



ORIGINAL ARTICLE

Ecosystem effects of the three capelin stock collapses in the Barents Sea

HARALD GJØSÆTER*, BJARTE BOGSTAD & SIGURD TJELMELAND

Institute of Marine Research (IMR), Bergen, Norway

Abstract

The Barents Sea capelin stock underwent drastic changes in stock size during the last three decades. Three stock collapses occurred in 1985–1989, 1993–1997, and 2003–2006. The collapses had effects both downwards and upwards in the food web. The release in predation pressure from the capelin stock led to increased amounts of zooplankton during the collapse periods. When capelin biomass was drastically reduced, its predators were affected in various ways. Cod experienced increased cannibalism, growth was reduced and maturation delayed. Sea birds experienced increased rates of mortality and total recruitment failures, and breeding colonies were abandoned for several years. Harp seals experienced food shortage, increased mortality because they invaded the coastal areas and were caught in fishing gears, and recruitment failures. There is evidence for differences in how the three capelin collapses affected the predators. The effects were most serious during the 1985–1989 collapse and can hardly be traced during the ongoing collapse. We conclude that these differences likely result from increased availability of alternative food sources during the two last periods of collapse.

Key words: *Barents Sea, capelin, ecological effects, stock collapse*

Introduction

In 1984 and the following years, an almost total recruitment failure was evident in the Barents Sea capelin, *Mallotus villosus* (Müller, 1776), stock, which then collapsed from 1985 due to lack of recruits. From a level of 4–7 million tonnes maintained during the 1970s, the stock was reduced to below 200,000 tonnes. The stock was rebuilt to pre-collapse levels in 1990, only to collapse once more in 1993, due to a new period of recruitment failure. In 2000, the stock was rebuilt to above 4 million tonnes, but collapsed for the third time from 2003. An intensive research activity to explain the reasons for and shed light on the mechanisms involved in the collapses was started in response to these large stock fluctuations, of which the first came totally unexpected to the research community. After 20 years much insight has been gained into the mechanisms involved, and although not all questions are answered there is agreement that changes in the ecosystem is the main reason behind the stock fluctuations (Hamre 1994; Gjøsæter 1995,

1998; Gjøsæter & Bogstad 1998; Hallfredsson & Pedersen 2006a,b).

Up to now, the causes and the underlying mechanisms have been at the centre of the research, but another interesting question is: what are the effects on the ecosystem when one of its key elements, the capelin, fluctuates to the extent seen during the last thirty years? The Barents Sea is probably one of the most intensively studied large marine ecosystems in the world, and numerous observations made during this period by the Institute of Marine Research (IMR) in Bergen, the Polar Institute of Fisheries and Oceanography (PINRO) in Murmansk and others give valuable information about the state of the ecosystem. These observations have given us new insight into how the ecosystem functions at the trophic levels near the capelin. The purpose of this paper is to document the ecosystem effects of the three capelin stock collapses and investigate possible differences in the ecosystem effects among them.

*Correspondence: Harald Gjøsæter, Institute of Marine Research, P.O. Box 1870 Nordnes, N-5817 Bergen, Norway. E-mail: harald.gjosæter@imr.no

Published in collaboration with the University of Bergen and the Institute of Marine Research, Norway, and the Marine Biological Laboratory, University of Copenhagen, Denmark

Material and methods

The Barents Sea is a high-latitude, shallow continental shelf area. It is bounded in the north by the archipelagos of Spitsbergen and Franz Josef Land, in the east by Novaya Zemlya, and in the south by the coasts of Norway and Russia (Figure 1). In the west, the boundary between the Barents Sea and the Norwegian Sea is usually drawn along the continental edge at about 10°–15°E. More than 20% of the area is shallower than 100 m, but troughs deeper than 400 m enter the area from the west and north-east. The oceanographic characteristics of the Barents Sea are mainly governed by large-scale current systems flowing through the area. The Norwegian Coastal Current flows along the coast of Norway and Russia, given the name Murman Coastal Current when it crosses the border between the two countries. It brings warm low-saline water masses to the Barents Sea. The Norwegian Atlantic Current flows into the Barents Sea from the south-west, dividing into two branches flowing eastwards and north-eastwards. It brings warm saline water to the area. Arctic water enters the Barents Sea through the channel between Spitsbergen and Franz Josef Land and, more important, between Franz Josef Land and Novaya Zemlya (Loeng 1991). Where the warm water masses entering from south and west meet the cold water masses from the north and east,

the Polar Front, a semi-stationary frontal zone, is formed. This front divides the Barents Sea roughly into a temperate zone and an arctic zone (Figure 1).

Various parts of the Barents Sea ecosystem have been studied for several decades during surveys conducted by IMR, PINRO, and others. In recent years, multipurpose surveys have been conducted, where the aim is to study a range of abiotic and biotic parts of the system. Previously, surveys were mostly aimed at covering one or a few fish stocks in addition to hydrography and plankton. In the present paper, information from a whole series of surveys (mostly documented in unpublished cruise reports) has been used, as well as published material.

The largest fish stocks in the area are the Northeast Arctic cod, *Gadus morhua* Linnaeus, 1758, stock, the Northeast Arctic haddock, *Melanogrammus aeglefinus* (Linnaeus, 1758), stock, the Barents Sea polar cod, *Boreogadus saida* (Lepechin, 1774), stock, the Barents Sea capelin stock and the Norwegian Spring-spawning herring, *Clupea harengus* Linnaeus, 1758, stock. The latter is only found in the Barents Sea during the young stages; it migrates out of this nursery area at the age of 3 or 4 years, to join the adult stock living in the Norwegian Sea. In recent years, blue whiting, *Micromesistius poutassou* (Risso, 1827), has expanded its distribution area into the western Barents Sea. The sizes of these stocks, back to 1973, are shown in Figure 2. A stock of harp seals,

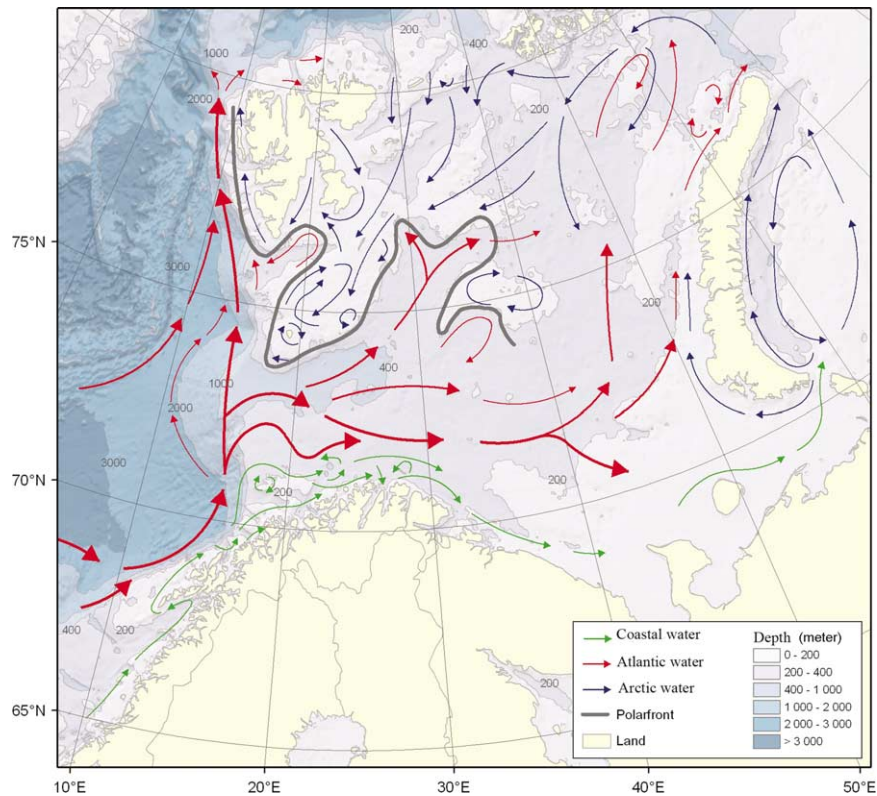


Figure 1. Bathymetric map showing the Barents Sea and adjacent areas, including water masses and ocean currents.

