The rise and fall of the Barents Sea capelin (*Mallotus villosus*): a multivariate scenario

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Hopkins, C. C. E. & Nilssen, E. M. 1991: The rise and fall of the Barents Sea capelin (*Mallotus villosus*): a multivariate scenario. Pp. 535–596 in Sakshaug, E., Hopkins, C. C. E. & Øritsland, N. A. (eds.): Proceedings of the Pro Mare Symposium on Polar Marine Ecology, Trondheim, 12–16 May 1990. *Polar Research 10(2).*

The Barents Sea capelin is a major forage species for many apex predators, for example, fish, marine mammals, sea birds, and man. The fishery for Barents Sea capelin increased exponentially in the early 1970s with the demise of the Atlanto-Scandian herring fishery along the Norwegian coast. The collapse of the herring spawning-stock resulted in the disappearance of young herring from the southern Barents Sea and the diet of the larger (ca. 3+ ages), piscivorous cod. Since then the only major dietary alternative for these larger cod has been capelin. The over-all trend in the biomass of the Barents Sea cod, however, has been one of decline since the late 1940s. As there was a marked decrease in the biomass of the 3+ ages of cod from ca. $3 \cdot 10^6$ tonnes to ca. $1 \cdot 10^6$ tonnes from 1974 to 1983, this would have simultaneously caused a great reduction in the predation pressure from cod on the capelin.

The Barents Sea capelin is an r-strategist. Its weight-at-age is inversely related to population size, and thus the number of cohorts and subsequently age-at-maturity are positively related to population size. Principal components analysis (PCA) indicates that the biomass of 2+ ages of capelin and population characteristics *already* exhibited a declining trend from about 1975, despite a declining cod stock. Coupling of independent Russian and Norwegian data clearly shows that the percentage occurrence of prawns in the stomach of 3+ cod increased disproportionately from the mid-1970s *despite* a decrease in the cod biomass, probably indicating a lack of capelin as primary-choice prey. The *nominal* capelin catch between 1978 and 1983 is probably an unreliable estimate of fishing mortality. A drastic decline in the capelin stock occurred after 1983/1984, with marked predation from the potentially strong 1983 cod year-class.

The capelin, as an r-strategist, is very difficult to manage in the fluctuating biological and climatic environment of the Barents Sea. Fisheries for capelin should be limited within the framework of multispecies perspectives, with much of its production being primarily used to sustain an elevated long-term yield of cod.

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Introduction

The capelin (*Mallotus villosus*) is a major forage species in several highly exploited, boreal shelf-ecosystems, such as those off Newfoundland, Iceland, and in the Barents Sea (Winters & Carscadden 1978). The capelin is a fatty fish which feeds directly on the abundant, lipid-rich zooplankton (such as the copepod *Calanus finmarchicus*, and euphausiids), and it in turn forms one of the most important components of the diet of cod (*Gadus morhua*) in these ecosystems (Prokhorov 1965; Lilly 1987; Pálsson 1983). This short "fatty food chain" is a key feature maintaining the relatively high productivity of northern, high latitude ecosystems (Hopkins et al. 1989a). Furthermore, capelin figure both directly and indirectly in the food chains leading to seals, whales and sea-birds (Winters & Carscadden 1978; Hamre 1988; Brown & Nettleship 1984; Furness & Barrett 1985; Barrett et al. 1987)).

Prior to the early 1970s capelin stocks off Canada, Iceland, Greenland, Norway and Russia were only exploited by local people for their own needs (Jangaard 1974). Since then capelin have been the target of more or less intensive fisheries, and collapses have occurred in Canada and Iceland in the latter part of the 1970s and 1982 respectively (Carscadden 1984; Vilhjálmsson 1983; Anon. 1989a). Various explanations have been provided to account for these collapses, ranging from belief that the primary causes were of natural origin (for example climatic) to putting the blame firmly on over-exploitation of key components of the ecosystem (Carter 1979, 1980; Brown & Nettleship 1984; Carscadden 1984; Hamre 1988).

The collapse of capelin stocks have far reaching effects on the rest of the ecosystem, with decreased individual and population growth rates of various fish, birds and mammals at higher levels in the food web (Carscadden & Reddin 1982; Hamre 1988; Vader et al. 1990). As the cod production decreases, this also detrimentally affects the livelihood of the cod-fishermen. It is thus of foremost importance to gain a better insight into the reasons affecting the collapse of capelin stocks.

This paper provides a critical analysis of the interplay of some of the key events that affected the rise and fall of the Barents Sea capelin stock. The inter-relationship between the major fishery stocks of the Barents Sea are analysed and discussed. The data indicate that there are various warning signals that should be paid attention to in the future in order to maintain a sustainable yield for the benefit of man and the rest of the ecosystem.

Materials and methods

Data have been extracted from official fisheries statistics published by the Norwegian Directorate of Fisheries in the journal *Fisken og Havet* (Anon. 1988, 1989b). Other sources of data cited and re-analysed in this work are acknowledged in the text.

The data were stored in the DATA module of the statistics package SYSTAT (Wilkinson 1988a), and plotted as desired using the SYGRAPH facilities. Principal Components Analyses (PCA) were performed with the FACTOR module of SYSTAT. Where it has been desirable to fit a curve illustrating a basic trend in the data, this has been achieved by avoiding semi-subjective regression techniques and rather using "locally weighted scatterplot smooth" methods (Cleveland 1979) implemented in SYGRAPH (Wilkinson 1988b).

