and Godø (1993) have reviewed the available information on life history. Jakobsson (1992) has provided an overview of the development of the stock during the past 20 years including a discussion of factors which may explain the large fluctuations in abundance and growth which occurred in the 1980s. Recently, Jakobsen (1993) described and evaluated the history of management and discussed possible strategies for the future.

The cod reach maturity at an age of 6-9 years (Table 1), and the mature fish undertake spawning migrations southwards along the Norwegian coast (Fig. 1). Eggs and larvae are transported northwards in the upper water layers during April-August, and in August-

September the 0-group is distributed in the upper 100 m over large areas in the Barents Sea and off Svalbard. During autumn the 0-group descends towards the deeper layers.

The immatures feed at both the bottom and in the midwater layers and make seasonal east-west and north-south migrations (Maslov, 1944, 1960). The amplitude or range of these migrations increases with age, and at an age of 3-4 years, when capelin become a major food item, the cod follow the spawning migration of capelin to the coasts of northern Norway and Murman. Some older immatures will join the mature stock on its migration towards the spawning fields farther south, the so-called "dummy runs" (Trout, 1957; Woodhead, 1959).

In addition to seasonal displacements of cod concentrations, temperature-related displacements have been reported on both small and large time and space scales (see Nakken and Raknes (1987) for references). In periods of warm climate in the Barents Sea the cod distribution area is extended towards east and north, as

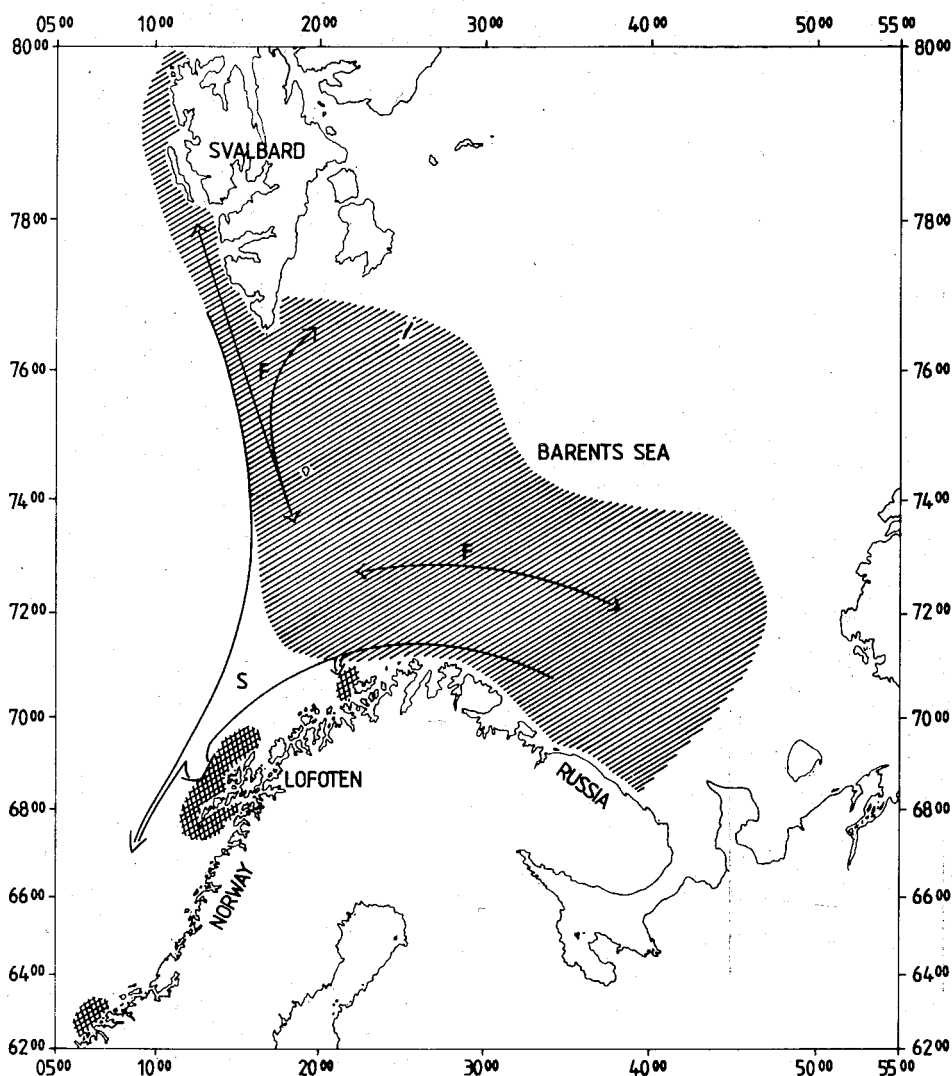


Figure 1. Main feeding area (hatched) and spawning areas (cross hatched) of Northeast Arctic cod with spawning (S) and feeding (F) migration routes (after Mehl, 1991).

compared to periods of cold climate when the fish tend to concentrate in the southwestern parts of the sea (Midttun *et al.*, 1981).

Landings have fluctuated considerably (Figs. 2 and 3). Official landing statistics date back to 1866 for spawning cod (skrei) and to about 1900 for total catches. Information on distribution, abundance, and biological characteristics for the various stages and age groups increased rapidly from 1950 owing to intensified scientific survey work. Systematic international scientific cooperation on stock monitoring started in 1958 when the ICES Arctic Fisheries Working Group was established; since the early 1960s as a stock assessment group at ICES.

Prior to 1920 the bulk of the landings came from two traditional coastal fisheries which have taken place for centuries: the fisheries for spawning cod (the skrei fisheries) during winter/spring on the spawning grounds (Fig. 1) and the fishery for immature cod (the spring cod fishery) that followed the capelin to its spawning fields along the northern coasts (Finnmark and Murmansk) in March to June.

During the 1920s and particularly in the 1930s an offshore fishery, predominantly with trawl, developed in the Barents Sea. The expansion continued after a period of low fishing activity during World War II (1940–1945). Simultaneously the efficiency of the coastal fleet increased. Average annual landings amounted to about

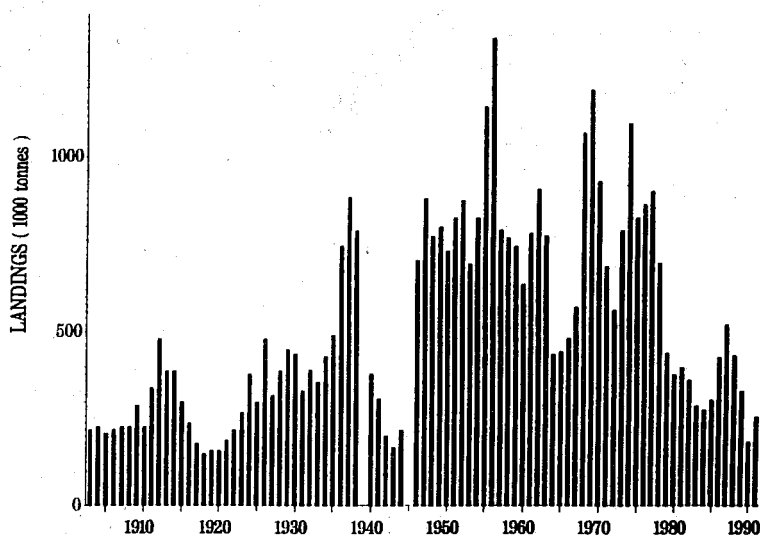


Figure 2. Landings (tonnes, thousands) of Northeast Arctic cod. (Sources: 1903–1929, Bergstad *et al.*, 1987; 1930–1960, Coop. Res. Rep. Cons. int. Explor. Mer, Ser. B. 1964; 1961–1991, ICES Coop. Res. Rep., 1962, 1993.)

Table 1. Data on reproductive biology and life history of Northeast Arctic cod.

		Sources
Age at first maturity (years)	6–12	1
Length at first maturity	65–100	1
Approximate absolute fecundity (millions of eggs per female)	1–19	2
Spawning season	March–April	2
Egg diameter (mm)	1.2–1.7	2
Length at hatching (SL, mm)	4.2–4.3	2
Length at end of yolk sac (days)	4.8–5.0	2
Age at end of yolk sac (days)	9	2
Length at metamorphosis (SL, mm)	10–12	2
Length by August–September (TL, mm)	25–140	2
Age at recruitment to fishery (years)	3–4	3
Minimum allowable catching size (TL, mm)		
Norwegian EZ	47	4
Russian EZ	43	4

Sources: 1 Jørgensen (1990), 2. Bergstad *et al.* (1987), 3. Reports of the Arctic Fisheries Working Group, 4. Reports of the Mixed Norwegian–Russian Fishery Commission.

800 000 t for the period 1946–1978, with peak landings exceeding 1 million tonnes in five of those years. During the 1980s, landings declined. The 1990 landings were among the lowest on record and about 25% of the average for the period 1946–1978. In the most recent years, landings have been increasing rapidly.

The present paper is an attempt to summarize and evaluate the published information on trends and fluctuations in the stock and to discuss their causes.

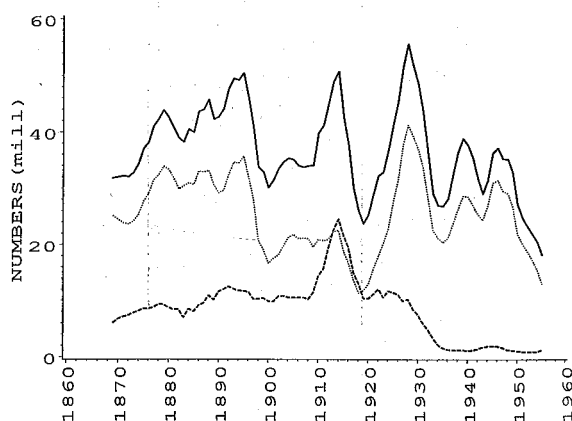


Figure 3. Landings (no. of fish, millions) of spawning cod from the Norwegian skrei fisheries. Running five-year mean values. — Total; ···· Nordland (Lofoten); ---- Southern district (Møre) (after Godø and Sundby (1993), redrawn from Sætersdal and Høyen (1964)).