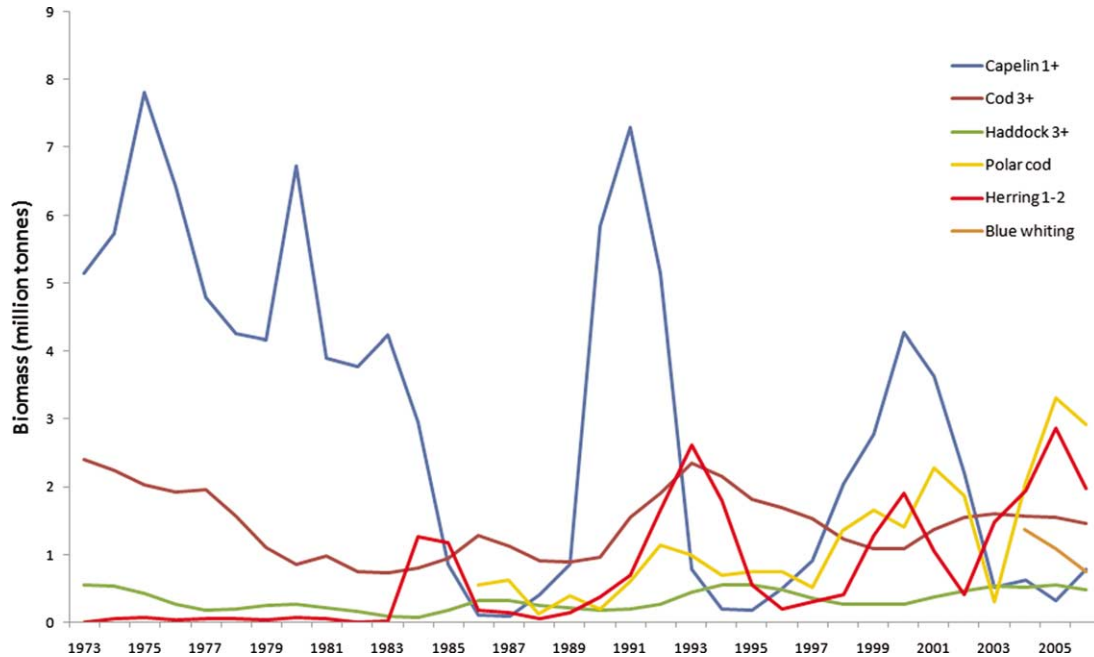


Figure 2. Stock history for the main fish stocks in the Barents Sea.

Phoca groenlandica Erxleben, 1777, also inhabits the Barents Sea, and minke whales, *Balaenoptera acutorostrata* Lacépède, 1804, fin whales, *Balaenoptera physalus* (Linnaeus, 1758), and humpback whales, *Megaptera novaeangliae* (Borowski, 1781), from the north-east Atlantic feed in the area during summer and fall. Some populations of sea birds utilize capelin as prey. The most important of these in terms of capelin consumed are the Brünnich's guillemot, *Uria lomvia* (Linnaeus, 1758), the Common guillemot, *Uria aalge* (Pontoppidan, 1763), the Black-legged kittiwake, *Rissa tridactyla* Linnaeus, 1758, and the puffin, *Fratercula arctica* (Linnaeus, 1758).

These stocks affect each other in a complicated interplay, which is only partly understood (Bogstad et al. 2000). The three stock collapses of capelin were drastic upheavals in this ecosystem (Figure 2). The mechanisms behind these collapses (we define a capelin collapse as a situation when the total capelin stock is less than 1 million tonnes when measured acoustically during fall) have been discussed in several papers (e.g. Hamre 1994; Gjøsæter 1995; Gjøsæter & Bogstad 1998), and will not be discussed here. It suffices to say that practically all studies so far have concluded that the causes of the collapses are natural changes in the ecosystem, first of all characterized by the presence of young herring in the Barents Sea; fishing on the capelin stock has played a minor role.

We focus on the recent series of capelin stock collapses starting in the mid-1980s, and some of the important data used in the analysis is available from that time onward only. The stock size of capelin has

been monitored from 1973 and some analyses are carried out on data from 1973 to 2006. To explore any differences in the variables among the various collapse events, and to test the hypothesis that the collapse periods affected the ecosystem differently, the period from 1973 to 2006 was divided into the following periods:

1. 1973–1985 (before any of the recent stock collapses, restricted amount of data);
2. 1986–1989 (the first capelin stock collapse);
3. 1990–1993 and 1998–2003 (inter-collapse periods with a big capelin stock); and
4. 1994–1997 and 2004–2006 (the second and third collapse period).

This division does not follow the definition of stock collapses given above strictly. The amount of capelin measured in the autumn is probably a better proxy for the available amount of capelin during next calendar year than the estimate from the autumn of that calendar year, especially for cod, which consume most of the capelin during the first half of the year. Therefore, we have used this amount when dividing into different periods above. The third capelin stock collapse period ended in 2007 when the stock was estimated to 1.9 million tonnes. We have chosen not to include data from 2007 in our analyses, but we utilize the knowledge about the length of the third collapse period.

We analysed information on the following factors, which have varied substantially during the last few decades:

- plankton biomass (data available from 1985 to 2006; Stiansen & Filin 2007);
- cod biomass (data available from 1973 to 2006; ICES 2007);
- cod diet (data available from 1984 to 2006; ICES 2007);
- cod mortality caused by cannibalism (data available from 1984 to 2006; ICES 2007);
- cod growth (data available from 1973 to 2006; ICES 2007);
- cod maturity (data available from 1973 to 2006; ICES 2007);
- harp seal distribution and mortality (data available from 1973 to 2006, various sources, see references in text); and
- seabird distribution and mortality (no time series data available, various sources, see references in text).

We wanted to study how the variability of these factors could be related to the amount of capelin. We also use information on the following factors, which could shed light on the mechanisms behind the variation of the factors listed above:

- polar cod biomass (data available 1986–2006; Anon 2006);
- blue whiting biomass (data available 2003–2006; Anon 2006); and
- herring biomass (data available 1973–2006; ICES 2006a).

Results

The capelin collapse periods

What characterized the three collapse periods? The lowest capelin stock size measured during the event was smaller during the first than during the second and third: 0.10 and 0.12 million tonnes during 1986 and 1987, 0.19 and 0.20 million tonnes during 1994 and 1995, and 0.62 and 0.32 million tonnes in 2004 and 2005. It should be noted that at such small stocks the estimates are highly uncertain, and may not be significantly different. In any case, compared to a 'normal' size of the capelin stock of above 4 million tonnes, these differences are small.

The collapse periods were of approximately equal length: the period with a stock size below 1 million tonnes lasted for five years both during the first and the second collapse period, while the third period only lasted for four years. Since the three collapses were all first and foremost caused by recruitment failure, the stock structure was also similar during the collapse events. However, the individual growth of capelin was somewhat better during the second and third collapse than during the first one. This is

also reflected in larger M-output biomasses MOB (estimated capelin biomass output through natural mortality; Hamre & Tjelmeland 1982; Bogstad et al. 2000) during the two last periods. During the second and third collapse the average annual MOB was almost twice as high as during the first collapse period (0.6–0.7 million tonnes vs. 0.4 million tonnes). The estimates of MOB are probably even more uncertain than the estimates of standing stock, since MOB is based on estimates of standing stock of each age group, the mean weight of each age group, and the natural mortality of each age group. Since the stock size of cod is known for the whole period, it is also possible to calculate the stock size and the MOB of capelin per unit of cod. Because the cod stock was larger during the two last collapse periods, the amount of capelin per unit cod stock was somewhat smaller during the two last collapse periods than during the first, and the MOB per unit cod stock was only slightly larger during the last periods than during the first.

The geographical distribution of the capelin stock during the collapse years may also affect the consequences of the collapses, since the overlap with other stocks might be affected. From the distribution maps of capelin from the annual autumn surveys, it is difficult to trace any differences. Perhaps there is a tendency for a larger distribution area, especially towards the south and east, during the second and third period, but there are differences among the individual years that make a comparison difficult. Besides, the surveys only give a snapshot of the distribution near the end of the feeding season, and may not be representative for the whole year.