Key system components

Hydrography and topography of the Barents Sea

The Barents Sea is in essence a neritic, shelf-sea with a mean depth of about 230 m (Zenkevitch 1963). Covering an area of approximately $1.5 * 10^6$ km^2, it is delineated by the coastline of northern Norway and the USSR in the south, by Bjørnøya (Bear Island) and Spitsbergen towards the west, and by Novaja Zemlja and Frans Josef Land at the east and the north. The southern part of the Barents Sea is ice-free throughout the year, and is dominated by the relatively warm intrusion of Atlantic Water masses. The northern part of the sea is covered by annually formed sea ice in winter, and is primarily under the influence of cold water masses of Arctic origin flowing from the north and northeast. The degree of Atlantic inflow into the Barents Sea can vary greatly, resulting in changes in temperature and ice-cover; this is considered to also have consequences for recruitment and distribution patterns of several fish species (see Tantsiura 1959; Loeng 1979; Loeng & Midtun 1984; Sætersdal & Loeng 1984; Nilssen & Hopkins 1991).

Recent descriptions of the Barents Sea, and its plankton and fish resources have been presented by Dragesund & Gjøsæter (1988), Bergstad et al. (1987), Skjoldal & Rey (1989), and Loeng (1989).

The Atlanto-Scandian herring and its demise

The Atlanto-Scandian herring spawns along the Norwegian coast from the Lofoten Islands southwards (Fig. 1). Prior to the 1970 collapse of the herring stocks (now generally acknowledged to be due to both "biomass" and "recruitment" overfishing, Dragesund et al. 1980), it was common for large numbers of the larvae to be transported northwards with the Norwegian Coastal Current. Larval and juvenile herring filled up the north Norwegian fjords, and juvenile herring accumulated in the Barents Sea in the Atlantic influenced waters south of the polar front. There they grazed on the abundant zooplankton, grew rapidly and formed an important part of the diet of the Norwegian Arctic cod (*Gadus morhua*) (Zatsepin & Petrova 1939). When about 4–5 years old the young herring migrated southwestwards out of the Barents Sea. There they joined the maturing herring grazing the rich waters near Jan Mayen and Iceland before spawning at the Norwegian coast (Fig. 1). However, the stock size of adult Atlanto-Scandian herring fell from about 10 million tonnes in 1957 to 20 thousand tonnes in 1971 (Fig. 2). After 1970 the migration of maturing and post-spawners to Jan Mayen and Iceland

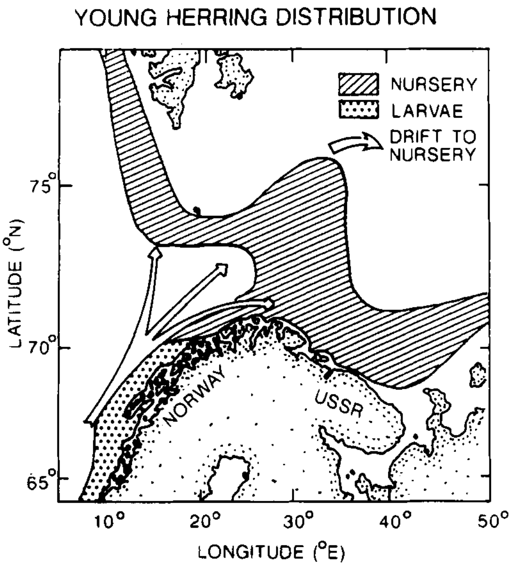

Fig. 1. Distribution and migrations of young stages of Atlanto-Scandian herring (after Dragesund & Gjøsæter 1988): Nursery areas, distribution of larvae, and drift to nursery areas. This is illustrative of the situation when strong year-classes occurred prior to the demise of the stock in the 1970s.

ceased, and too few recruits and survivors were produced to fill up the Barents Sea.

The capelin

The main spawning areas and distribution of Barents Sea capelin are shown in Fig. 3. Spawning occurs from the coast of Troms and Finnmark counties in the southwest, to the Murman Coast in the east; spawning may occur from February to June, with warmer hydrographic conditions increasing the proportion of more eastern, relatively late spawners (Prokhorov 1968; Olsen 1968; Ozhigin & Luka 1985). Larval capelin drift with the northeasterly flowing Atlantic waters. Maturing, and adult capelin feed primarily during the summer months in the north, towards the ice-edge, but move southwards with the advent of winter and the southwards progression of ice-coverage (Reed & Balchen 1982; Loeng 1981; Loeng et al. 1983).