## Fisheries and their influence on stock size

### Directed fisheries, landings

In the 1950s, Sætersdal and Høyen (1964) were concerned with the declining trend of the landings of spawning cod (Fig. 3). They compared time series of catch per unit of effort (c.p.u.e.) in the skrei- and springcod fisheries and concluded that, "the skrei population has apparently been less abundant as compared with the

population of young cod than it was before the war. This is the type of effect we must expect to find if the reduction of the stock of skrei is not largely a result of natural fluctuations, but has been caused by an increase in the total exploitation of the arctic cod. The number of old and large fish is reduced relatively to that of the younger and smaller fish". They also found that the mean age of the spawning cod decreased over the same period, as the reduction in abundance occurred, and interpreted this as an effect of increased exploitation.

The influence of fisheries on stock development and yield was the main subject of study of the Arctic Fisheries Working Group from the very beginning. Important results of the Group's work are summarized as follows:

1. In 1961, on the basis of c.p.u.e. studies, the Group recommended an increase in mesh size in order to protect small fish from being caught, and thus increase future stock biomass and yield.
2. In the mid-1960s, partly on the basis of cohort analysis in addition to catch-and-effort studies (the first VPA was carried out in 1965 (Gulland), it became evident that the overall fishing mortality rate was far above the rate giving maximum yield per recruit. The 1965 report from the Group (ICES, 1965) included a presentation of measures which could limit the catches (closed areas, increased mesh size, catch quotas, reduced effort).
3. From 1969 and onwards the Group consistently expressed concern at the future size of the spawning stock, considering that at low levels of spawning stock the risk of poor recruitment was increased.

4. In the mid-1980s the Group predicted, on the basis of high abundance indices of 0 to 2-year-old fish, a substantial increase in stock size and catches by the end of the 1980s. The predictions failed completely because of interrelations with other stocks, which the group did not foresee.

The increase in the spawning stock biomass in the early 1970s caused by the abundant 1963 and 1964 year classes probably convinced managers that the concern of scientists at that time was not justified. Fishing mortality rates remained high for many years, and in due course the stock decreased and the spawning stock fluctuated at low levels (Figs. 4 and 5). At the end of the 1980s, when it was evident that the stock was in a very poor condition, catches and fishing mortalities were drastically reduced through regulations implemented by Norway and the USSR.

In the early 1970s, Garrod and Jones (1974) calculated a spawning stock and recruitment relationship for the stock and used it to conclude:

1. If annual fishing mortality rates are sustained at a level of  $F = 0.43$  or above, the stock will tend to extinction. The maximum catch, 800 000 t, is obtained with a spawning stock equal to that observed in the early 1950s and a fishing mortality of  $F = 0.26$ .
2. Because of instability in recruitment at low spawning stock levels, only very large year classes contain enough recruits to offset the level of exploitation which has been characteristic of recent years (1965-1972).

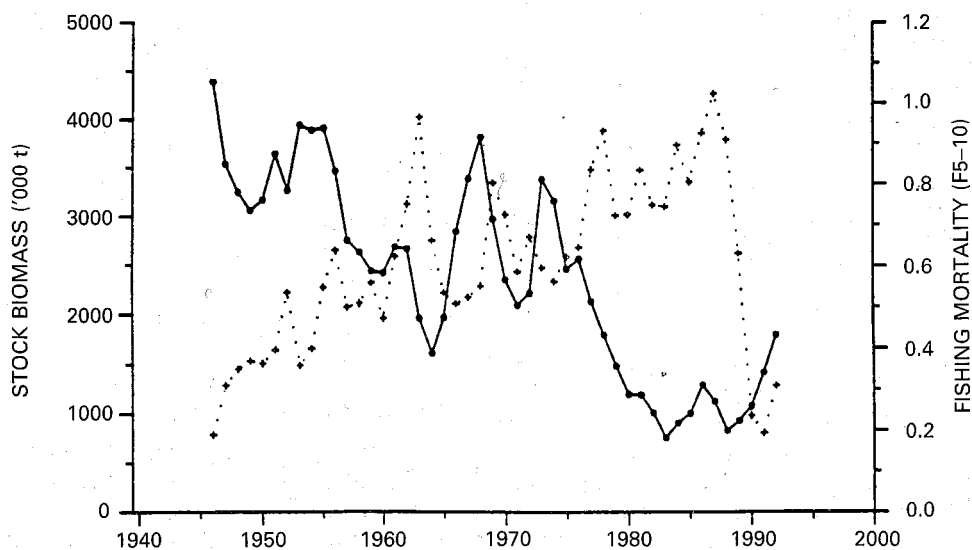


Figure 4. Northeast Arctic cod. Stock biomass (ages 3+) and fishing mortality (after Jakobsen (1993)).

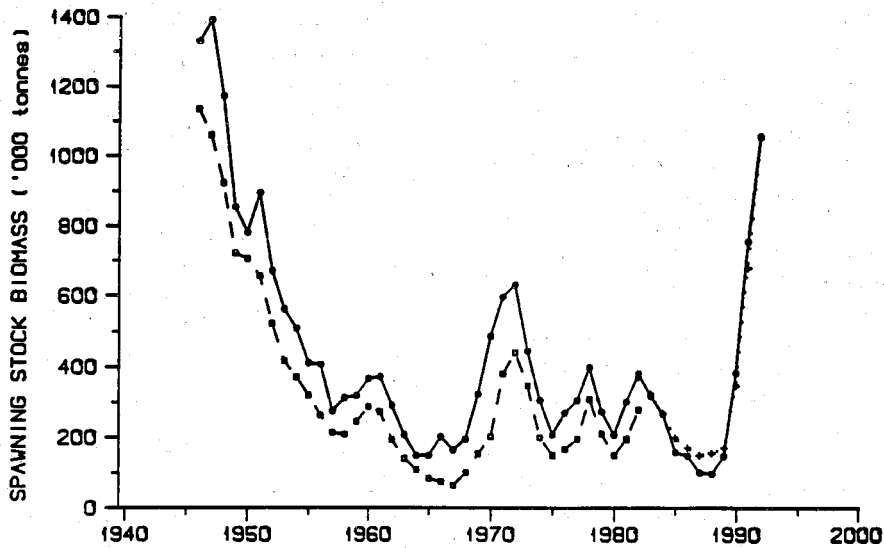


Figure 5. Northeast Arctic cod. Spawning-stock biomass for various maturity ogives (after Jakobsen (1993)).

The fact that the largest year class ever recorded, the 1970 year class, recruited to the fisheries and increased the annual catches for some years (Figs. 2 and 6) seems to have weakened the effect these findings ought to have had on the management of the fishery. In hindsight, it can be seen that the appearance and fate of that year class and the development of the stock in the following years supported Garrod and Jones (1974) conclusions. It

is also interesting to note that recent works on stock and recruitment relationships and the incorporation of such relationships in stock assessment work largely support the figures arrived at by Garrod and Jones (1974). Jakobsen (1992) estimated the level of fishing mortality where the recruitment to the stock in half of the observed years has been more than sufficient to balance the losses due to mortality ( $F_{med}$ ) at  $F = 0.46$ . Serebryakov

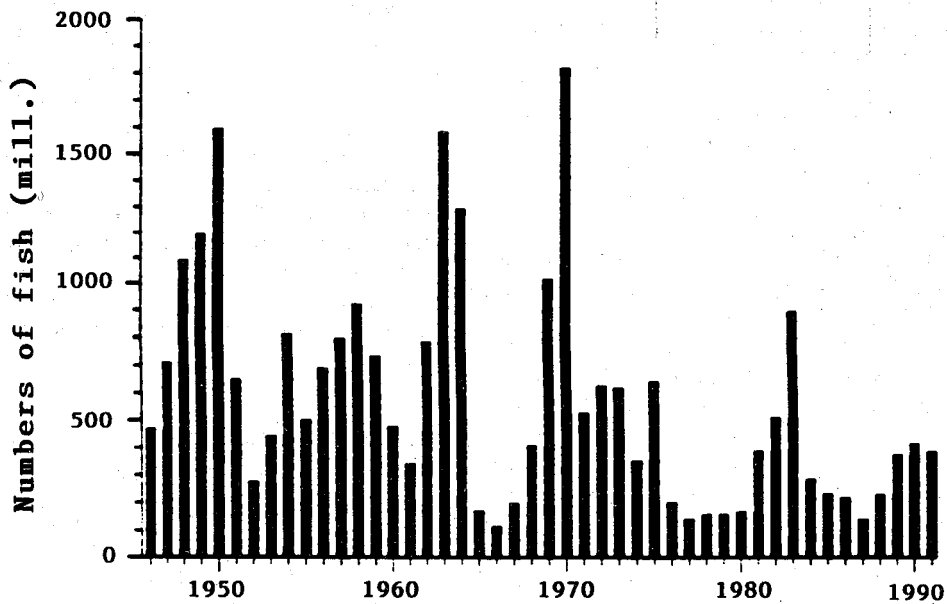


Figure 6. Northeast Arctic cod. Year-class abundance (no. of fish, millions) at age 3 (after Jakobsen (1993)).

(1991) and Jakobsen (1993) indicated that in order to maintain sufficient levels of recruitment a spawning stock of 500 000 t or more is needed, and Jakobsen (1993) concluded that a lower level of exploitation than  $F = 0.46$  should be aimed at in management.