Changes in the distribution of cod may have affected the geographical overlap between cod and capelin during the period. The overlap between these stocks is most extensive during the capelin spawning migration in January–March (Bogstad & Gjøsæter 2001), and we do not know about any time trends in the overlap at this time of the year. In autumn, the situation is somewhat different. For the cod, we have annual surveys in August–September from 2004 onwards, but the cod distribution was only sporadically mapped during the summer–autumn period before 2004. There were no clear changes in the distribution area of cod between the years 1991, 1995, 1996, 1997 and 2000. However, from these years to 2004, there was a clear expansion towards north and east, and during the period 2004–2007, we have seen a further expansion in those directions, which might be associated with increased sea temperatures. A more northern and eastern distribution of cod implies a more complete overlap between cod and capelin. Consequently, there is reason to believe that the overlap between cod and

capelin in summer–autumn might have been more extensive during recent years, although no quantitative analysis of the distribution charts has been made.

It is difficult to estimate the amount of other food available during the various capelin collapse periods. This will also vary among predators. The combined biomass of capelin, herring, blue whiting and polar cod, which would make up relevant food for cod, was 4.2-times higher during the second and third collapse period than during the first. If we add the biomass of cod and haddock to this amount, which would seem relevant for seals, we obtain 2.7-times higher biomass during the second and third capelin collapse periods than during the first. These estimates are imprecise, since the populations of blue whiting and polar cod is not well known for the first part of the time series. However, the amount of blue whiting is known to have increased substantially in recent years, and the reason why no acoustic stock size estimates were made prior to 2003 is that blue whiting was not common in the Barents Sea. The stock of polar cod was estimated at a very low level in the early 1970s, and probably built up gradually to the levels measured acoustically from 1986 onwards. It should also be noted that during 1980s and early 1990s redfish (*Sebastes* spp.) was an important prey item for cod, but then the biomass of young redfish decreased strongly, with a corresponding decrease

in the proportion of redfish in the cod diet (ICES 2007).

Plankton

Figure 3 shows how the zooplankton standing stock in August–September has varied during the period 1985–2006. The biomass of capelin is also shown. Visual inspection of the data reveals opposite trends in the biomasses of capelin and zooplankton. Regression analysis confirms this; there is a significant negative relationship between the two variables capelin biomass and total zooplankton abundance ($R^2_{\text{adj}} = 0.25$, $P < 0.01$). This effect is even clearer when only the size fraction 1–2 mm of zooplankton is taken into consideration ($R^2_{\text{adj}} = 0.36$, $P < 0.01$).

Cod

Cod is the main predator on capelin and capelin is the main prey for cod, and these two stocks will obviously interact. Figure 4 shows how these two stocks have varied in size during the period 1973 till present. There is no relationship between the variation in standing stocks ($R^2 = 0.0$).

Figure 5 shows the total consumption estimates of cod per prey category based on the stomach content analysis undertaken since 1984 (Mehl & Yaragina 1992; Bogstad & Mehl 1997), and Figure 6a,b shows the consumption/biomass ratio for age 3–6

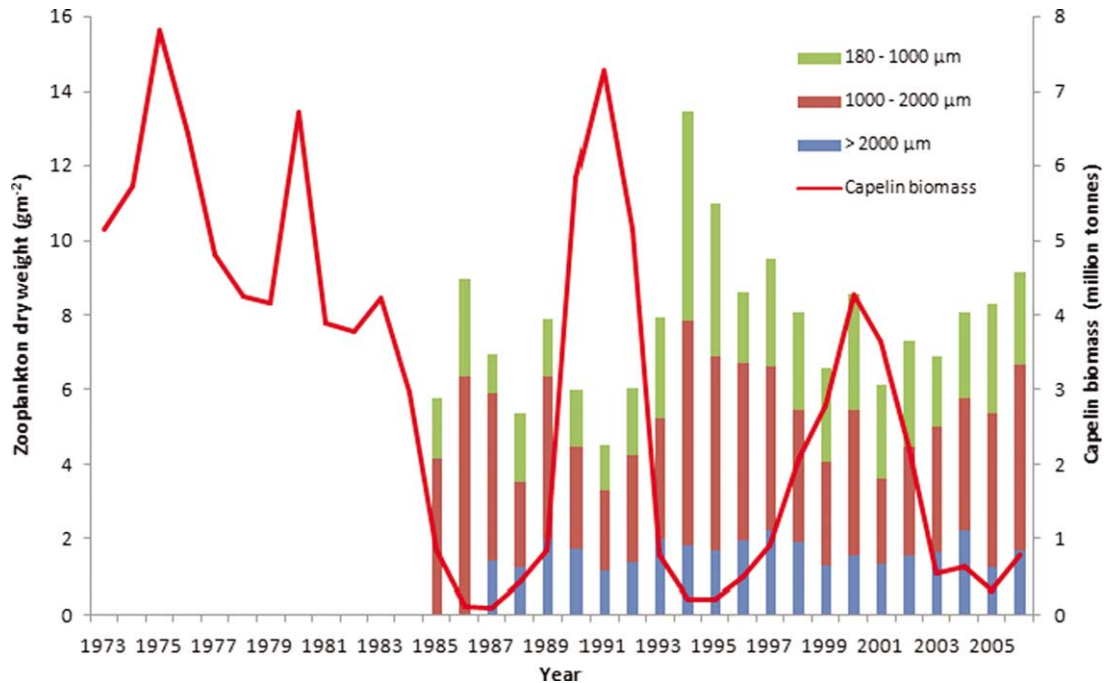


Figure 3. Standing stocks of zooplankton, distributed on three size categories, and capelin. Before 1987, the plankton was only divided into two size groups.

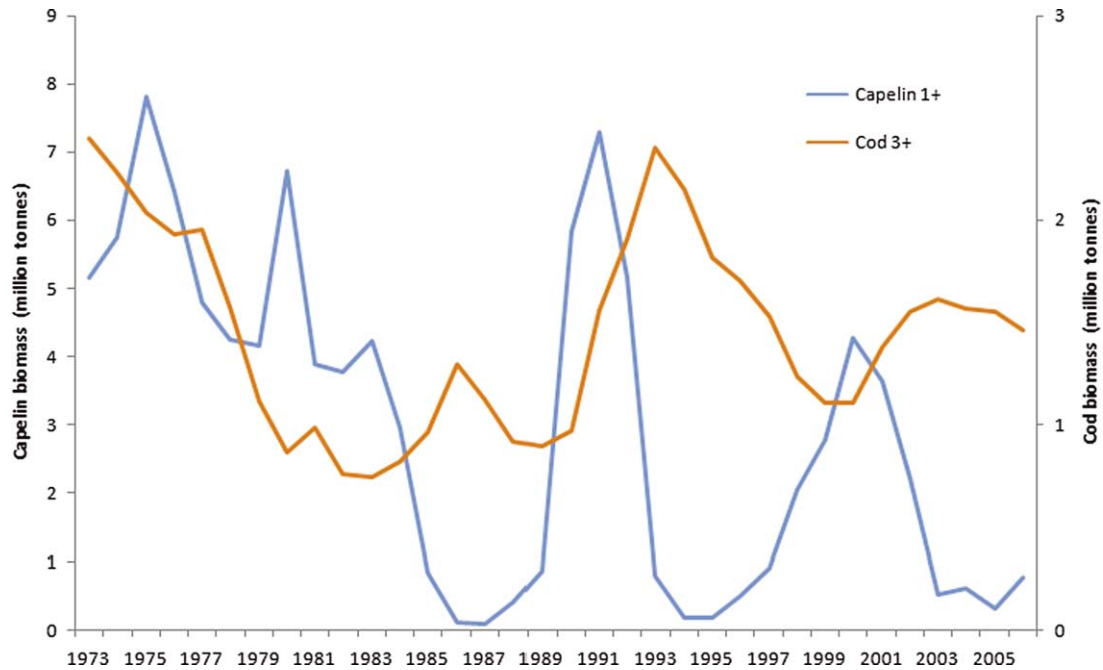


Figure 4. Standing stocks of cod and capelin.