Catch. – Local communities in the northernmost counties of Troms and Finnmark have historically

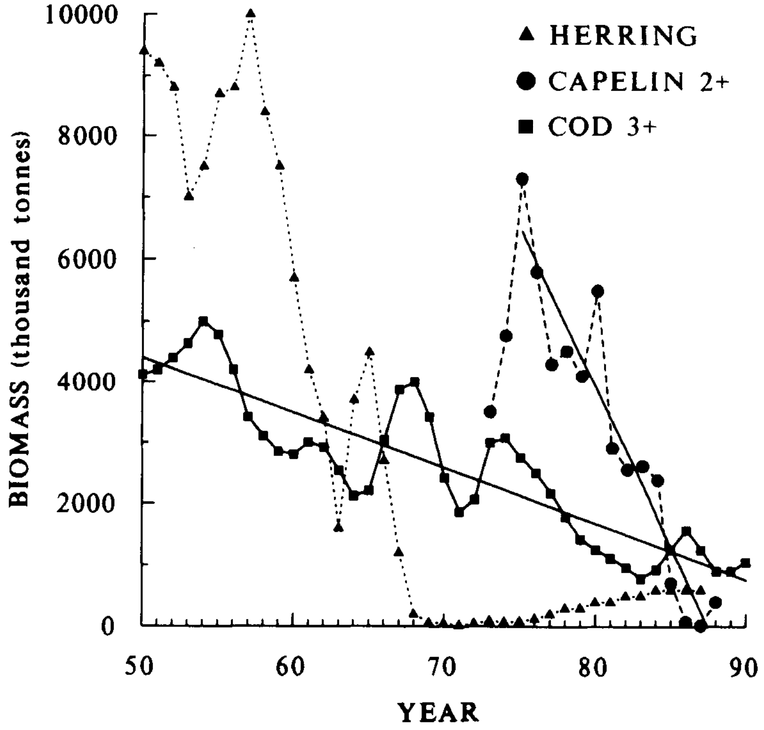

Fig. 2. Stock size estimates of Barents Sea cod (at age 3+), Atlanto-Scandian herring (spawning stock), and Barents Sea capelin (at age 2+). The declining trend-lines are fitted to both cod (all years) and capelin (1975–1985) data. Note: herring is shown merely to illustrate the lack of significant recruitment of young herring to the Barents Sea after 1970. (Data extracted from Dragesund et al. 1980; Anon. 1989b).

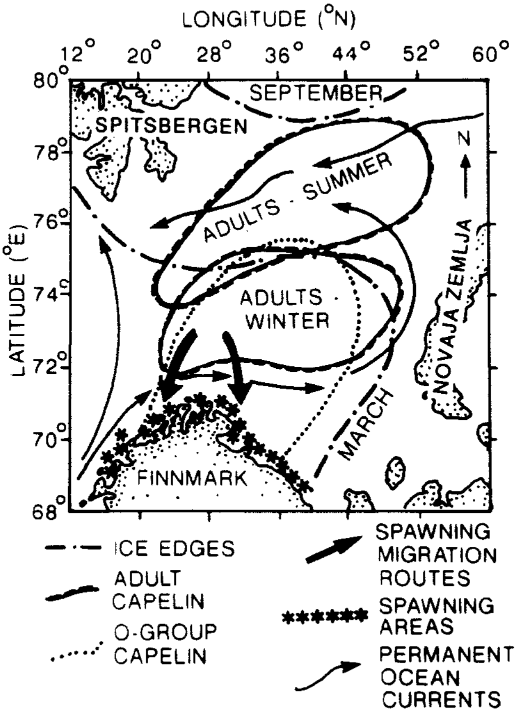

Fig. 3. The Barents Sea showing spawning areas and the distributions of adult capelin in summer and winter. The positions of the ice edge at mean maximum and mean minimum extensions, the Polar Front, and the main currents are also indicated (after Reed & Balchen 1982).

utilised capelin as sources of bait, fertilizer and food when the spawners arrive at the coast in February–March (Møller & Olsen 1962; Nitter-Egenæs 1967; Jangaard 1974)).

Catch statistics exist for capelin from 1950 onwards (Fig. 4). Less than 200 thousand tonnes were landed before 1960, with Norway taking >99% of the catch during a "winter" fishery (based mainly on maturing fish on their way to the coastal spawning grounds). A rapid development of the purse seine, increases in vessel size and engine power, and improvements in sonar occurred in the 1960s. The decrease of the adult herring stocks resulted in a northwards movement of the purse seiners, and thus the fishing effort, into the Barents Sea, generating a marked rise in the catch of capelin. It is clear that the capelin catch rose steadily from about 1965 (Fig. 4), approximately as the herring stock declined. However, there are no categorical data to indicate whether it was due to a real surge in capelin abundance or to a switch-over in effort, previously aimed at herring, towards capelin. As one of the major aims of the herring fishery in the Barents Sea was to catch fish for the herring meal reduction factories, an intensified fishery in this area would probably also have caught capelin. Capelin provide high quality fish meal and oil (Jangaard 1974; Ackman 1982; Falk-Petersen et al. 1990), so those caught would have been used for this purpose.

In 1968 the Norwegians also added a "summer" fishery (aimed at both maturing and semi-juvenile capelin of high fat content, on the grazing grounds situated further north towards the ice edge, see Fig. 3). Before 1973 the Soviet catch of capelin had been < 50 thousand tonnes, but after 1973 their catch rose exponentially. A peak of 2.9 million tonnes was reached in 1977 for the total (all nations) Barents Sea catch. Between 1978 and 1983 the nominal catch varied between 1.5 and 2.4 million tonnes, before declining to 123 thousand tonnes in 1986. The commercial fishery was closed in 1987 and 1988, by order of the joint Soviet-Norwegian Fisheries Commission, in order to preserve the stock.

Abundance. – Independent stock assessments (using combined hydroacoustic and trawl surveys) of the Barents Sea capelin did not start until the early 1970s (Dommasnes & Røttingen 1985) (Fig. 2). It is pertinent to note that data are restricted to fish of > 2 years old, as hydroacoustical assessments of the surface-dwelling younger fish are difficult to obtain with hull-mounted echo-sounders (Dommasnes & Røttingen 1985).