The time series of stock size and fishing mortality are shown in Figure 4. For a period of more than 30 years the annual fishing mortality was well above any calculated safe level ( $F < 0.46$ ). Consequently, the number of fish removed (the total mortality) from the stock was on average higher than the number recruited to the stock, and stock numbers and biomass decreased. Hence, the main trend in Figure 4, the decline from a stock biomass of about four million tonnes in 1955 to less than one million tonnes in the 1980s was caused by the fisheries. The fluctuations around this main trend were caused by variation in recruitment (Fig. 6). Ulltang (1987) demonstrated that accumulated yields for the period 1970–1982 as well as the stock size in the mid-1980s would have been considerably higher than experienced if the fishing mortality rate, particularly on small fish, had been reduced during the 1970s.

#### Discards in directed fisheries

Estimates of discards are relatively few. In its early assessments the Arctic Fisheries Working Group (1961) used discarding rates of 30% by numbers for English trawlers (ICES, 1965). Observations in the mid-1960s indicated cod discards up to 24 and 40% by numbers for Norwegian and British trawlers (Hysten, 1966; Garrod, 1967). In 1973, Hysten and Smedstad (1974) observed discarding rates of 24 and 39% by numbers for bottom trawl and midwater trawl respectively. According to ICES (1990), discarding was known to have taken place in the 1980s, particularly in 1986–1987, owing to the poor condition of young fish in these years.

The proportion of young fish discarded at sea has probably fluctuated with the size composition of the stock, with the market demand for small fish, and with the effective mesh size used. Actual mesh sizes increased from about 80 mm and/or less in the 1950s to 110–120 mm in the 1960s, and since the early 1980s have been 125 and 135 mm in the Russian and Norwegian zones, respectively. In addition to mesh size regulations, an area closure system was established in the 1980s; areas where the amount of undersized fish (Table 1) in the catches exceed 15% by numbers are closed in fishing. It is thus not surprising that discarding rates on average were considerably reduced during the period 1946–1990 for which estimates of stock size exists. A consequence of a reduction in discarding rates over this period is that the abundances at age 3 (Fig. 6), which are calculated from landings, might be underestimated for the early part of the period.

#### Mortality of fish escaping through meshes

Mortality of fish that are injured when escaping through the meshes in trawls will reduce the recruitment of fish to the fisheries and the expected gains of increased mesh sizes. According to Soldal *et al.* (1993) Scottish and Russian investigations in the 1980s indicated that mortality rates of escaped cod were high. On the other hand, in their review of Norwegian experiments on demersal gadoid species Soldal *et al.* (1993) concluded that the mortality of cod was negligible and that of haddock less than 10%. On that basis they expected high survival rates of gadoids that escape through the meshes in demersal trawls.

#### Bycatches in shrimp and capelin fisheries

The fisheries for shrimps with small-meshed bottom trawls in the Barents Sea region developed rapidly, from landings amounting to some few thousand tonnes in the mid-1970s to 126 000 t in 1984. Since the early 1980s these fisheries have been managed using a closed area system in order to limit the catch of young gadoids; areas where the number of specimens of cod + haddock exceed 3 per 10 kg shrimp catch are closed to shrimp fishing. Hysten and Jacobsen (1987) estimated the number of cod caught in the shrimp fisheries in 1983–1986 as ranging from 7 million in 1983 to 49 million in 1985, mainly 1–4 year olds. Assuming a natural mortality rate ( $M = 0.2$ ) for the cod aged 1 and 2 years equal to that of older fish they found that the number of cod aged 1–3 years removed by the shrimp fisheries of the 1982 and 1983 year classes would generate losses in yield from these year classes of 20 000 and 30 000 t, respectively. Since 1 and 2 group fish were predominant in the shrimp catches and these age groups are probably subject to somewhat higher natural mortalities than  $M = 0.2$ , it is likely that actual losses were less.

Catches of various age groups of cod in capelin fisheries (purse seine and trawl) are regularly monitored by the coastguards. Areas are closed for fishing when bycatches of cod exceed specified limits agreed upon by Norway and Russia. The total amount of cod bycatch in the capelin fisheries is unknown. In recent years it is assumed to be low because of strict enforcement of the closed area system.

#### Seismic exploration, pollution, and changes in freshwater run-off

During the past 10–15 years seismic exploration has been undertaken at an increasing rate at locations within the cod distribution area. Engås *et al.* (1993), studying distribution and catch rates at and around an area of seismic shooting (airguns) before, during, and after the

shooting, found that catch rates were reduced (up to 70%) in the vicinity of the shooting area when shooting started, and significant reductions were observed at distances of 15–20 nautical miles from that area during the shooting period. The cod evidently avoided the seismic area and the bigger fish that showed the most pronounced avoidance did not reappear in the area within 5 days of shooting at the end of the observation period.

Studies of the effect on fish eggs and larvae from airgun shooting have indicated that lethal injuries are caused very close to the explosion (1–3 m). Unless future investigations reveal damage at greater distances, and taking into consideration the great extent of horizontal and vertical distribution of cod eggs and larvae, it must be concluded that seismic shooting, as performed nowadays, hardly affects the mortality of cod eggs and larvae.

Monitoring of various pollutants in the environment as well as in fish meat and liver has not revealed concentrations that with the present state of knowledge can have influenced the stock.

In several papers, Skreslet (1981) has focused on freshwater runoff as an important factor for the formation of survival conditions for cod larvae. During the past decades the runoff from many Norwegian rivers has been adjusted through storage of water for hydroelectric power; in particular, the peak in runoff to the sea in spring due to snow melting in the mountains has been levelled off compared with earlier periods. However, Sundby (1979) found no relation between freshwater outflow and survival indices of Northeast Arctic cod for the period 1946–1978.

## Interactions with other species

The cod is prey throughout its entire life from the egg stage and predator from the time the yolk sac is finished. Studies on interactions between cod larvae and other species during the northward drift have been directed mainly towards the diet, abundance, distribution, and behaviour of cod eggs and larvae in relation to food availability, and effects on larval growth and survival. These studies and findings are discussed in the section on Environmental Influences. In the present section, interactions between other species and cod older than 8–10 months, at the end of the 0-group drift, are considered.

The bulk of quantitative information available originates from the joint project between the Institute of Marine Research (IMR), Bergen, and the Polar Research Institute (PINRO), Murmansk, on multispecies assessment studies, and is present in Bogstad and Tjelmeland (1992a).

## Food, feeding and consumption

Figure 7 shows the main food web in the Barents Sea (Ajiad *et al.*, 1992). Cod feeds on fish and crustaceans and its food habits vary with size (age). At onset of feeding, phytoplankton is included in the larval food, but various stages of *Calanus* are the most important food items for cod larvae at all stages. The importance of euphausiids in the diet increases towards the end of the pelagic stage of the 0-group, and euphausiids, amphipods and various size groups of shrimps continue to be important prey for fish up to considerable sizes (30–50

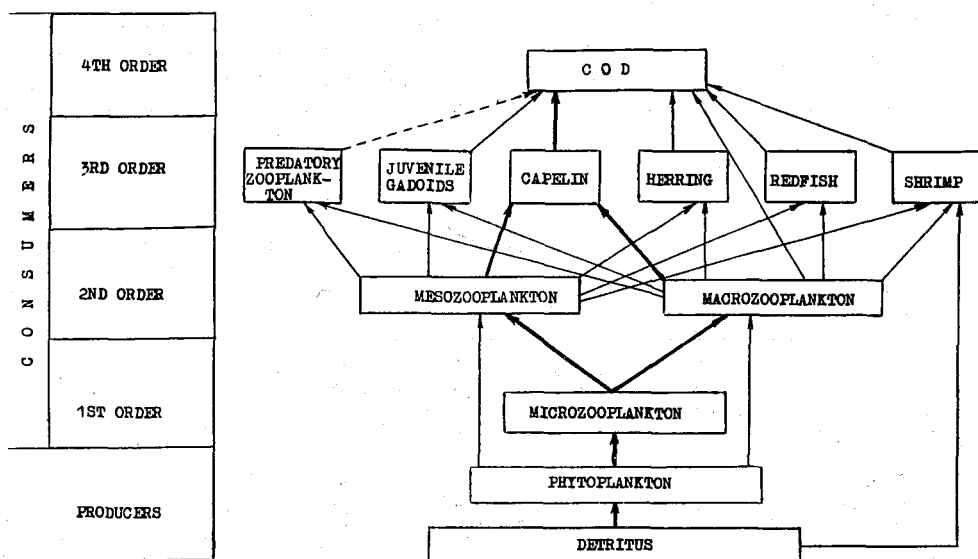


Figure 7. Main food webs in the Barents sea ecosystem (after Ajiad *et al.* (1992)).

cm). Ponomarenko (1984) considered the abundance of euphausiids prior to the first wintering season of the cod as an important factor for cod survival. For cod between 30 and 70–80 cm in length fish (capelin, herring, polar cod, sandeel, young gadoids) on the average make up about 70% of the food. Capelin and juvenile herring are the most important prey species. Cod above 80 cm in length eats almost exclusively fish including young cod up to 30–34 cm in length. Since the stock of Norwegian spring spawning herring collapsed in the 1960s capelin has been the major food resource for cod.