cod, for the first and second half of the year separately. These age groups were chosen in this analysis since they are those who are most dependent on capelin as food. Since the standing stock of capelin measured in autumn is not necessarily representative for the amount of capelin available for cod during that calendar year, MOB has been estimated. A noticeable relationship exists between the MOB and the consumed amount of capelin ($R^2_{\text{adj}}=0.60$, $P<<0.01$). It should be noted that in some years the estimated consumption of capelin is higher than the estimated MOB. The consumption

estimates could be overestimates, or the MOB could be underestimates. The latter depend on survey estimates, and the survey reports from the collapse periods comments that the probability of underestimating stock size is probably higher when the stock size decreases. Other interesting relationships can also be seen from Figure 5. For example, the consumption of crustacean prey (shrimp, *Pandalus borealis* Krøyer, 1838, amphipods and krill) is inversely related to the available amount of capelin (MOB) ($R^2_{\text{adj}}=0.23$, $P=0.01$) and that of capelin actually consumed ($R^2_{\text{adj}}=0.29$, $P<0.01$). The

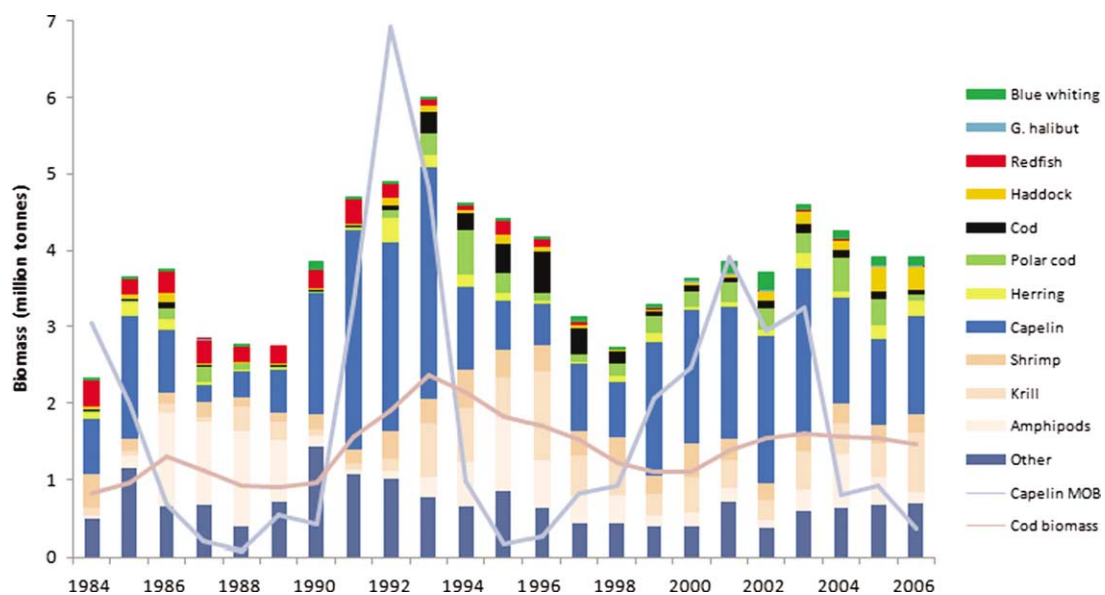


Figure 5. Total consumption of the cod stock, estimated from stomach samples.

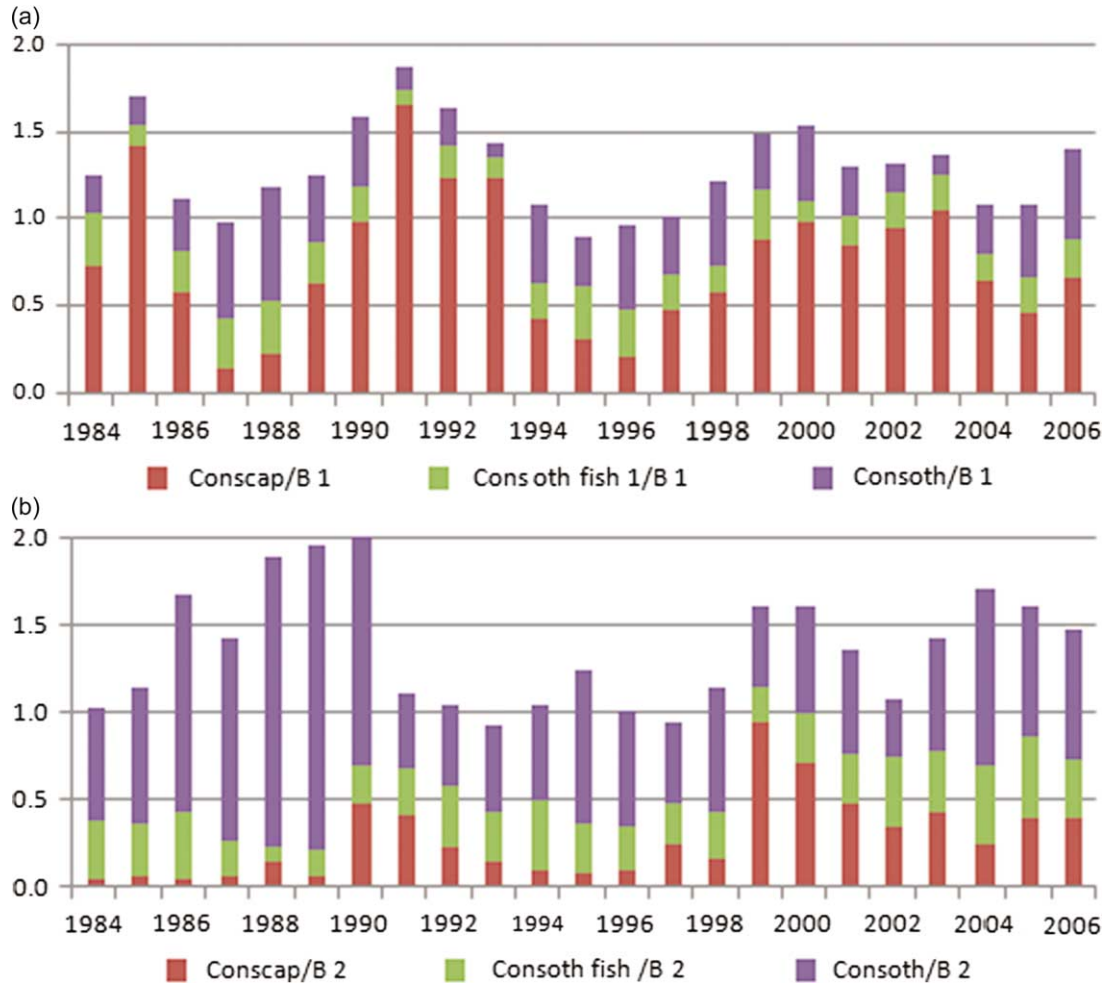


Figure 6. Consumption/biomass ratio for age 3–6 cod by half-year, estimated from stomach samples and VPA estimates of stock abundance.

relative abundance of shrimp appears to covary with that of capelin, and there is no relationship between the amount of shrimp and capelin consumed by cod. Contrary to expectance, there is no relationship between the availability of capelin and the consumed amount of fish food other than capelin.

The consumption/biomass ratio for age 3–6 by half-year (Figure 6a,b) shows that the consumption of capelin decreased markedly during all the three capelin collapses. The cod could only to a limited extent compensate for the lack of capelin by eating other food during the first half of the year. Also, the figure shows the consumption of ‘other’ food (mainly krill, amphipods and shrimp) in the second half of the year, particularly during the first collapse. The consumption of other fish was somewhat higher during the second and third collapses than during the first collapse.

There are negative relationships (although not statistically significant) both between the availability of capelin and the amount of young cod consumed by cod, and between the capelin consumed by cod

and the amount of young cod consumed by cod. However, the instantaneous mortality coefficient for the two youngest age groups of cod calculated based on these cannibalism estimates (M2, Figure 7) are significantly negatively correlated with capelin stock size (M2 Age 1: $R^2_{\text{adj}}=0.19$, $P=0.02$, M2 Age 2: $R^2_{\text{adj}}=0.18$, $P=0.03$).