It is generally considered that the capelin stock began their decline from the early 1980s (e.g. Hamre 1985; Røttingen 1990). However, examination of the data from the peak of 1975 onwards (Fig. 2), shows that there are reasons to believe that a declining, significantly linear trend (evident from the standardised residuals; $r^2 = 0.90$, d.f. = 13, $P = < 0.001$) has taken place since the mid 1970s. 1980 deviates most, but represents a single "outlier" in the overall declining trend. It is thus reasonable to ask, whether the decline of the capelin stock began as early as 1975, and not as late as about 1983 as generally proposed.

Demography and individual growth rates. – The age-composition of the Barents Sea capelin, using research survey material (Anon. 1989b, table 1.4.2), is shown in Fig. 5. The proportion of 4

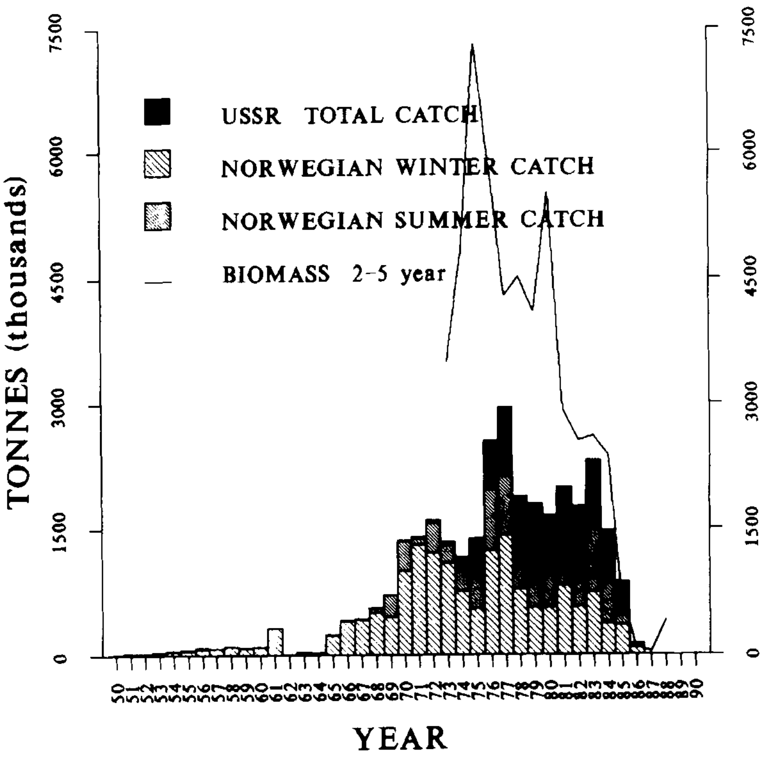

Fig. 4. Total fishery landings of Barents Sea capelin (1950–1988) showing distribution of Norwegian summer and winter catch and total U.S.S.R. landings (from Ervik & Roman 1975; Hamre 1985; Anon. 1989b).

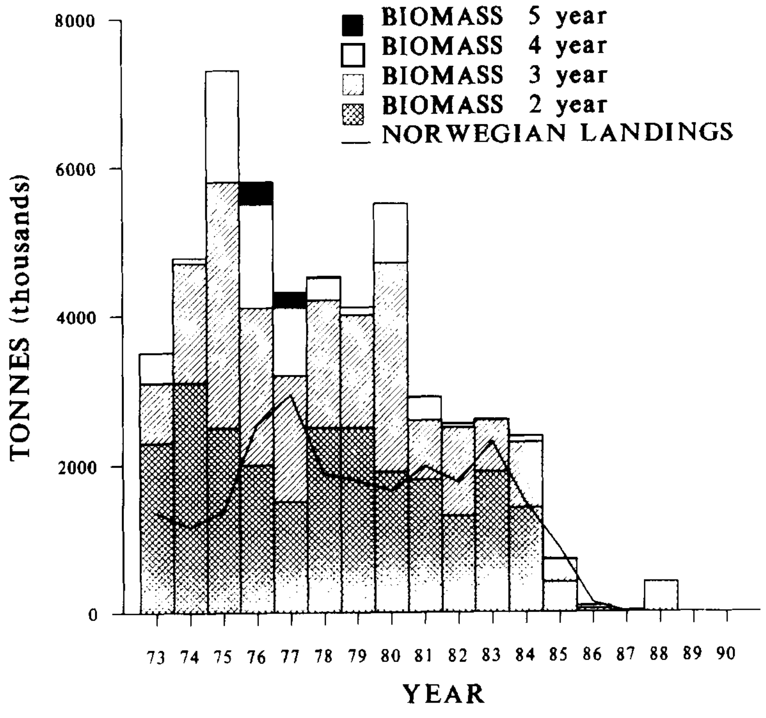

Fig. 5. Biomass at age (ages 2+) of Barents Sea capelin from scientific surveys. Total fishery landings are also shown (data extracted from Anon. 1989b, table 1.4.2).

and 5 year-olds was greatest between 1975 and 1978, when both the stock size and catch were at about their peaks. On the other hand, the decrease in the stock size is correlated with the elimination of the older age-groups, resulting in 1985 and 1986 in most of the adult stock being composed of two year-olds. The age at maturity of capelin in the Barents Sea has generally varied between two and five years old (Dommasnes 1984). As capelin are mainly semelparous (Hamre 1985), the data are indicative of a general tendency for elevated age-at-maturity (towards 4 and 5 year-olds) at large stock size, and reduced age-at-maturity (towards 2 year-olds) at small stock size.