Table 2 gives the stock's consumption of the main prey species during the period 1984–1989 (Bogstad and Mehl, 1992). Capelin and amphipods were predominant and a shift from capelin to amphipods appeared along with the collapse in the capelin stock in 1986–1987 (Mehl, 1989; Hamre, 1988, 1991; Jakobsson, 1992). Herring and young gadoids amounted to only a few percent of the total biomass consumed, but the mortality of these groups due to cod predation increased in 1985–1986 and led to a pronounced reduction in the 1984–1986 year classes of cod, as well as in the 1984 and 1985 year classes of herring (Mehl, 1989; Hamre, 1991; Jakobsson, 1992). As early as in the mid-1970s Ponomarenko and Ponomarenko (1975) anticipated the circumstances that had become apparent by the mid-1980s from Table 2. On the basis of estimates of the cod and haddock stock's food demand and the production capacity of the capelin stock they concluded that if the two gadoid stocks were to recover, the capelin stock and fishery would decline and the cod would have to change to other food. In the event, the capelin stock was heavily reduced from 1984 to 1986 and fishing was banned from 1987 to 1989; the cod changed to food resources other than capelin, including increased cannibalism, in 1984–1986.

The unexpected feature of Table 2, at least to the present author, was the predominance of amphipods in the food of cod during the years when capelin was

lacking (particularly 1987 and 1988). Even large cod 50–70 cm in length fed heavily on amphipods (*Parathemisto*) and although no time series of the latter's abundance exist the general impression from acoustic recordings and midwater trawl hauls is that amphipod abundance reached a peak in 1986–1988. Was the abundance of amphipods really higher in these years? If so, then was it because of less predation from capelin, as suggested by Skjoldal *et al.* (1992), or did other factors contribute to the increase?

During the last decade much effort has been put into modelling the interrelations between cod and other species in the Barents Sea, with the ultimate aim to establish interrelationships which can be used in stock assessment and predictions of stock development and catch quotas. At present a cod/capelin interrelationship (Bogstad and Tjelmeland, 1992b) that takes into account the cod stock's need for capelin as food is used when capelin quotas are estimated and advice is given by ICES. Ongoing research is focused on other main food items for cod (herring, shrimp, and redfish) as well as on cannibalism (see Bogstad and Tjelmeland (1992a) for references).

#### Cannibalism

Cannibalism in cod increases when other prey species are scarce compared with small cod. It was high in 1986–1988, when stocks of both capelin and juvenile herring were low (Orlova, 1992). Tables 3 and 4 give estimates of the mortality rate of young cod due to cannibalism (Ajiad *et al.*, 1992; Korzhev and Tretyak, 1992). Cannibalism of the 0-group takes place during the last quarter of the year, when the fry have descended to deeper layers and become available to the large fish. Sundby *et al.* (1989) calculated mortality rates from estimates of abundance of 0-group and three-year-olds for the year classes of 1979–1983. Depending on assumed catching

Table 2. The Northeast Arctic cod stock's consumption of main prey species in 1984–1989 (per cent of biomass). Total in million tonnes.

	1984	1985	1986	1987	1988	1989
Amphipods	1	3	25	35	44	27
Shrimp	19	5	4	8	5	5
Capelin	40	56	33	11	22	31
Herring	3	5	4	1	0	0
Cod	2	1	4	2	1	0
Haddock	2	1	3	0	0	2
Redfish	15	6	8	14	8	9
Others	17	23	19	29	20	26
Total	2.1	3.5	2.9	2.1	2.4	2.5

Source: Bogstad and Mehl (1992).



Table 3. Natural mortality rates of Northeast Arctic cod at age 0–3 years due to cannibalism in 1984–1989 (from Ajiad *et al.* (1992)).

Age	1984	1985	1986	1987	1988	1989
0	0.28	0.48	0.51	1.31	0.30	0.00
1	0.05	0.11	0.25	0.38	0.35	0.00
2	0.04	0.01	0.04	0.07	0.10	0.00
3	0.02	0.01	0.01	0.03	0.04	0.00

Table 4. Consumption of cod by cod in the Barents Sea (Ajiad *et al.*, 1992) and by harp seal during the seal invasions to the Norwegian coast in 1987–1988 (Ugland *et al.*, 1993) (millions of individuals).

Age	Cannibalism				Harp seal
	0	1	2	3	
1982	–	–	13	4	16 (at age 5+6)
1983	–	43	12	6	22 (at age 4+5)
1984	188	56	17	10	66 (at age 3+4)
1985	339	111	23	13	103 (at age 2+3)
1986	344	147	27	–	33 (at age 1+2)
1987	255	186	–	–	

efficiencies of 0-group ( $q = 0.1$  and  $q = 0.25$ ) they arrived at total instantaneous mortality rates in the range 0.5–1.0 and 0.1–0.6. The estimates of the mortality rates in Table 3 thus seem to be comparable with those which are arrived at for other year classes by using a different method.

#### *Influence of birds and marine mammals*

Birds and marine mammals can influence the stock of cod in two ways: directly by predation, or indirectly, through competition, by utilizing the same food stocks as cod (pelagic fishes and crustaceans). Their diet is probably closely related to the prey that is available at the lowest cost/benefit in terms of foraging time and effort; the predation pressure they exert on the various fish stocks (including cod) might therefore be dependent more on the relative abundance and availability of the various prey species than on their own stock sizes. A few of the species of birds in the area are highly specialized feeders (guillemot and puffin) but most species eat what is available.

The total food consumed by birds and marine mammals in the Barents Sea area is estimated at 4–8 million tonnes, depending on the biomass and energy content of the various prey species (Gabrielsen and Ryg, 1992). There exist no long-term time series of diets of birds and marine mammals which enable us to quantify their influence on stock size fluctuations of cod. Gabrielsen and Ryg (1992) estimated that marine mammals (seals and whales) in the region consumed 7–10 times more

food in terms of energy equivalents than did birds. From an aerial survey in 1991, Borkin *et al.* (1992) estimated that the total population of birds in the Barents Sea is 14 million, 59% of which are fulmars and 37% kittiwakes. The total consumption of fish by fulmars and kittiwakes was estimated at ~90 000 t annually, mainly capelin.

Barrett *et al.* (1990) calculated that predation on gadoids by shags and cormorants may affect the year-class strength of saithe and cod. Their estimates would account for a substantial part of the mortality of the prerecruits of saithe and cod in the period 1985–1988, and at levels comparable to the levels of cannibalism estimated by Mehl (1989). Barrett *et al.* (1990) questioned their own estimates, pointing at the inaccuracies in the data set used; nevertheless, their results indicated that predation from birds might have a significant influence on the mortality of small-sized cod (aged 0–2 years) in some years.

The most abundant seal species in the Barents Sea is the harp seal. Bjørge *et al.* (1981) and Haug *et al.* (1991) studied the diet of harp seal caught in fishing nets along the Norwegian coast during the seal invasions (1978–1988). Their findings supported previous conclusions that harp seal are opportunistic feeders, eating what is available. In 1978–1981 when capelin was abundant, capelin and capelin roe constituted the bulk of the diet of the examined animals, while in 1986–1988, when the stock of capelin was at a minimum, various fish species including cod were predominant in the stomachs. Ugland *et al.* (1993) estimated the harp seal's consumption of various fish species as well as several year classes

of cod during the seal invasions in 1987–1988 to be at levels comparable to the levels of cannibalism (Table 4).

Observations made in recent years of the diet of minke whales in the Barents Sea region (Haug *et al.*, 1993) have revealed large differences in stomach contents between years and areas. In the summer of 1992 herring and other fish species, including cod, were observed to be the most important constituent of the diet off the coasts of Murmansk and Finnmark, while capelin was the important food item in the Bear Island–Svalbard area. Although 0-group cod dominated the biomass of the pelagic organisms in large parts of the area investigated, they were not found in whale stomachs.

## Environmental influences

### Periodicity in time series of temperature and yield

Loeng *et al.* (1992) used Fourier analysis to find principal periodicities (cycles) in time series of temperature at several locations in the Northeast Atlantic, including the mean temperature (0–200 m) in the Kola section (Fig. 8). In several papers, Ottestad (1986) used a similar approach searching for cycles in the time series of annual yield from the Lofoten skrei fishery. Table 5 gives the most dominant cycles found in the two studies.

Ottestad (1986) also found cycle lengths of 23, 42.2, and 57 years. The technique he used allowed for cycle lengths between 8.5 and 72 years.

There is good agreement between dominant cycle lengths in the two studies, raising the possibility that variations in yield (and thus variations in abundance) of spawning cod are related to variations in ocean climate. The mechanism of any possible causal relationship is not, however, explained by the above evidence.

### The significance of temperature

The significance of temperature for the development of the stock of Northeast Arctic cod has been investigated by numerous authors (see Loeng (1989) for references). Sætersdal and Loeng (1987) assessed the relative strength of the year classes in the period 1902–1987 and compared the occurrence of year classes of high, medium, and low abundance with temperature data from the Barents Sea during the same period. They found that year classes of high abundance were either associated directly with high temperatures or occurred at the onset of a shift to a warmer regime in the area. Table 6 summarizes their findings, demonstrating clearly that medium and high year-class abundance have occurred more often in warm years than in cold years.

The average numbers of three-year-old cod in year classes of high, medium, and low abundance in the period 1943–1985 for which absolute estimates are available (Fig. 6) were approximately 400, 800, and 1400 million respectively. Applying these figures to the frequency distributions in Table 6 results in average year-class abundances in cold and warm years of 480 and 710 million individuals, respectively. The average year-class strength for 1977–1981, which is the coldest period experienced during the past 50 years, was 200 million (Fig. 6) and about one-third of an average year class (600 million) for the period 1943–1985.

Sætersdal and Loeng's (1987) observations are in agreement with results from Russian workers (see Mukhina *et al.*, 1987), who found increased larval transport (current velocity) into the Barents Sea in years when abundant year classes were formed. Variations in temperatures in the area are mainly determined by variations in inflow. Why does the production of recruits in the stock vary with temperature conditions and inflows of Atlantic waters?