Capelin constitutes high-energy food for cod, and lack of capelin may hamper growth, energy storage and maturity (Yaragina & Marshall 2000). For analysis of growth and maturation, the period 1985–2006 was chosen, as data from before 1985 were calculated in a different way than data for 1985 and later years (ICES 2001, 2007). Figure 8 shows how the growth of the age groups 3–6 of cod has fluctuated during the period 1985–2006 compared to the capelin stock size. Since the stock size of cod varies, the stock size, the MOB and the amount of capelin consumed by cod were divided by the stock size of cod to obtain more relevant independent variables to compare with cod growth. For all age groups of cod there were significant relationships

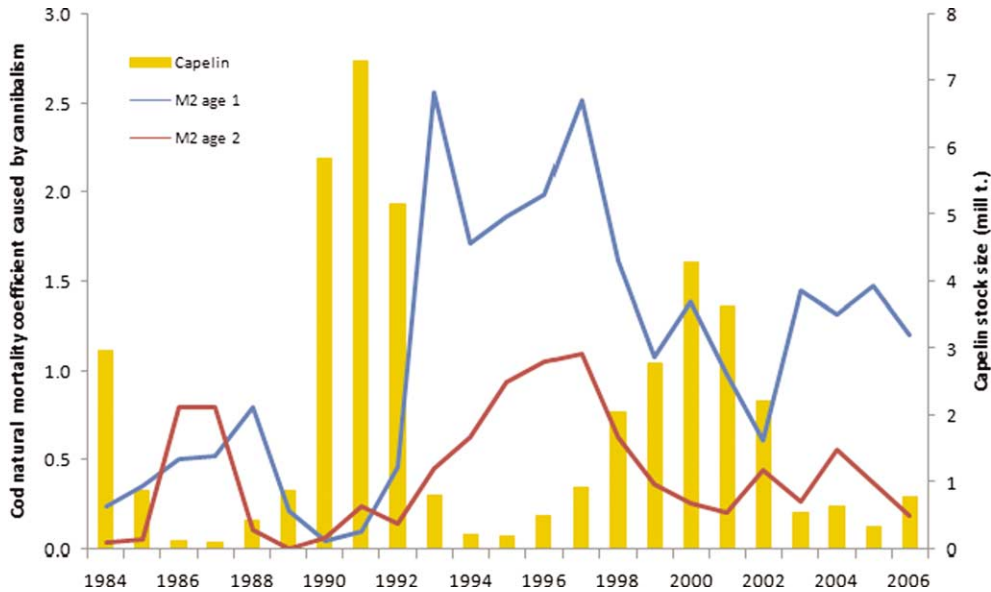


Figure 7. Natural mortality coefficients caused by cannibalism, estimated from cod stomach samples.

between yearly growth and the capelin biomass per cod ($P=0.0009$, 0.0001 , 0.0002 , and 0.0048 for age groups 3–6, respectively). When using the MOB of capelin per cod as independent variable, the relationships were significant for two of the age groups ($P=0.041$, 0.072 , 0.024 , and 0.193 for age groups 3–6, respectively). Using the consumed amount of capelin per cod as independent variable gave no significant results, only weak positive relationships were found.

Figure 9 shows how the maturity rate at age 7–9 cod has fluctuated during the period 1985–2006. There was a significant drop in maturity during the first capelin collapse, but no clear trends and little variation can be seen in the period after 1990. There were positive relationships between the rate of maturation by age and the capelin stock size for these three age groups for the whole period, but none of them were significant.

Marshall et al. (1998, 2006) showed that there was a substantial decrease in weight at length of prespawning female cod, hepatosomatic index (HSI; liver weight/fish weight) as well as total egg production per unit SSB (TEP/SSB) during the first capelin collapse. The lowest values were observed in 1987. A lesser decrease in these quantities was observed during the second capelin collapse, while such data for the third collapse period were not analysed in those papers.

Harp seals

There are no direct measurements of the population size of the harp seal in the Barents Sea. Pup production is estimated based on surveys, and based on these estimates and various other population parameters the total population size is modelled (ICES 2006b), Figure 10. The stock size estimates

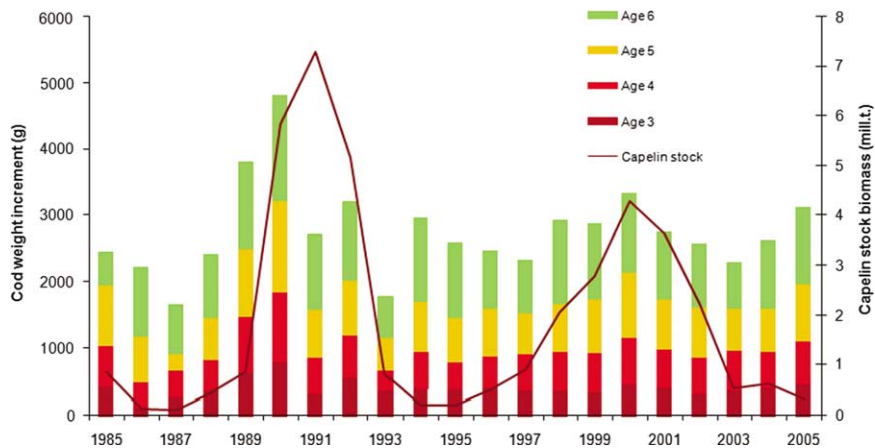


Figure 8. Growth (annual weight increment) of cod in various age groups, and the standing stock of capelin.

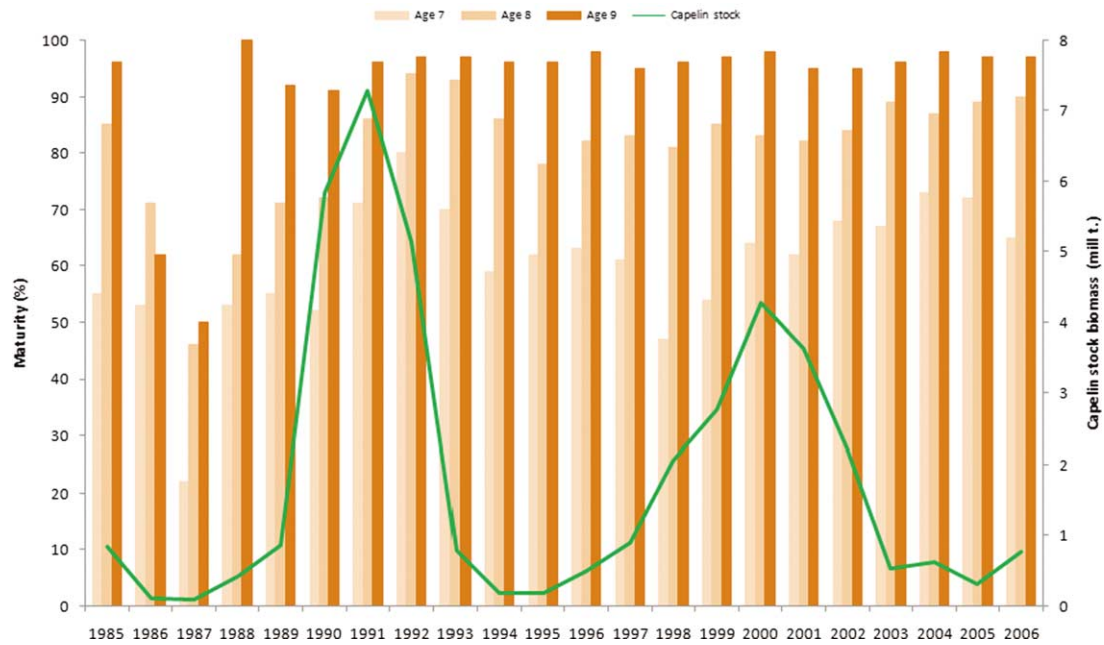


Figure 9. Maturity rate (%) of some age groups of cod and capelin stock biomass.

are considered uncertain. It is seen that during the period analysed here, the stock has increased from about 1.15 million individuals to about 2 million individuals. Contrasting a steady increase of about 5% per year during most of the period shown here, there was a levelling off during the late 1980s. According to Russian surveys the number of breeding females drastically decreased during the period 1985–1988 (Markussen & Øritsland 1991).