Recent work has suggested that age-at-maturity of capelin is determined by growth, such that faster growing fish become sexually mature at a younger age than those with slower growth rates (Winters 1974; Hamre & Tjelmeland 1982; Forberg & Tjelmeland 1985). In order to examine this further, a plot of mean individual body weight of 2, 3, and 4 year-old Barents Sea capelin as a function of survey year with a rough classification of their abundance (numbers) at age (data extracted from Anon. 1989b, table 1.4.2) is shown in Fig. 6. A general trend is seen for increasing individual weight from the early 1970s to the present time, as stock size also exhibited a decreasing trend. A generally similar, though less clear, trend is seen for 3 year-olds between 1974 and 1982/1983, before weight decreased drastically. A plot of mean individual weight of 2 year-old fish from the various year-classes as a function of their abundance (numbers) is shown in Fig. 7, indicating a highly significant (see fitted Cleveland smoother in fig. 7) negative correlation between these factors. Body weight at age in the mid 1980s (low stock size) was double that of the early 1970s (large stock size).

Finally, the biomass and numerical abundance data for 2–4 year-old capelin has been treated by Principal Components Analysis (PCA) (Fig. 8). The data input were ordered according to year-

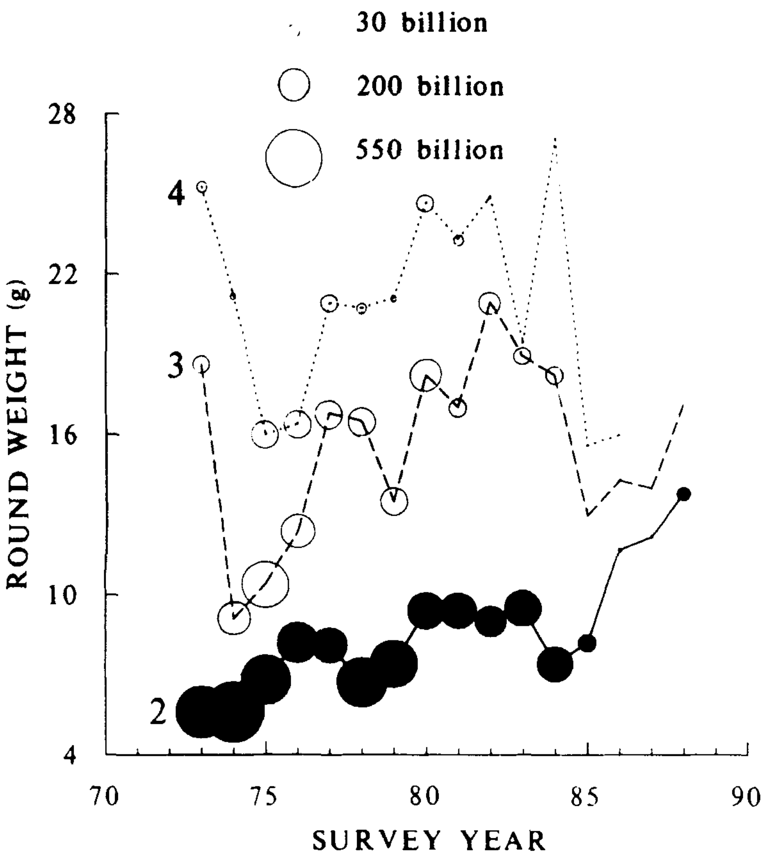

Fig. 6. Mean individual body weight (round weight, g) of 2, 3, and 4 year-old Barents Sea capelin as a function of survey year with circles indicating their abundance (numbers) at age. Area of circles are proportionate with abundance (data extracted from Anon. 1989b, table 1.4.2).

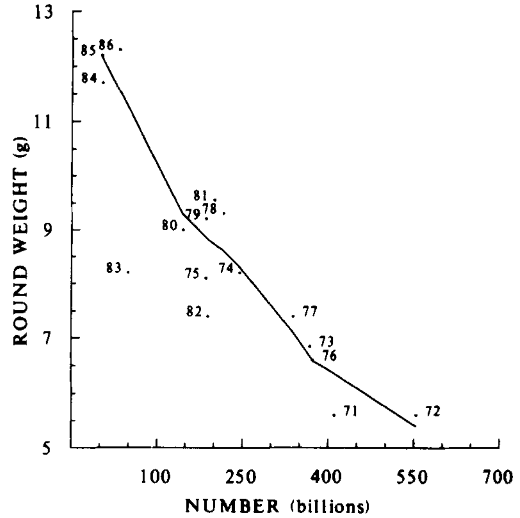

Fig. 7. Mean individual weight (round weight, g) of 2 year-old Barents Sea capelin from year-classes 1971–1986 as a function of their abundance (numbers). The Cleveland smoother trend-line (see Materials and methods) is shown fitted.