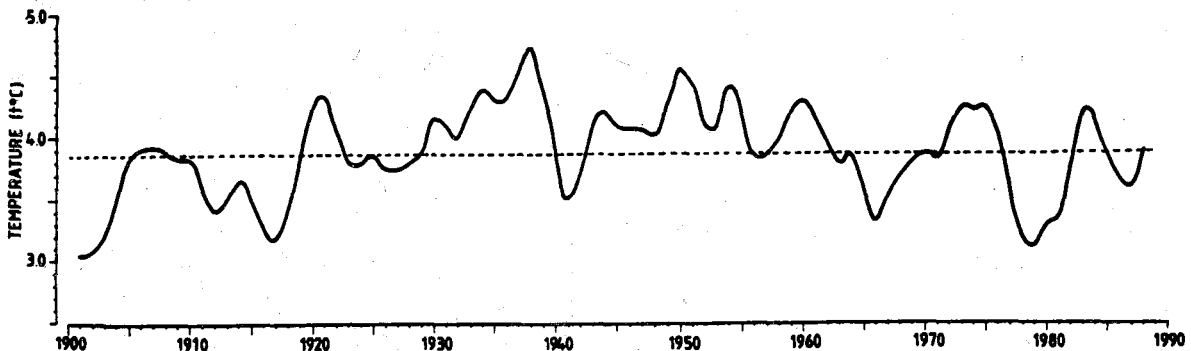


Figure 8. Three-year moving average of yearly temperature in the Kola section during the period 1900–1990 based on data from Bochkov (1982) and from PINRO, Murmansk (pers. comm.). The stippled line indicates the mean value for the period 1921–1980 (Loeng, 1991).

Table 5. Dominant periods (years) as estimated by Fourier analysis.

Temperature (Loeng <i>et al.</i> , 1992)	8.8	11.7	-13.6	17.5
Annual yield (Ottestad, 1986)	8.5	10.7	13.7	17.5

### Eggs, larvae, and early juveniles

Ellertsen *et al.* (1989) reviewed the available information on spawning and distribution of eggs, distribution and feeding of early larvae as well as prey abundances. Their main findings were:

1. Year classes of high or medium abundance occur in years with medium or high temperature at the spawning grounds in March–April.
2. At the main spawning ground (Lofoten), spawning takes place during the same period each year. The date of 50% spawning varied by less than 5 days around 1 April during the 10 years of observation.
3. Egg mortality between spawning and hatching was 90% in the two years of observation (1983–1984). The causes of mortality are not well known, but predation by herring has been observed.
4. Eggs hatched after 20–35 days, depending on temperature. The peak of hatching varied by approximately two weeks between two years of extreme temperatures (1981 and 1983).
5. The cod larvae feed mainly on nauplii of *Calanus finmarchicus*.
6. Onset of *Calanus* spawning as well as maximum occurrence of *Calanus* nauplii (suitable food for larvae) varied considerably from year to year depending on temperature. In the warm year of 1960 (4.4°C), maximum abundance was 50 days earlier than in the cold year of 1981 (1.9°C), 1 April and 20 May respectively.

They concluded their discussion as follows: "In years with normal environmental temperatures, a high proportion of cod larvae will experience food concentrations high enough for growth and survival in most of the distribution area of first feeding larvae, due to the match between larvae and their prey. In years with extreme temperatures both high and low, the mismatch

Table 6. Occurrence percent of year classes of various abundances in cold and warm years (From Loeng, 1989).

	Year-class abundance		
	Low	Medium	High
Cold years	35	7	11
Warm years	31	14	12

in time may contribute significantly to the weak year classes produced in these years."

Observations of reared cod larvae in closed and controlled systems have shown that shortage of food and demand for space generate extensive cannibalism (Folkvord *et al.*, 1993); the bigger ones eat the smaller ones. Lack of suitable food may take place at later stages than the first feeding period. Many workers, including Folkvord *et al.* (1993), have pointed out that the time after metamorphosis might be a critical period because of the rapidly increasing demand for food at this stage. Hence the abundance of older copepodite stages and adult *Calanus*, which are the main food items for juvenile cod at that stage, may limit growth and survival.

### Post-larvae and 0-group

Loeng and Bjørke (1992) analysed mean lengths of postlarvae (July) and 0-group fish (August/September) of several species in the area and found a fairly close covariation in mean lengths of cod, haddock, and herring during the period 1965–1992. The mean length of cod and haddock in August–September seemed to depend mainly on the growth during their first three months of life (April–June), while the mean length of herring in August–September was more related to the growth during July–August. Their study indicated a weak length/temperature relationship for cod in accordance with previous findings (Loeng and Gjøsaeter, 1990).

The time series (1965–1992) of abundance indices and mean lengths of 0-group cod, together with mean temperatures in the central Barents Sea, are presented in Figure 9. All data are from the 0-group surveys, 20 August–10 September each year (ICES, 1992). The curves for abundance and length appear similar; in years of low abundance of 0-group the growth has also been reduced. Low abundance and low growth also seem to occur more often in years with low temperatures.

Sundby *et al.*, 1989 found density-dependence of the mortality rate of cod between the postlarvae (early juveniles) and 0-group stages. This may indicate that lack of suitable food (starvation) rather than predation is the primary cause of the reduction in numbers at this stage too. Reduced growth would be an indicator of starvation but can hardly be measured in practice since predators will preferentially remove the weak (small) specimens. If for instance cannibalism within a cohort occurs at this stage in nature, as it does in controlled systems, reduced growth can only be expected when cod densities and abundances become low.

### Age group 1 and older fish

Figure 10 shows the mean ambient bottom temperature for various age groups of cod in February. The temperatures were calculated from survey data using fish density

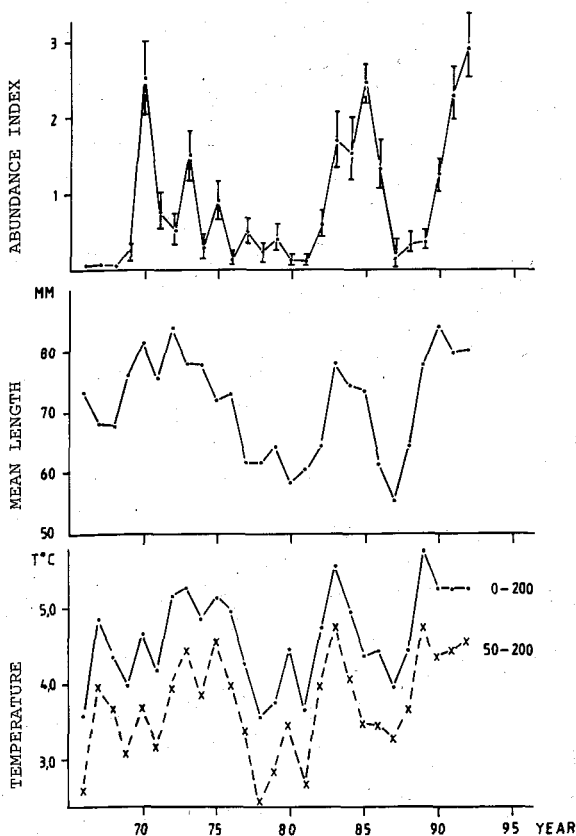


Figure 9. Indices of abundance (upper) and mean lengths (middle) of 0-group cod, and mean temperature in the Kola section in August–September 1965–1992. (Source: ICES, 1965–1992.)

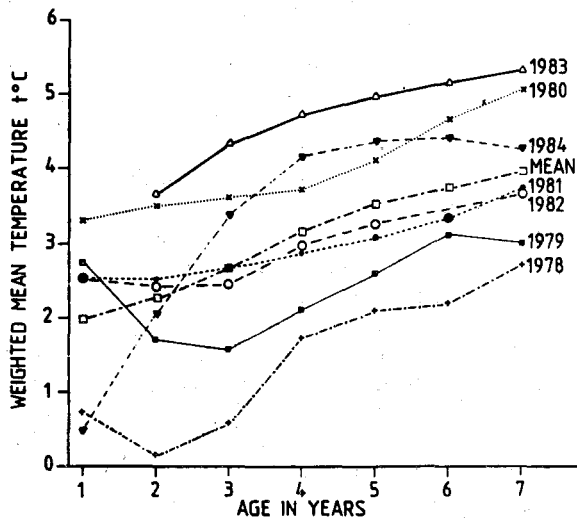


Figure 10. Weighted mean values of bottom temperatures for the various age groups of cod in February for the years 1978–1984. MEAN is the arithmetic mean for the whole period (Nakken and Raknes, 1987).

as weight in the calculation. Young fish were distributed in colder waters farther east than older age groups. For all age groups the mean temperature in February varied within a range of about 3°C over the years of observation. Ranges in temperature at fixed sections within the distribution area were also large, 1.5–2.5°C during the same period (Nakken and Raknes, 1987, Fig. 2; Skjoldal *et al.*, 1992, Fig. 3), but significantly less than the variations in the temperature of the environment of the fish. Variations in environmental parameters at fixed stations and/or sections do not necessarily represent the variations in the environment of the stock or certain age groups (see also Nilssen and Hopkins (1992)).

Figure 10 shows a systematic increase in ambient temperature by age of ~0.35°C per year for fish aged three years and older, indicating that these age groups maintain their distributions within the temperature field relative to each other and independent of the absolute temperature. Shevelev *et al.* (1987) suggested that cod year classes migrated westward at an average of 80 nautical miles per year. Independent of fish age, westward displacements of cod also coincide with decreasing temperatures in the area (Eggvin, 1938; Konstantinov, 1967, 1969; Nakken and Raknes, 1984). These temperature-related displacements have brought about great changes from year to year in the availability of fish at the various fishing grounds in the spring cod fisheries. Similar west/east and south/north displacements have also been observed for several other species (Loeng, 1989; Nilssen and Hopkins, 1992) some of which are important food items for the cod (capelin, shrimps). Hence, temperature-related migrations of cod might partly be the result of the fish adjusting its feeding area to suitable prey distributions as well as a direct response to temperature.