In late autumn the harp seals leave the northern ice-filled feeding areas to migrate southwards to the whelping areas in the White Sea. Seal ‘invasions’ to Finnmark has been a regular phenomenon during

winter–spring in periods, e.g. in 1901–1903, 1916–1918, and recently from 1978 to 1988 (Markussen & Øritsland 1991). The feeding in the northern area is dominated by pelagic amphipods, polar cod and occasionally capelin (Falk-Petersen et al. 2004). The feeding on capelin in the northern area depends probably on the distance between the ice border and the northernmost capelin concentrations. During their return from the northern feeding areas in autumn the harp seals probably switch to a more fish-rich diet. It is not clear how much of the fish prey consists of capelin, because samples of seals for stomach analysis in these periods are scarce. Based

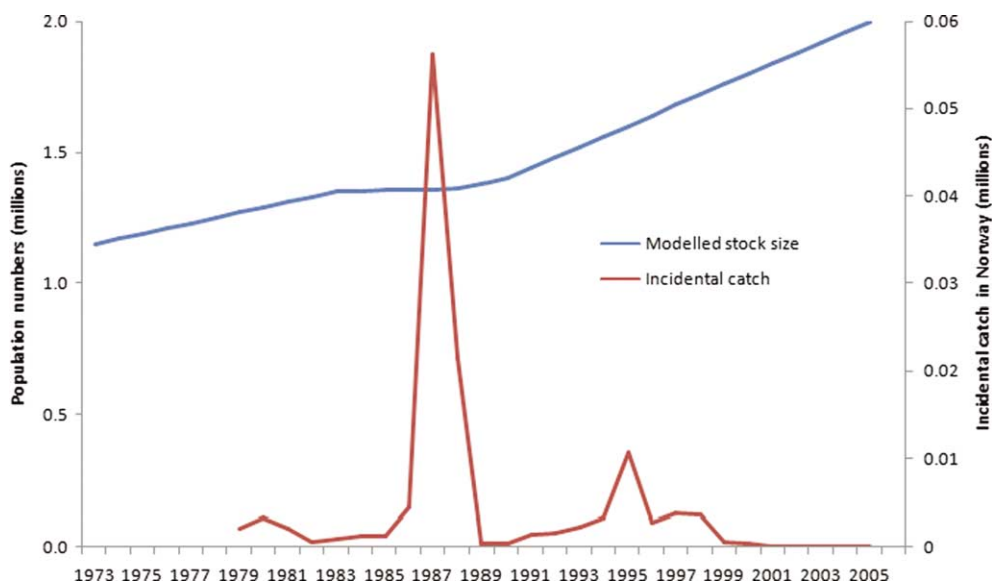


Figure 10. Modelled standing stock of harp seals in the Barents Sea, and number of incidental catches on the Norwegian coast.

on stomach data from incidental catches of seals at the Finnmark coast, Haug et al. (1991) concluded that they were opportunistic feeders, and that the food consisted of herring, capelin, and various gadoid species. When the capelin stock collapsed in 1985–1986 there was a dramatic increase of seals at the Norwegian coast of Finnmark and further south (Figure 10) during winter–spring (ICES 2006b). Also during the second capelin stock collapse period there was an increase in the number of incidental catches, indicating increased invasions, especially in 1995, where also the condition of the seals was poor compared to the condition of the seals in 1993 (Nilssen et al. 1998). Seal invasions have apparently not been a major problem in recent years.

Seabirds

Several species of seabirds feed in the Barents Sea, and fatty fish, including capelin, constitutes major prey for some of these. The most important in terms of capelin consumed are the Brünnich's guillemot, the Common guillemot, the Black-legged kittiwake, and the puffin (Furness & Barrett 1985; Barrett & Krasnov 1996; Barrett et al. 1997, 2002; Wassmann et al. 2006). Although fish prey and in particular capelin is important food for several species of seabirds, it has been difficult to quantitatively demonstrate major effects on seabird mortality, breeding success, etc., caused by the capelin stock collapses (Barrett & Krasnov 1996). One reason for this might be that the studies of such parameters are normally carried out in local colonies, and the availability of prey within the foraging range from the colony may be totally independent of the total stock size of the prey (Furness & Barrett 1985). However, Vader et al. (1990) associated a sudden collapse in the guillemot numbers in 1986–1987 with the capelin stock collapse in the same period (Vader et al. 1990; Krasnov & Barrett 1995). The largest change in birds was in the number of common guillemots, especially the Bear Island population, which contained 245,000 of the total of 266,000 breeding pairs of common guillemots before the first collapse, but was reduced by 85–90% (Barrett et al. 1997). Barrett (2002) reported that chick growth of puffin at Hornøya, Eastern Finnmark was lower near the end of the first capelin stock collapse (1988–1989) than during the corresponding years near the end of the second one (1996–1997), perhaps because the chicks compensated by eating small cod during the second stock collapse. It is unknown whether later capelin stock declines have had similar effects on the seabird populations in the Barents Sea. Due to a complete lack of time series data on seabird population sizes that could be

statistically compared to similar series of stock sizes of fish prey, it is difficult to pursue this theme any further.

Discussion

The ecological effects of capelin stock collapses demonstrated here are partly working downwards, partly upwards in the food chain. The downward effect on plankton standing stock in autumn, demonstrated for the whole period of analysis, has not changed among the different collapse periods. For instance, the medium-sized zooplankton, for which the negative relationship with capelin stock size was strongest, had nearly equal abundance during the first and the two last capelin stock collapses. We interpret this as if they were equally affected by the release in predation pressure. The smallest and largest size fractions of plankton were less affected. The smallest size fraction is probably less important as food for adult capelin, while the largest size fraction is poorly represented in the plankton samples from the WP2 nets, which make up the majority of the samples underlying the abundance estimates of zooplankton.

The upward effects, on the other hand, seem to have been different for the different time periods 1–4. Our analyses show that the cod was severely affected by cannibalism during all three collapse periods, but the largest mortality coefficients for age 1 and 2 were calculated for the second collapse period (Figure 7). The growth (Figure 8) and the maturation (Figure 9), on the other hand, were most seriously affected during the first collapse period, but only to a small degree during the two last collapse periods.

The reason why cannibalism, in contrast to the other effects, seems to be less important during the first capelin stock collapse is probably that the geographical overlap between juvenile and adult cod was much larger in the 1990s than it was during the 1980s. Figure 11 shows the overlap index

$$I = \sum_{i=1}^N \frac{Y_i O_i}{0.25 N}$$

between cod of age 1 and 2 and older cod, where Y_i is the fraction of age 1 or age 2 in sample i , and O_i is the fraction of an older age (4–8), all other age groups disregarded. The figure shows that the overlap was at a minimum during the first collapse for both age 1 and age 2 as younger age groups and for all ages 4–8 as older age groups. The overlap decreases with increasing age difference. The temporal variation in overlap pattern is the same for data in quarters 1 and 3, although more pronounced in

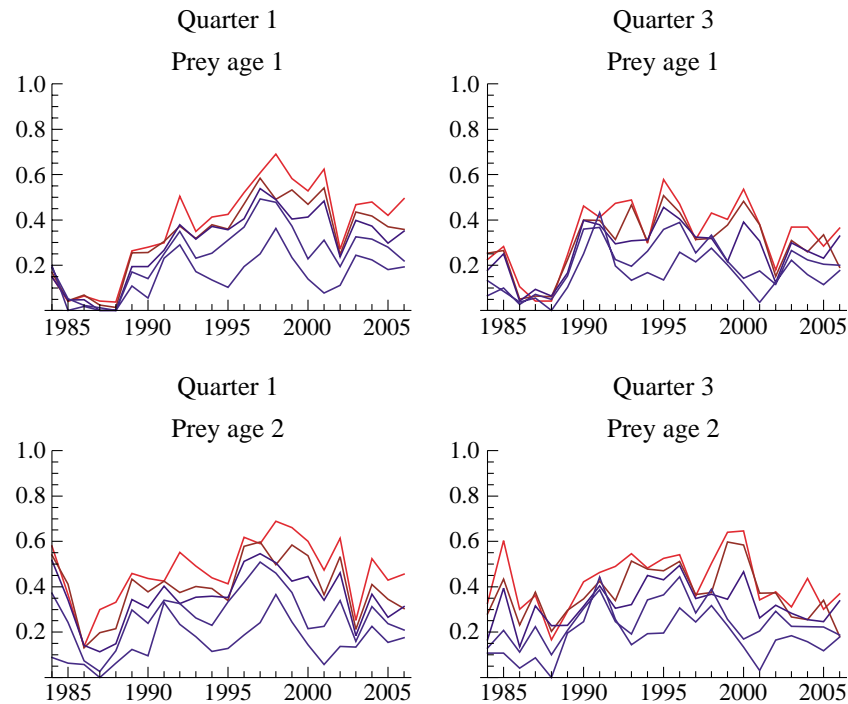


Figure 11. Overlap between cod ages 1 and 2 and cod of ages 4–8, ranging from red (age 4) to blue (age 8), in the first and third quarters of the year. (The colour version of this figure is available in the online version.)

quarter 1. Quarters 2 and 4 are not shown, because of too little data.