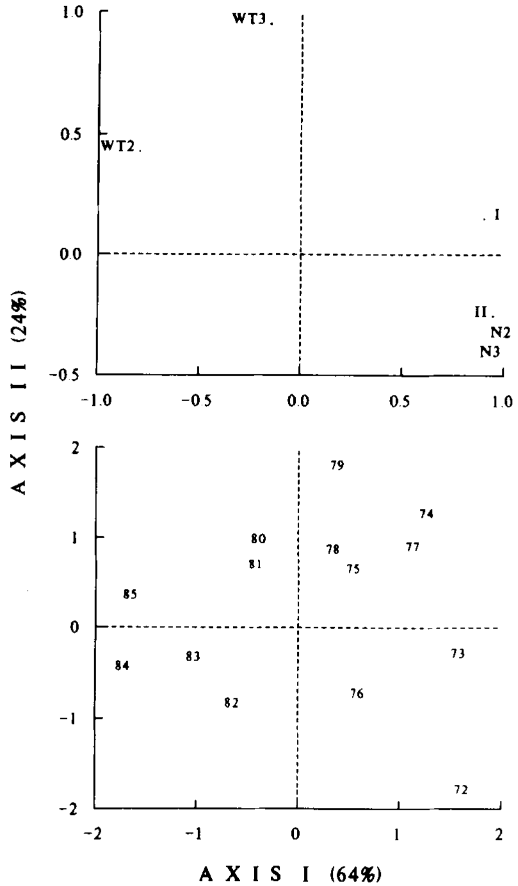

Fig. 8. Principal Components Analysis of individual body weight and numerical abundance data for Barents Sea capelin. The data is ordered according to year-class (1971–1985) for mean round weight (g) as 2 (WT$_2$) and 3 (WT$_3$) year-olds; the estimated numerical abundance (obtained by dividing the biomass by the mean individual weight) as 2 (N2), and 3 (N3) year-olds; the estimated total numbers of 2+ fish when the year-class itself was 1 year-old (I) and 2 years-old (II).

class (1971–1986) for mean round weight (g) as 2 (W_2), and 3 (W_3) year-olds; estimated numerical abundance as 2 (N2), and 3 (N3) year-olds; estimated total numbers of 2+ ages of fish when the year class was itself 1 year-old (I) and 2 years-old (II). The aim of this exercise is to examine individual growth (here reflected by weight-at-age, encompassing both size and time aspects of "growth") in the context of a given year-class's own experience of its own abundance and that of other fish in the population (see Fig. 8 for further details). The data matrix is thus primarily ordered by logical transition of age-groups from specific year-classes. The displacement of individual weight (W) and abundance (N) at opposite ends of Axis 1 (variance explained by axes 1 and 2 = 64% and 24% respectively, providing a ratio of 2.7 between the two) indicates a negative correlation, thus implying density dependence. Furthermore, a slightly better correlation is achieved using the estimates of "total" abundance, indicating that not only is the growth of a particular year-class dependent on its own abundance, but also that the additional abundance of the other year-classes present plays an important rôle. The PCA thus clearly denotes an overall density dependent growth in the Barents Sea capelin. As yet, it remains to determine exactly what proximate or ultimate factors steer "density" dependence in Barents Sea capelin.

The PCA data, and those analysed for demography and age at maturity, indicate the following scenario for Barents Sea capelin:

1. Weight at age is density dependent, especially in 2 years-olds.

2. At large stock size, as seen about the mid 1970s, the spawning stock tended to be composed of older fish, while decreasing stock size resulted in the "shedding" of the older age-groups of spawners. As capelin are semelparous, this resulted in a "bump-down" effect on the spawning

stock until only the two-year olds were left to carry the spawning stock.

3. This basic trend would have resulted in a greater proportion of maturing fish being taken for a given unit weight of TAC (total allowable catch), thus causing an increased relative exploitation of the spawning stock.

4. Faster growth rates and younger age at maturity are well-known factors which increase the production/biomass (P/B) ratio (Cole 1954; Banse & Mosher 1980; Peters 1983; Plante & Downing 1989), thus providing a compensatory turn-over of the stock. However, as capelin never mature at less than 2 years-old, the drastic decrease in the biomass and numbers of 2 year-old capelin seen from 1983 onwards would have exclusively been at the cost of the spawning stock. No further biological compensation was possible, and the stock collapsed.

5. Finally, irrespective of young or old age-at-maturity, plotting of data for weight against population size/density for 2 year-old Barents Sea capelin (see Fig. 7) provides a simple yet valuable indicator of trends in maturity, individual growth and population size. Thus, the key information regarding the population trends for the Barents Sea capelin may be deciphered from the 2 year-olds.

The deep-water prawn

The fishery landings of *P. borealis* from the Barents Sea have been registered from 1977 onwards, but redesigned, more dependable survey assess-