### Other factors affecting year-class strength

As pointed out above the biomass of the spawning stock, i.e. the number of eggs spawned, has reached levels insufficient to maintain full recruitment. Recently, increased attention has been given to the quality and size of eggs (Kjesbu *et al.*, 1992). Large old fish, having already spawned several times, spawn eggs of varying size and varying specific gravity (buoyancy), while first-time spawners (small fish) and fish in poor condition spawn small eggs with quite stable specific gravity. Hence the eggs from established spawners are more widely vertically distributed and thus subjected to greater horizontal spreading, factors that are considered favourable for larval survival. In addition, bigger eggs give the larvae bigger yolks and widen the window for adaptation to first feeding.

Another factor of importance for larvae survival is turbulence (Rothschild and Osborn, 1988; Sundby and Fossum, 1990). Turbulence favours larval feeding by increasing the contact rate between larvae and their food particles.

## Changes in growth and maturation

Long-term changes in length-at-age and age at sexual maturity of Northeast Arctic cod are described by Jørgensen (1990 and 1992). Figure 11 shows the time series of mean length-at-age of first-time spawners. There is a trend towards increased length-at-age over the period 1932–1987, which is more pronounced for the older age groups. At the end of the 1930s and the beginning of the 1940s a marked reduction in mean length-at-age occurred for all age groups. It coincided with the fall in temperature in 1939–1941 (Fig. 8) and with a complete disappearance of spawning capelin at the coast of Finnmark in the years 1938–1942 (Olsen, 1968).

From 1945 to 1980 an overall increase in length-at-age of 5–10 cm is seen (Fig. 11), most markedly for the older fish (9 and 10 years). Jørgensen (1990) interpreted this as a possible density-dependent effect, but in his more comprehensive later study on growth (1992) he found neither a significant relationship between length increment and stock size nor an overall trend in length-at-age throughout the period of investigation (1953–1989). Length-at-age showed marked short-term variations (1–5 years) with amplitudes of 10–15 cm. Growth-in-length was positively related to increasing ratio of capelin to

cod stock abundance and also to increasing water temperature.

The pronounced increase in length-at-age of seven and eight-year-olds from 1982/1983 to 1987 (Fig. 10) (year classes 1975–1980), was also observed for the immatures of these year classes (Nakken and Raknes, 1987). It was explained as an effect of increasing environmental temperatures in the period (Fig. 10), although it occurred during a period (1978–1983) when both total stock size (Fig. 4) and the number of immatures in the stock declined rapidly.

The large changes in growth of cod observed during the years 1985–1989 when the stock of capelin collapsed are shown in Figure 12. Growth was particularly low in 1986 and 1987; the mean weight of five-year-olds by 1988 being two to three times less than that of five-year-olds in 1985 and 1991. At the end of the 1980s, when the stock of capelin recovered and capelin again became important as food (Table 2), the mean weights increased to the levels observed in 1985 and preceding years. The consequences of the dramatic reduction in cod growth were also dramatic (Mehl and Sunnanå, 1991); the 1986 predictions from ICES of stock biomass development in 1987 and 1988 were too high and so also were the recommended catch quotas for 1987 and 1988. Hence fishing mortality rates which were expected to decrease in these years stayed at a record high level (Fig. 4).

Jørgensen (1990) observed considerable reductions in age-at-maturity for the postwar period (Fig. 13); the median age-at-maturity decreased from about 10 years in 1945–1950 to 7–8 years in the early 1980s. Over these years the range of age covered by the maturity ogive also decreased. Jørgensen discussed his findings in relation to

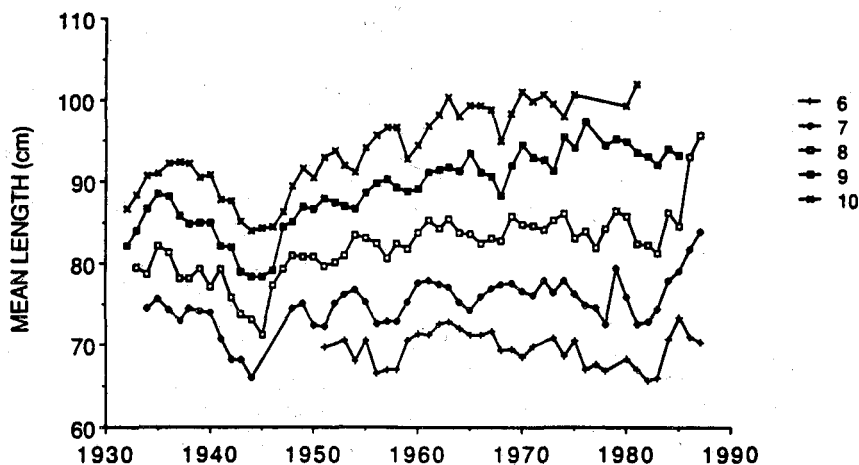


Figure 11. Mean length-at-age of first-time spawners of ages 6 through 10 caught by long-line at Lofoten. All means are based on a minimum of 10 observations (Jørgensen, 1990).

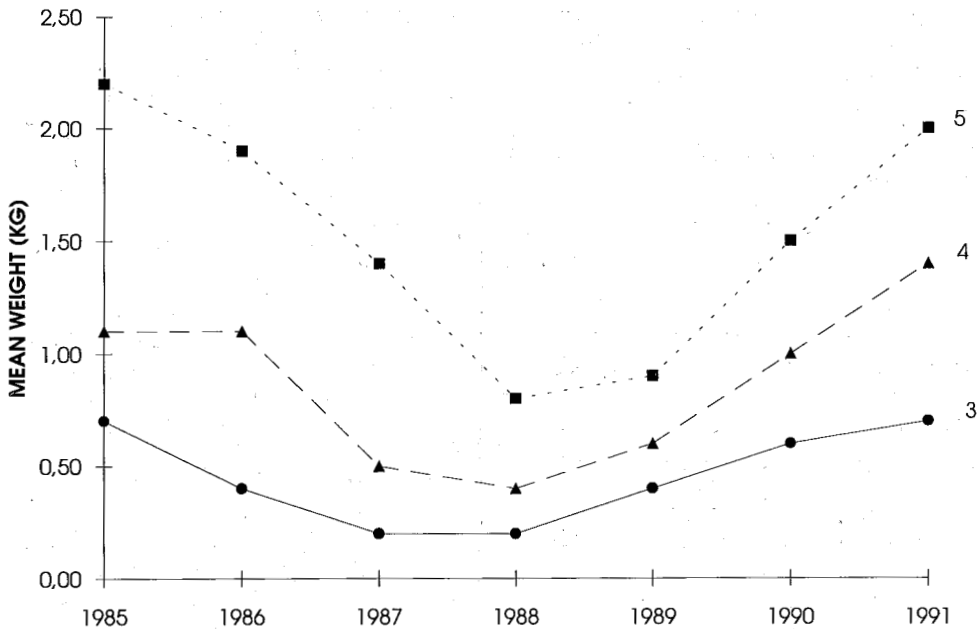


Figure 12. Mean weights (kg) of cod, age groups 3-5 years, as observed during surveys in February each year (data from Korsbrekke *et al.*, 1993).

genetic changes due to selective fishing, as had been suggested by other authors, and concluded: "Since the changes predicted by life history theory as a result of intensified exploitation and reduced abundance are exactly the same as those expected from phenotypic compensatory mechanisms, observed changes in length and/or age at maturity are *per se* no proof of genetic changes." He further concluded that the response of the

stock, i.e. the general trend to mature at younger ages (Fig. 13), was probably an adaptation to the increased mortality.

### Concluding remarks

Owing to environmental factors and interactions Northeast Arctic cod show a 20-fold range of year-class abundance at age 3 (100 million to 1900 million fish), with an average of 600-700 millions. The fish is recruited to the directed fisheries at age 3-5 years and appears as by-catch in small-meshed fisheries as young as 0-group. Measures taken to protect small-sized fish (increased mesh size, increased minimum catching size, and closed areas) have largely reduced the influence of fisheries on year-class abundance at age <4 years during past decades. The development of year-class abundance from age 4-5 onwards depends heavily on the fishing pressure to which it is exposed, and the declining trend of stock biomass from 1955 to 1988 was caused mainly by fishing; the number of fish removed from the stock by fisheries and by natural mortality exceeded by far the number recruited to the fishable stock in these years. The stock responded to the decline in abundance by shorter generation time (maturation at earlier age). Fisheries may also have had an adverse effect on recruitment by reducing the spawning stock and along with that the abundance of established spawners (large fish) to

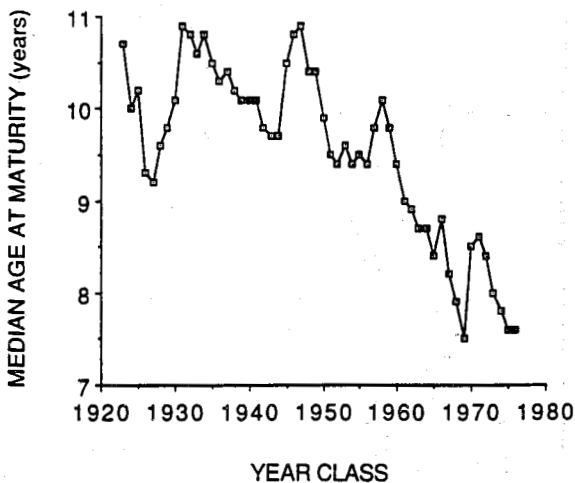


Figure 13. Median age at maturity for the year classes 1923 to 1976 (Jørgensen, 1990).

low levels. Other man-made activities, such as pollution, seismic exploration, and modification of freshwater runoff, have had no detectable effect on stock abundance.