Yaragina et al. (2009) studied data on frequency of occurrence (FO) of capelin and cod in cod stomachs for the period 1947–2005. They found no significant relationship between these two quantities, although some years with low FO of capelin coincided with years with high FO of cod.

Since we do not have comparable data for cod growth and maturity before 1985, we do not know the status before the first collapse. Both growth and maturation rate was at a minimum in 1987, and increased rapidly after the first collapse period. The growth rate dropped somewhat also during the second and third collapse period, while the maturation rate seemed to stabilize at the high level attained after the first collapse period. Obviously, both the growth and the maturation of cod are affected by several factors other than the availability of capelin prey. A thorough analysis of these factors should be done, but lies outside the scope of the present paper. It should be noted that the considerable changes in exploitation pattern and stock size around 1990 may have had a significant impact on growth and maturation of cod. The fishing mortality was in the 0.7–0.9 range during the 1980s, but dropped to around 0.3 in 1990–1991 before it increased again. Also, the stock size more than doubled from 1990 to 1993, increasing from 1 to above 2 million tonnes.

It is difficult to document effects of the capelin stock collapses to other capelin predators, like the harp seals and various species of seabirds, since time series data for these predators are mostly lacking. However, there are numerous accounts of drastic changes taking place during the first capelin stock collapse, e.g. seabirds that failed to breed and left the colonies, seals that invaded the coast and died by the thousands when caught in fishing nets, etc. Hamre (1994), among others, even called the events a crisis. In later years, however, fewer accounts, if any, have been seen describing substantial changes in the upper trophic levels of the ecosystem or its various components that could be associated with the capelin stock collapses. However, the aftermath of the first collapse may actually have influenced the effects during the second and third collapse. For instance, the common guillemot colony at Bear Island, which was reduced by 85–90% during the first collapse (Barrett et al. 1997), probably did not have time to recover before the next collapse came, and consequently this may indirectly have prevented a similar situation during the second and third collapses. For seals there has seemingly not been an equivalent decline in the population after the first collapse (Figure 10), so the same argument cannot be used to explain an apparent lack of effects during the second and third collapse periods. This gives at least circumstantial evidence that the ecosystem effects of lack of capelin have had less drastic effects

in recent years. These evidences are strengthened by the few quantitative data available for the top predators. The development of the harp seal population and the number of animals that drowned in fishing nets along the coast (Figure 10) both indicates that the first capelin stock collapse had drastic effects while later collapses have not hampered the steady increase in population size.

It seems reasonable to conclude that (1) there have been ecological effects of the capelin stock collapses both upwards and downwards in the food webs, and (2) there are differences in ecological effects upwards among the three capelin collapse periods, and the first period (1986–1989) stands out as the period with the most severe effects. What are the mechanisms behind this difference? Two hypotheses may be put forward.

1. A better supply of capelin during the second and third collapse periods.
2. A better supply of other food for the predators during the second and third collapse periods.

The first hypothesis implies that, even if the stock size measurements of capelin seem to show that the second and third collapse was just as grave and lasted as long as the first one, the predators managed to find more capelin to feed on during the later periods. This is possible to test for the cod but not for the other predators. The results from the consumption estimates based on cod stomach sampling show that the average consumption of capelin was almost doubled during the last two periods compared to the first. This seems to support the first hypothesis. However, when calculated per cod, the consumption is only slightly larger during the later periods and not statistically different from the first period. We may conclude that the cod stock was able to consume more capelin during the two last collapse periods, because of higher numbers and growth rates of capelin, but this was counteracted by a larger cod stock during the later periods, and the consumption per cod was only marginally higher. Consequently, this hypothesis cannot explain why cod did better during the later periods.

Since no time series of consumption estimates are available for the other capelin predators, it is unknown how the somewhat higher level of capelin during the second and third collapse than during the first collapse affected the seals. However, like the cod, the number of seals increased during this period and would need more capelin to maintain the per capita ration of capelin.

The second hypothesis says that a higher intake of other food compensated for the lack of capelin during the second and third collapse. The total

estimated annual food intake of cod was higher during the second and third collapse than during the first (4.06 and 3.03 million tonnes, respectively). However, the consumption per cod (weighted average over all age groups) was somewhat lower. The same can be seen when analysing the different prey categories separately. Consequently, although the cod stock was able to consume more food during the second and third capelin stock collapse periods, the consumption per cod was lower, and since it is the consumption per capita that matters for effects like maturation and growth, the consumption estimates do not support the findings that the effects on the cod were more severe during the first collapse. The picture is somewhat more complicated when analysing each age group of cod separately. Of those age groups mostly dependent on capelin as food (age 3 and above), some (most notably age 4–8) showed a similar decline in consumption during the first and second capelin stock collapse periods, while older cod have had an increasing trend in food consumption during the whole period, although the variation from year to year is large.

The possibility that the consumption estimates of cod do not tell the whole story can not be ruled out. The growth of some cod age groups show no significant relationship with the total consumption per cod, and the possibility that the consumption estimates might give a misleading picture of the true annual food intake should not be ruled out. The reason might be, for example, that sampling is non-representative in time and/or space. On the other hand, the consumption and the growth are inter-related. The growth will decrease (over time) when the consumption decreases. And the consumption per predator is not directly comparable when the size of the predator changes.

Although the consumption estimates for cod do not directly support the second hypothesis, the hypothesis should not be abandoned. When growth and maturity of some cod age groups show an increase with time, there is a possibility that at least some cod age groups were able to compensate better with other food during the second and third collapse period. The energy content of different prey will also vary, both with species and time of the year. A direct comparison of prey weights might consequently be too simplistic. It should be noted that the crustaceans (krill and amphipods) which replaced capelin in the cod diet during the first capelin collapse are less digestible and have lower energy content than the fish which replaced capelin during the second and third collapse. Also, the energy spent catching krill and amphipods may be higher than the energy spent catching the same amount of fish prey.

Seals and seabirds have other fish than capelin on the diet. Polar cod is probably important food both for harp seals (Sakshaug et al. 1994; Nilssen et al. 1995; Lindstrøm et al. 1998) and seabirds (Mehlum & Gabrielsen 1993; Barrett & Krasnov 1998), and herring is important for harp seals (Haug et al. 1991). It seems reasonable to think that both seals and birds exploited the increased amounts of these and other fish species when the capelin stock was heavily reduced during the second and third collapse period. The reason why sea mammals and seabirds did better during the two last capelin collapse periods would most easily be explained by this hypothesis. However, at least for some birds, a connection between the collapse periods resulting from that the colonies reduced in size during the first collapse period were not able to regain their pre-collapse sizes until the second and third collapses came, could partly explain the findings.

This hypothesis is also supported by circumstantial evidence. The temperature in the Barents Sea has increased over most of the period analysed here (Stiansen & Filin 2007). This is at least partly caused by increased inflow of Atlantic water, rich in nutrients and zooplankton. Some fish stocks known to be preyed on by cod and other top predators have increased in size during this period, most notably the polar cod but also the blue whiting, herring and juveniles of various stocks (Figure 2).

The first capelin stock collapse was termed an 'ecosystem crisis', while the later collapses that were equally grave in terms of availability of capelin as food for predators were hardly noticed. The most likely explanation for this is that other forage fishes were much more abundant during the second and third collapse. This partly mitigated the situation and stabilized the upper trophic levels.