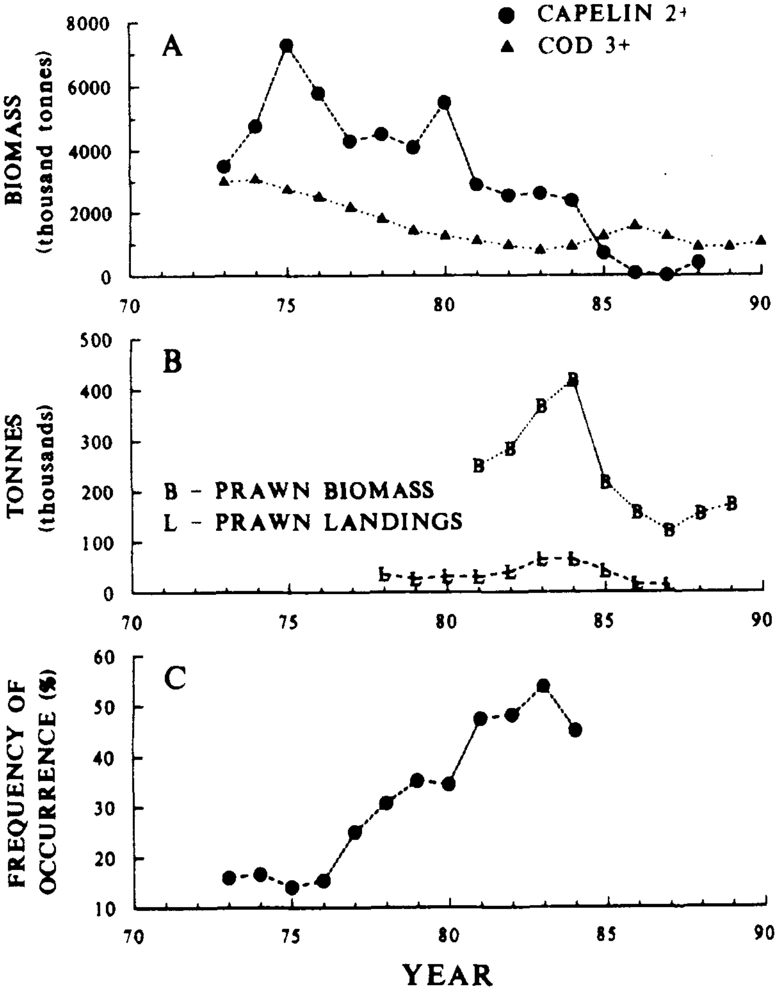

Fig. 9. A. Biomass of Barents Sea cod (at age 3+) and capelin (at age 2+). B. Fishery landings and biomass of deep-water prawn. C. Frequency of occurrence of deep-water prawn in cod stomachs. (Data sources: A & B after Anon. 1989b; C after Ponomerenko & Yaragina 1984).

ments of stock size were, however, first implemented in the early 1980s (Fig. 9B) (Tavares & Øynes 1980). Fishery landings varied from 27–65 thousand tonnes, peaking in 1983 and 1984 before decreasing sharply to only 14 thousand tonnes in 1987. The stock increased steadily between 1981 and 1984. A dramatic decrease was observed in 1985 (about 50% of 1984 level), which continued to reach a minimum in 1987. A slight increase in 1988 and 1989 has been ascribed to a reduction in predation by cod at the same time as many of the trawling grounds were closed for prawn trawling due to excessively large by-catches of undersized cod and haddock (Anon. 1989b).

The Norwegian-Arctic cod: an apex predator

Abundance and year-class strength. – A measure of the year-class strength of Barents Sea cod, presented as biomass at age 3+ between 1950 and 1988, is shown in Fig. 2. A series of oscillating peaks and troughs can be seen, based on the recruitment of strong and weak year-classes respectively. There is a highly significant trend of decreasing stock size over the period (see trend line in Fig. 2).

Between 1974 and 1983 there was a particularly marked decrease in cod biomass. The 1983 year-class initially gave the impression of being one of the stronger year-classes produced (Sætersdal & Loeng 1984), but there has been a steady reduction in the annual biomass forecast of this year-class prior to its recruitment to the fishery (Anon. 1989b); this had been partly ascribed to increased predation of the 1984–1987 year-classes by older cod, a higher incidence of dumping of undersized cod in 1986–1987, and reduced weight-at-age (see also Mehl 1989).

Food and changes in feeding habits. – The Barents Sea cod is well known as being a generalised, opportunistic carnivore, feeding on several types of prey whenever they are available (Zatsepin & Petrova 1939; Ponomarenko & Yaragina 1978). Compared with more southerly areas, the numbers of prey species recorded are relatively small, and stomach contents are dominated by few "key" prey (Brown & Cheng 1946; Novikova 1962; Ponomarenko & Yaragina 1978). Barents Sea cod is a particularly good example of Jones & Hall's (1973) description of a predator growing its way through increasing sizes of prey, as small cod have a preponderance of krill and prawns in their diet, while large cod become increasingly piscivorous, sometimes even being cannibalistic on younger cod (Ponomarenko & Yaragina 1978, 1979, 1984).

A comparison of the stock assessment data for cod, herring and capelin indicate that cod during the period 1950 to 1960 probably had a greater biomass of prey available before the herring stocks collapsed than afterwards. Unfortunately the quantity of capelin present in the Barents Sea when the herring were still in abundance is unknown. That capelin were present at that time is known from the catches of spawners on the coast of Finnmark (Ervik & Roman 1975). We can also safely say that the capelin stock sustained the combined exploitation of both cod and the capelin fishery after about 1970.

Stomach content data of Barents Sea cod have been collected by the USSR since 1947 (see Ponomarenko & Ponomarenko 1975; Ponomarenko & Yaragina 1978; Ponomarenko et al. 1978; Ponomarenko & Yaragina 1984). These data show a clear dominance of herring compared to capelin in the diet of large cod before 1970. From 1963 to 1969 the percentage occurrence of capelin increased steadily from about 10% to 50%, before decreasing to 30–40% during the first half of the 1970s (Ponomarenko & Yaragina 1978). The increase is probably associated with the demise of the herring and its replacement by capelin, while the succeeding fall may be a sign of the steep step-up of fishery landings seen about 1969 (Fig. 4).