Year classes of high and medium abundance occur more frequently in warm climatic periods than in cold periods, and the recruitment to the stock is positively related to the inflow of Atlantic water to the area. A temperature-related degree of synchrony between early larval abundance and *Calanus* spawning and development seems to affect larval survival and thus year-class abundance at later stages. The observation that 0-group size and abundance in August–September are positively related and also related to temperature indicates that inflows of Atlantic water prior to and during the larval drift offer favourable conditions for growth and survival of cod juveniles during their first 5–6 months of life. Variation in the abundance at age 3 is also strongly dependent on interactions between species and size groups beyond the larval and 0-group stages. Predation from birds and marine mammals as well as cannibalism have caused year-to-year variations in juvenile cod mortality depending on the abundance of other prey items (capelin, herring). Unless such variations are foreseen and quantified by utilizing knowledge of trends in the most important prey and predator stocks in the area, predictions of year-class abundance at age 3 from estimates of 0-group abundance are of limited value.

Growth studies have revealed large short-term variations in length and weight-at-age for all age groups caused by varying availability (abundance and distribution) of prey. Neither an overall trend in length-at-age nor a significant relationship between length increment and stock size were found for the period 1953–1989, when stock size declined. The growth of cod increases with increasing temperature. However, a growth-temperature relation based on field data includes the effect of interrelations and depends on the availability of prey under various temperature regimes.

The importance of capelin as a major food resource has been clearly demonstrated and the significance of herring as another main prey item is pointed at by many authors (Øiestad, 1994).

The reliability of the conclusions arrived at on the causes which have influenced the development of the stock have been discussed in many of the papers referred to. Besides the need for improvement in observations, sampling, and analytical tools (models), there is a need to improve the fishery statistics. In earlier periods, as well as in recent years, the official statistics do not fully reflect the actual landings. According to a press release from the Norwegian Ministry of Fisheries in April 1993 the total international landings of Northeast Arctic cod in 1992 were 90 000–120 000 t higher than the official ones. Since such unreported landings as well as discards

were not corrected for when annual stock estimates were established, the time series of stock size, fishing mortalities, and year-class abundance at age 3 do not fully reflect the actual development over the 50 years' period considered. These discrepancies do not, however, affect the main conclusion that the stock during a period of 40 years suffered from overfishing and declined to very low levels. The present increase in stock size and yield is a combined effect of moderate fishing pressure since 1989 and improved recruitment and growth in recent years.

## References

- Ajiad, A. M., Mehl, S., Korsbrette, K., Dolgov, A. V., Korzhev, V. A., Tretyak, V. L., and Yaragina, N. A. 1992. Trophic relationships and feeding-dependent growth in the Northeast Arctic cod. Proc. Fifth PINRO-IMR Symposium, Murmansk, August 1991. Institute of Marine Research, Bergen.
- Barrett, R. T., Røv, N., Loen, J., and Montevecchi, W. A. 1990. Diets of shags (*Phalacrocorax aristotelis*) and cormorants (*P. carbo*) in Norway and possible implications for gadoid stock recruitment. Mar. Ecol. Prog. Ser., 66: 205–218.
- Bergstad, O. A., Jørgensen, T., and Dragesund, O. 1987. Life history and ecology of the gadoid resources of the Barents Sea. Fish. Res., 5: 119–161.
- Bjørge, A., Christensen, I., and Øritsland, T. 1981. Current problems and research related to interactions between marine mammals and fisheries in Norwegian coastal and adjacent waters. ICES CM 1981/N: 18.
- Bogstad, B., and Mehl, S. 1992. The Northeast Arctic cod stock's consumption of various prey species 1984–1989. Proc. Fifth PINRO-IMR Symposium, Murmansk, August 1991. Institute of Marine Research, Bergen.
- Bogstad, B., and Tjelmeland, S. (Eds.). 1992a. Interrelations between fish populations in the Barents Sea. Proceedings of the Fifth PINRO-IMR Symposium, Murmansk, 12–16 August 1991. Institute of Marine Research, Bergen.
- Bogstad, B., and Tjelmeland, S. 1992b. A method for estimation of predation mortalities on capelin using a cod-capelin model for the Barents Sea. Proc. Fifth PINRO-IMR Symposium, Murmansk, August 1991. Institute of Marine Research, Bergen.
- Borkin, I. V., Chernook, V. I., Ponomarev, Y. I., and Bogomolov, V. Y. 1992. Results of aerial surveys of seabirds in the Barents Sea. Proc. Fifth PINRO-IMR Symposium, Murmansk, August 1991. Institute of Marine Research, Bergen.
- Eggvin, J. 1938. Trekk fra Nord-Norges oseanografi sett i sammenheng med torskefisket. FiskDir. Skr. Ser. Havunders., 5: 33–46.
- Ellertsen, B., Fossum, P., Solemdal, P., and Sundby, S. 1989. Relation between temperature and survival of eggs and first-feeding larvae of northeast Arctic cod (*Gadus morhua* L.). Rapp. P.-v. Réun. Cons. int. Explor. Mer, 191: 209–219.
- Engås, A., Loekkeborg, S., Ona, E., and Soldal, A. V. 1993. Effects of seismic shooting on catch and catch-availability of cod and haddock. Fisken Havet No. 9, 1993: 1–129.
- Folkvord, A., Blom, G., Dragesund, O., Johannessen, A., Nakken, O., and Nævdal, G. 1993. A conceptual framework for enhancing and stabilizing recruitment of marine stocks. Symposium on "Seafish Ranching of Cod and other Marine Species", Arendal, 15–18 June 1993.