References

- Anon. 2006. Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea in August–October 2006 (vol. 1). IMR/PINRO Joint Report Series, No. 2/2006. ISSN 1502-8828.
- Barrett RT. 2002. Atlantic puffin *Fratercula arctica* and common guillemot *Uria aalge* chick diet and growth as indicators of fish stocks in the Barents Sea. Marine Ecology Progress Series 230:275–87.
- Barrett RT, Anker-Nilssen T, Gabrielsen GW, Chapdelaine G. 2002. Food consumption by seabirds in Norwegian waters. ICES Journal of Marine Science 59:43–57.
- Barrett RT, Bakken V, Krasnov V. 1997. The diets of common and Brünnich's guillemots *Uria aalge* and *U. lomvia* in the Barents Sea region. Polar Research 16:73–84.
- Barrett RT, Krasnov YV. 1996. Recent responses to changes in stocks of prey species by seabirds breeding in the southern Barents Sea. ICES Journal of Marine Science 53:713–22.
- Bogstad B, Gjøsæter H. 2001. Predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) in the Barents Sea: Implications for capelin stock assessment. Fisheries Research 53:197–209.
- Bogstad B, Haug T, Mehl S. 2000. Who eats whom in the Barents Sea? NAMMCO Scientific Publications 2:98–119.
- Bogstad B, Mehl S. 1997. Interactions between Atlantic cod (*Gadus morhua*) and its prey species in the Barents Sea. In: Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No. 97-01. University of Alaska Fairbanks. p 591–615.
- Falk-Petersen S, Haug T, Nilssen KT, Wold A, Dahl TM. 2004. Lipids and trophic linkages in harp seal (*Phoca groenlandica*) from the eastern Barents Sea. Polar Research 23(1):43–50.
- Furness RW, Barrett RT. 1985. The food requirements and ecological relationships of a seabird community in north Norway. Ornis Scandinavica 16(4):305–13.
- Gjøsæter H. 1995. Pelagic fish and the ecological impact of the modern fishing industry in the Barents Sea. Arctic 48:267–78.
- Gjøsæter H. 1998. The population biology and exploitation of capelin (*Mallotus villosus*) in the Barents Sea. Sarsia 83:453–96.
- Gjøsæter H, Bogstad B. 1998. Effects of the presence of herring (*Clupea harengus*) on the stock–recruitment relationship of Barents Sea capelin (*Mallotus villosus*). Fisheries Research 38:57–71.
- Hallfredsson EH, Pedersen T. 2006a. Effects of predation from 0-group cod on mortality rates of capelin larvae in the Barents Sea. In: Hallfredsson EH, editor. 2006. Fish predation on capelin larvae *Mallotus villosus* in the Barents Sea, in relation to recruitment. Doctor scientiarum thesis, The Norwegian College of Fisheries Science, University of Tromsø, Norway.
- Hallfredsson EH, Pedersen T. 2006b. Effects of predation from juvenile herring on mortality rates of capelin larvae in the Barents Sea. In: Hallfredsson EH, editor. 2006. Fish predation on capelin larvae *Mallotus villosus* in the Barents Sea, in relation to recruitment. Doctor scientiarum thesis, The Norwegian College of Fisheries Science, University of Tromsø, Norway.
- Hamre J. 1994. Biodiversity and exploitation of the main fish stocks in the Norwegian–Barents Sea ecosystem. Biodiversity and Conservation 3:473–92.
- Hamre J, Tjelmeland S. 1982. Sustainable yield estimates of the Barents Sea Capelin stock. ICES C. M. 1982/H:45, 24 pp.
- Haug T, Krøyer AB, Nilssen KT, Ugland KI, Aspholm PE. 1991. Harp seal (*Phoca groenlandica*) invasions in Norwegian coastal waters: Age composition and feeding habits. ICES Journal of Marine Science 48:363–71.
- ICES. 2001. Report from the Arctic Fisheries Working Group, Bergen, Norway, 24 April–5 May 2001. ICES C.M. 2001/ACFM:19, 380 pp.
- ICES. 2006a. Report of the Northern Pelagic and Blue Whiting Fisheries Working Group, Copenhagen 24–30 August 2006. ICES C.M. 2006/ACFM:34, 294 pp.
- ICES. 2006b. Report of the ICES/NAFO Working Group on Harp and Hooded Seals, St. John's, Newfoundland, 30 August–3 September 2005. ICES C.M. 2006/ACFM:06, 52 pp.
- ICES. 2007. Report of the Arctic Fisheries Working Group, Vigo, Spain, 18–27 April 2007. ICES C.M. 2007/ACFM:16, 651 pp.
- Krasnov YV, Barrett RT. 1995. Large-scale interactions between seabirds, their prey and man in the southern Barents Sea. In: Skjoldal HR, Hopkins CCE, Erikstad KE, Leinaas HP, editors. Ecology of Fjords and Coastal Waters. Amsterdam: Elsevier. p 443–56.
- Lindstrøm U, Harbitz A, Haug T, Nilssen KT. 1998. Do harp seals *Phoca groenlandica* exhibit particular prey preferences? ICES Journal of Marine Science: Journal du Conseil 55(5):941–53.
- Loeng H. 1991. Features of the physical oceanographic conditions of the Barents Sea. Polar Research 10(1):5–18.
- Markussen NH, Øritsland NA. 1991. Food energy requirements of the harp seal (*Phoca groenlandica*) population in the Barents

- and White Seas. In: Sakshaug E, Hopkins CCE, Øritsland NA, editors. Proceedings of the Pro Mare symposium on Polar Marine Ecology, Trondheim, 12–16 May 1990. Polar Research 10(2):603–08.
- Marshall CT, Kjesbu OS, Yaragina NA, Solemdal P, Ulltang Ø. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? Canadian Journal Fisheries Aquatic Sciences 55:1766–83.
- Marshall CT, Needle CL, Thorsen A, Kjesbu OS, Yaragina NA. 2006. Systematic bias in estimates of reproductive potential of an Atlantic cod (*Gadus morhua*) stock: Implications for stock-recruit theory and management. Canadian Journal Fisheries Aquatic Sciences 63:980–94.
- Mehl S, Yaragina NA. 1992. Methods and results in the joint PINRO–IMR stomach sampling program. In: Bogstad B, Tjelmeland S, editors. Interrelations Between fish Populations in the Barents Sea, Proceedings of the Fifth PINRO–IMR Symposium, Murmansk 12–16 August 1991. p 5–16.
- Mehlum F, Gabrielsen GW. 1993. The diet of high-arctic seabirds in coastal and ice-covered pelagic areas near the Svalbard archipelago. Polar Research 12:1–20.
- Nilssen KT, Haug T, Øritsland T, Lindblom L, Kjellqvist SA. 1998. Invasions of harp seals *Phoca groenlandica* ERXLEBEN to coastal waters of Norway in 1995: Ecological and demographic implications. Sarsia 83:337–45.
- Nilssen KT, Haug T, Potelov V, Timoshenko YK. 1995. Feeding habits of harp seals (*Phoca groenlandica*) during early summer and autumn in the northern Barents Sea. Polar Biology 15:485–93.
- Sakshaug E, Bjørge A, Gulliksen B, Loeng H, Mehlum F. 1994. Structure, biomass distribution, and energetics of the pelagic ecosystem in the Barents Sea: A synopsis. Polar Biology 14:405–11.
- Stiansen JE, Filin AA, editors. 2006. Joint PINRO/IMR report on the state of the Barents Sea ecosystem 2006, with expected situation and considerations for management. IMR/PINRO Joint Report Series No. 2/2007. ISSN 1502–8828.
- Vader W, Barrett RT, Erikstad KE, Strann KB. 1990. Differential responses of common and thick-billed murrelets to a crash in the capelin stock in the southern Barents Sea. Studies in Avian Biology 14:175–80.
- Wassmann P, Reigstad M, Haug T, Rudels B, Carroll ML, Hop H, et al. 2006. Food webs and carbon flux in the Barents Sea. Progress in Oceanography 71:232–87.
- Yaragina NA, Bogstad B, Kovalev YuA. 2009. Variability in cannibalism in north-east Arctic cod (*Gadus morhua*) during the period 1947–2006. Marine Biology Research 5:75–85.
- Yaragina NA, Marshall CT. 2000. Trophic influences on interannual and seasonal variation in the liver condition index of Northeast Arctic cod (*Gadus morhua*). ICES Journal of Marine Science 57:42–55.

Editorial responsibility: Geir Ottersen

Copyright of *Marine Biology Research* is the property of Taylor & Francis Ltd and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.