Ponomarenko & Yaragina (1984) found that annual variations in the frequency of prawn occurrence in cod stomachs and in the biomass of cod between 1947 and 1983 were inversely correlated. Berenboim et al. (1986) have shown a clear negative correlation between cod biomass and prawn biomass in the period 1980–1985. Ponomarenko & Yaragina's (1984) data clearly show a steady increase in the frequency of occurrence of prawns in cod stomachs from 1975 to 1983 (Fig. 9C). The rationale behind this is that reduced cod stocks release predation pressure on the prawn stocks allowing them to increase. This is theoretically quite acceptable. However, it is paradoxical for the period 1975–1983; for as if we have been led to believe, the stock size of the capelin had not yet begun to decrease before 1983, and fisheries exploitation was relatively constant (see Hamre 1988), then there would have been an abundance of food for the cod. We believe that the trend in

Fig. 9C, representing a "switch" towards taking more prawn per unit biomass of cod, primarily reflects the effects of increasing food limitation on the Barents Sea cod stock. It agrees well with our postulation that a decline in the capelin stock started about 1975 (see trend-line in Fig. 2).

The birth of the relatively strong 1983 year-class of cod provided a renewed, massive predation on the Barents Sea ecosystem, with sharpened competition occurring between man and cod for a limiting resource. The 1983 year-class, and especially some of the following year-classes of cod have exhibited all the signs of food limitation, with some of the worst growth and condition indices registered for Barents Sea cod (Anon. 1988; 1989b; Mehl 1989).

The initially strong 1983 year-class "steam-rollered" its way up the food chain, with drastic consequences. As most of the cod stock of the Barents Sea became dominated by a single cohort the degree of size-related intra-specific competition increased greatly, with one prey item after another being reduced in turn as it became of the correct size to be eaten. The buffer of a stable age structure of a predator has been removed with dire consequences. In 1984, the prawn, already the target of increasing human exploitation, became the main prey of cod (mainly one year-old 1983 year-class). In 1985 and 1986, the 1983 year-class, having reached the necessary body size to feed piscivorously, began to eat large amounts of capelin (Anon. 1989b). However, in 1986 and 1987 the collapse of the capelin stock resulted in their almost disappearing from the diet of these normally piscivorous cod. Alternative crustacean food, such as amphipods, increased in relative terms, and cannibalism on younger cod became more prevalent (Anon. 1989b). Such "junk-food" consumption by large Barents Sea cod is rare (cf. Ponomarenko & Yaragina 1978, 1979) and indicates a general lack of fish as prey.

Conclusions

The data presented and analysed here indicate that the rise and fall of the Barents Sea capelin is best seen in the light of a multivariate scenario. The rise of the capelin fishery occurred after 1970 as a replacement for that aimed at the Atlanto-Scandian herring. The capelin fishery reached a mean annual yield of about 2 million tonnes between 1977 and 1984, in the absence of the recruitment of any major year-classes of the Barents Sea cod. The present analysis has detected a clear trend for increased weight at maturity (i.e. higher growth rates) related to a decrease in numerical abundance of the capelin stock. Being semelparous, this trend is correlated with a steadily decreasing age at maturity. Although such changes are partly compensated by increased turn-over rates of the capelin stock (i.e. increased $P/\bar{B}$ ratio), the approximately constant exploitation of the whole stock probably resulted in a relatively greater exploitation of the spawning stock compared to the immature stock. After 1984 the 2 year-old capelin decreased drastically in numbers and the spawning stock collapsed.

Was this collapse due to human exploitation alone? It is difficult to provide a categorical answer. We suggest that a decline in the capelin stock size and its demography was already evident from about 1976 onwards; the trend exhibited in Fig. 2 suggests an alarming rate of decline. Catch statistics, in the absence of fisheries inspectors stationed onboard, are notoriously poor at providing accurate statistics of fishing mortality. Although a complex climatically-driven chain of events has been proposed as steering the balance between cod, capelin and herring (Hamre 1988), we consider that the present evidence clearly implicates the capelin fishery as an important *contributory* factor to the lost potential biomass of the 1983 year-class of cod, and the lack of food for the higher trophic levels.

The closure of the capelin fishery in the Barents Sea, in the presence of a steadily reduced biomass of the 1983 cod year-class, will hopefully allow the capelin stock to rise relatively swiftly. In the absence of good recruitment of Atlanto-Scandian herring to the Barents Sea, the presence of capelin is vitally important for cod, seabirds and marine mammals. The ecological and fisheries evidence suggests that as capelin play such an important rôle as a forage species, their natural buffering capacity should be given a high priority and their production channelled for the benefit of the higher trophic levels, including the cod. Given the importance of climatic forcing functions, which are obviously beyond human control, on the multispecies relationships in the Barents Sea (Hamre 1988; Nilssen & Hopkins 1991), it seems reasonable to promote a policy of prudence and restraint in setting TACs for capelin. Capelin meet all the criteria of an r-strategist (see Horn

1978; Adams 1980), and as such will be difficult to regulate and manage in a fisheries context.

Acknowledgements. – This work was conducted as part of the project *Inter-relationships between prawn and cod*, supported in part by the Norwegian Fisheries Research Council (NFFR: Project No. I 500.003).

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