- Gabrielsen, G. W., and Ryg, M. 1992. Sjøfugl og sjøpattedyr. In *Økosystem Barentshavet*, pp. 203–229. Ed. by E. Sakshaug. Mesna Trykk, Lillehammer.
- Garrod, D. J. 1967. Population dynamics of the Arcto-Norwegian cod. *J. Fish. Res. Bd. Can.*, 24(1): 145–190.
- Garrod, D. J., and Jones, B. W. 1974. Stock and recruitment relationship in the northeast cod stock and the implications for management of the stock. *J. Cons. int. Explor. Mer*, 36: 35–41.
- Gjøsæter, H., and Loeng, H. 1987. Growth of the Barents Sea capelin, *Mallotus villosus*, in relation to climate. *Environ. Biol. Fish.*, 20(4): 293–300.
- Gulland, J. A. 1965. Estimation of mortality rates. Annex to Arctic Fisheries Working Group Report of Meeting in Hamburg, 18–23 Jan. 1965. ICES CM 1965 (3).
- 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 CM 1988/H: 42.
- Hamre, J. 1991. Interrelation between environmental changes and fluctuating fish populations in the Barents Sea. In: *Proceedings from an international symposium on long-term variability of pelagic fish populations and their environment*, Sendai, Japan, 1989, pp. 259–270. Ed. by T. Kawasaki, S. Tanaka, Y. Toba, and A. Taniguchi.
- Haug, T., Gjøsæter, H., Linstrom, U., and Nilssen, T. 1993. Studies of minke whale (*Balaenoptera Acutorostrata*) ecology in the northeast Atlantic: preliminary results from studies of diet and food availability during summer 1992. *IWC SC/45/NA 3*: 1–31.
- Haug, T., Krøyer, A. B., Nilssen, K. T., Ugland, K. I. and Aspholm, P. E. 1991. Harp seal (*Phoca groenlandica*) invasions in Norwegian coastal waters: composition and feeding habits. *ICES J. mar. Sci.*, 48: 363–371.
- Hysten, A. 1966. On the estimation of cod and haddock discarded by trawlers using different chafers. Appendix to Liaison Committee Report to the North-East Atlantic Fisheries Commission, 1966. *Coop. Res. Rep., Cons. int. Explor. Mer, Ser. B*.
- Hysten, A., and Jacobsen, J. A. 1987. Estimation of cod taken as bycatch in the Norwegian fishery for shrimp north of 69°N. *ICES CM 1987/G: 34*.
- Hysten, A., and Smestad, O. 1974. Observations from the Barents Sea in spring 1973 on the discarding of cod and haddock caught in bottom and midwater trawls fitted with double cod ends. *ICES CM 1974/F: 45*.
- ICES. 1965. Liaison Committee Report to the North-East Atlantic Fisheries Commission. Annex 1: Report of the Arctic Fisheries Working Group. *Coop. Res. Rep. Cons. int. Explor. Mer, Ser. B*.
- ICES. 1990. Reports of the ICES Advisory Committee on Fishery Management, 1989. *Coop. Res. Rep. Cons. int. Explor. Mer, No. 168 (Part 1)*.
- ICES. 1965–1992. Preliminary Report of the International 0-Group Fish Survey in the Barents Sea and Adjacent Waters in August–September. *ICES CM 1965–1992. Demersal Fish Committee*.
- Jakobsen, T. 1992. Biological reference points for northeast Arctic cod and haddock. *ICES J. mar. Sci.*, 49: 155–166.
- Jakobsen, T. 1993. Management of Northeast Arctic cod – past, present, and future? *Proceedings Symp. Management Strategies for exploited fish population, Anchorage, Alaska, October 21–23, 1992 (in press)*.
- Jakobsson, J. 1992. Recent variability in the fisheries of the North Atlantic. *ICES mar. Sci. Symp.*, 195: 291–315.
- Jørgensen, T. 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua* L.). *J. Cons. int. Explor. Mer*, 46: 235–248.
- Jørgensen, T. 1992. Long-term changes in growth of North-east Arctic cod (*Gadus morhua*) and some environmental influences. *ICES J. mar. Sci.*, 49: 263–277.
- Kjesbu, O. S., Kryvi, H., Sundby, S., and Solemdal, P. 1992. Buoyancy variations in eggs of Atlantic cod (*Gadus morhua* L.) in relation to chorion thickness and egg size: theory and observations. *J. Fish Biol.*, 41: 581–599.
- Konstantinov, K. G. 1967. Forecasting of the distribution of fish concentrations in the Barents Sea according to the temperature factor. *Fish. Res. Bd Can. Transl. Ser., No. 1132*, 28 pp.
- Konstantinov, K. G. 1969. Effect of natural factors and fishing on the abundance of groundfish in northern seas. *Fish. Res. Bd Can. Transl. Ser., No. 1559*, 12 pp.
- Korsbrekke, K., Mehl, S., Nakken, O., and Nedreaas, K. 1993. Investigations on demersal fish in the Barents Sea Winter 1993. Report Department of Marine Resources, Institute of Marine Research, No. 14 1993: 1–47.
- Korzhev, V. A., and Tretyak, V. L. 1992. Effect on cannibalism on recruitment to the Northeast Arctic cod stock. *Proc. Fifth PINRO-IMR Symposium, Murmansk August 1991. Institute of Marine Research, Bergen*.
- Loeng, H. 1989. The influence of temperature on some fish population parameters in the Barents Sea. *J. Northw. Atl. Fish. Ser.*, 9: 103–113.
- Loeng, H., and Bjørke, H. 1992. Larval fish growth in the Barents Sea. *International Symposium on Climate Change and Northern Fish Populations, Victoria, B.C., Canada, October 13–16, 1992 (poster session): 1–5*, 5 figs.
- Loeng, H., Blindheim, J., Ådlandsvik, B., and Ottersen, G. 1992. Climatic variability in the Norwegian and Barent Seas. *ICES mar. Sci. Symp.*, 195: 52–61.
- Loeng, H., and Gjøsæter, H. 1990. Growth of 0-group fish in relation to temperature conditions in the Barents Sea during the period 1965–1989. *ICES CM 1990/G: 49*.
- Maslov, N. A. 1944. The bottom fishes of the Barents Sea and their fisheries. *Trudy PINRO. 8: 3–186 (in Russian)*.
- Maslov, N. A. 1960. *Soviet Fish. Invest. North European Seas, Moscow*, pp. 185–231.
- Mehl, S. 1989. The Northeast Arctic cod stock's consumption of commercially exploited prey species in 1984–1986. *Rapp. P.-v. Réun. Cons. int. Explor. Mer*, 88: 185–205.
- Mehl, S. 1991. The Northeast Arctic cod stock's place in the Barents Sea ecosystem in the 1980s: an overview. *Polar Research*, 10(2): 525–534.
- Mehl, S., and Sunnanå, K. 1991. Changes in growth of North-east Arctic cod in relation to food consumption in 1984–1988. *ICES mar. Sci. Symp.*, 193: 109–112.
- Midttun, L., Nakken, O., and Raknes, A. 1981. Variation in the geographical distribution of cod in the Barents Sea in the period 1977–1981. *Fisken Havet No. 4, 1984: 1–16*.
- Mukhina, N. V., Mukhin, A. I., and Dvinina, E. A. 1987. Oceanographic conditions and reproduction of Arcto-Norwegian cod of the Barents Sea in 1980–1985. In *The effect of oceanographic conditions on distributions and population dynamics of commercial fish stocks in the Barents Sea*. Ed. by H. Loeng. *Proceedings of the Third Soviet–Norwegian Symposium, Murmansk, 26–28 May, 1986. Institute of Marine Research, Bergen, 1987: 145–158*.
- Nakken, O., and Raknes, A. 1984. On the geographical distribution of cod in the Barents Sea in the period 1977–1984. *ICES CM 1984/G: 20*.
- Nakken, O., and Raknes, A. 1987. The distribution and growth of Northeast Arctic cod in relation to bottom temperatures in the Barents Sea, 1978–1984. *Fish. Res.*, 5: 243–252.
- Nilssen, E. M., and Hopkins, C. C. E. 1992. Regional variability in fish-prawn communities and catches in the Barents



- Sea, and their relationship to the environment. ICES mar. Sci. Symp., 195: 331-348.
- Øiestad, V., 1994. Historic changes in cod stocks and cod fisheries: Northeast Arctic cod. ICES mar. Sci. Symp., 198: 17-30.
- Olsen, S. 1968. Some results of the Norwegian capelin investigations 1960-1965. Rapp. P.-v. Réun., Cons. int. Explor. Mer, 158: 18-23.
- Orlova, E. L. 1992. Prey size preference in cod feeding on capelin and herring in the southern Barents Sea. Proc. Fifth PINRO-IMR Symposium, Murmansk, August 1991. Institute of Marine Research, Bergen.
- Ottestad, P. 1986. Time-series described by trigonometric functions and the possibility of acquiring reliable forecasts for climatic and other biosphere variables. J. Interdiscipl. Cycle Res., 17 (1): 29-49.
- Ponomarenko, I. Y., 1984. Survival of bottom-dwelling young cod in the Barents Sea and its determining factors. In Proceedings Sovjet-Norwegian Symposium on Reproduction and Recruitment of Arctic cod, Leningrad, 26-30 September 1983, pp. 213-229. Ed. by O. R. Godø and S. Tilseth. Institute of Marine Research, Bergen.
- Ponomarenko, V. P. and Ponomarenko, I. Y. 1975. Consumption of the Barents Sea capelin by cod and haddock. ICES CM 1975/F: 10.
- Rothschild, B. J., and Osborn, T. R. 1988. Small-scale turbulence and plankton contact rates. J. Plankton Res., 10: 465-474.
- Serebryakov, V. P. 1991. Predicting year-class strength under uncertainties related to survival in the early life history of some North Atlantic commercial fish. NAFO Sci. Coun. Stud., 16: 49-55.
- Shevelev, M. S., Tereschenko, V. V., and Yaragina, N. A. 1987. Distribution and behaviour of demersal fish in the Barents and Norwegian seas, and the factors influencing them. In The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea. Ed. by H. Loeng. Proceedings of the Third Soviet-Norwegian Symposium, Murmansk, 26-28 May, 1986, pp. 181-190. Institute of Marine Research, Bergen.
- Skjoldal, H. R., Gjørsæter, H., and Loeng, H. 1992. The Barents Sea ecosystem in the 1980s; Ocean climate, plankton and capelin growth. ICES mar. Sci. Symp., 195: 278-290.
- Skreslet, S. 1981. Information and opinions on how freshwater outflow to the Norwegian coastal current influences biological production and recruitment to fish stocks in adjacent seas. The Norwegian Coastal Current. Proceedings from the Norwegian Coastal Current Symposium, Geilo, September 1980, pp. 712-748. Ed. by R. Sætre and Martin Mork. University of Bergen.
- Soldal, A. V., Engås, A., and Isaksen, B. 1993. Survival of gadoids that escape from a demersal trawl. ICES mar. Sci. Symp., 196: 122-127.
- Sundby, S. 1979. Om sammenhengen mellom ferskvannsavrenninger og en del biologiske parametre. Fisken Havet, Ser. B; 1979(7): 15-26.
- Sundby, S., Bjørke, H., Soldal, A. V., and Olsen, S. 1989. Mortality rates during the early life stages and year-class strength of Northeast Arctic cod (*Gadus morhua* L.). Rapp. P.-v. Réun. Cons. int. Explor. Mer, 191: 351-358.
- Sundby, S., and Fossum, P. 1990. Feeding conditions of Arcto-Norwegian cod larvae compared with the Rothschild-Osborn theory on small-scale turbulence and plankton contact rates. J. Plankton Res., 12: 1153-1162.
- Sundby, S., and Godø, O. R. 1993. Life history of the Arcto-Norwegian cod stock. Unpublished manuscript.
- Sætersdal, G., and Hysten, A. 1964. The decline of the skrei fisheries. FiskDir. Skr. Ser. Havunders., 13(7): 56-69.
- Sætersdal, K., and Loeng, H. 1987. Ecological adaptation of reproduction in Northeast Arctic cod. Fish. Res., 5: 253-270.
- Tjelmeland, S. 1992. A stochastic model for the Barents Sea capelin stock with predation from an exogenous cod stock. Proc. Fifth PINRO-IMR Symposium, Murmansk, August 1991. Institute of Marine Research, Bergen.
- Trout, G. C. 1957. The Bear Island cod: migrations and movements. Fishery Invest., Lond., Ser. 2, 21(6), 51 pp.
- Ugland, K. I., Jødestøl, K. A., Aspholm, P. E., Krøyer, A. B. and Jakobsen, T. 1993. Fish consumption by invading harp seals off the Norwegian coast in 1987 and 1988. ICES J. mar. Sci., 50: 27-38.
- Ulltang, Ø. 1987. Potential gains from improved management of the Northeast Arctic cod stock. Fish. Res., 5: 319-330.
- Ulltang, Ø. 1993. Risk analysis and biological knowledge. ICES CM 1993/D: 16.
- Ushakov, N. G., Korzhev, V. A., and Tretyak, V. L. 1992. Northeast Arctic cod importance in capelin stock dynamics. Proc. Fifth PINRO-IMR Symposium, Murmansk, August 1991. Institute of Marine Research, Bergen.
- Woodhead, A. D. 1959. Variations in the activity of the thyroid gland of the cod, *Gadus callarias* L., in relation to its migrations in the Barents Sea. II. The "dummy run" of the immature fish. J. mar. biol. Ass. U.K., 38: 417-422.