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Climatic variations and some examples of their effects on the marine ecology of Icelandic and Greenland waters, in particular during the present century

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Interactions between capelin *(Mallotus villosus)* and other species and the significance of such interactions for the management and harvesting of marine ecosystems in the northern North Atlantic

by

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Introduction

There are few if any environmental variables which exert such a profound influence on the development, habitation and behaviour of terrestrial life as the weather. Everyone is familiar with the daily, seasonal and annual changes in weather and we are all witness to their effects in one way or another. The close interaction between the atmosphere and the ocean is well known and information relating to climatological changes in general is, therefore, indicative of variations in sea temperatures. This is especially true for the uppermost layers of the water column, but with time the deeper layers are also affected.

Although the history of direct, systematic measurements of climatological variables and sea temperatures only goes back to the last century, it has proven possible to reconstruct climatic conditions in past ages and even eons. This has been done not only by sifting through old annals but also by the investigation of records imprinted in the earth itself, mainly in the form of erosion scars, sediment layers and glaciers.

On the basis of various estimates of sea temperatures, both obtained by measurements of the $^{18}O/^{16}O$ isotope ratio as well as by the study of biological communities in the sediment layers, McIntyre and associates (1976) published a paper showing the mean sea surface temperature distribution 18,000 years ago with a typical present day temperature distribution for comparison (Fig. 1). These illustrations indicate that during the last glaciation the sea temperature in certain areas of the northern Northeast Atlantic, such as south of Iceland, was many degrees lower than at present. However, it is clear that in times of glaciation all the oceans were not equally cooled and in some areas the temperature may even have been appreciably higher than at present.

A team of scientists headed by W. Dansgaard of the University of Copenhagen and S. J. Johnsen of the University of Iceland investigated changes in the $^{18}O/^{16}O$ isotope ratio in ice cores drilled through the Greenland icecap. One of their conclusions was that following the last glaciation there was a climatic warming which peaked some 4,500-7,000 years ago. The period 600-1150 C.E. was also relatively warm with a marked cooling towards the end of the 12th century. Since then climate remained cold throughout the 19th century (Dansgaard *et al.* 1971). Studies of variations in the length of the glaciers in Greenland and Iceland corroborated these findings (Thórarinsson 1974) as does available historic information about climatic and ice conditions in Iceland during the last millennium (*e.g.* Thoroddsen 1916; Bergthórsson 1969; Eythórsson and Sigtryggsson 1971).

Since the beginning of systematic monitoring of air and sea temperatures in the last century, the recorded changes have shown large spatial fluctuations. Thus, variations may have been relatively small when considering large parts of the globe, while they have been appreciable or even dramatic in boreal and cold-temperate regions. This is clearly demonstrated in Figure 2 (Hansen *et al.* 1983), which shows variations in 5 year running means of temperature in the period 1880-1980 for the globe as a whole as well as for the areas north of 64°N. The main feature of this change in climate over the Nordic Seas (*i.e.* the Barents and Norwegian Seas, Icelandic waters, the Irminger Sea, the Davis Strait and the waters off Labrador, Newfoundland and the east coast of the Canadian main-

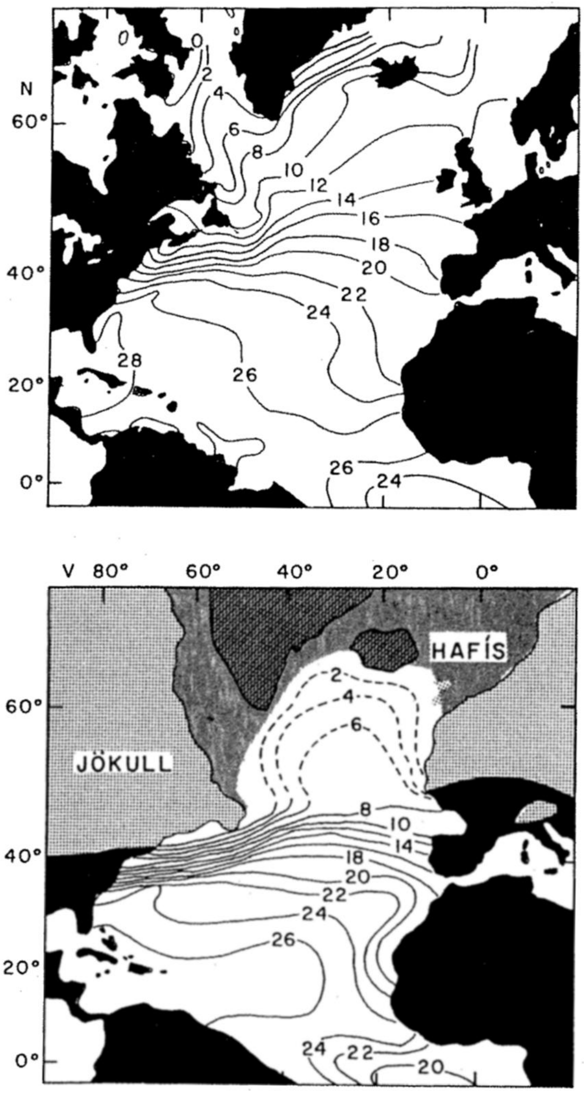

Figure 1. Mean sea surface temperature distribution 18,000 years ago (lower part) and at present (upper part). From Stefánsson 1991 (based on McIntyre *et al.* 1976).

land) is the rise in air temperature during the first decades of the present century with corresponding increase in sea temperature, decreasing extension of drift ice and a general improvement of climate, especially in the period 1920-1940. In the latter half of the 1960s the climate deteriorated suddenly with subsequent lowering of sea temperatures. Conditions improved again in the 1970s but have been more variable in the last two decades than during the warm period. An extensive review of the effects of the sudden deterioration of the marine climate in the latter half of the 1960s and its repercussions during the following years on various ecosystems in the North Atlantic area has been given by many authors and an overview for most of these by Jakobsson (1992).

These climatological changes are among the largest in recorded history of temperature changes. The purpose of the present paper is to review climatological variations in the Iceland-Greenland area and some of the associated hydrobiological changes during the present century.

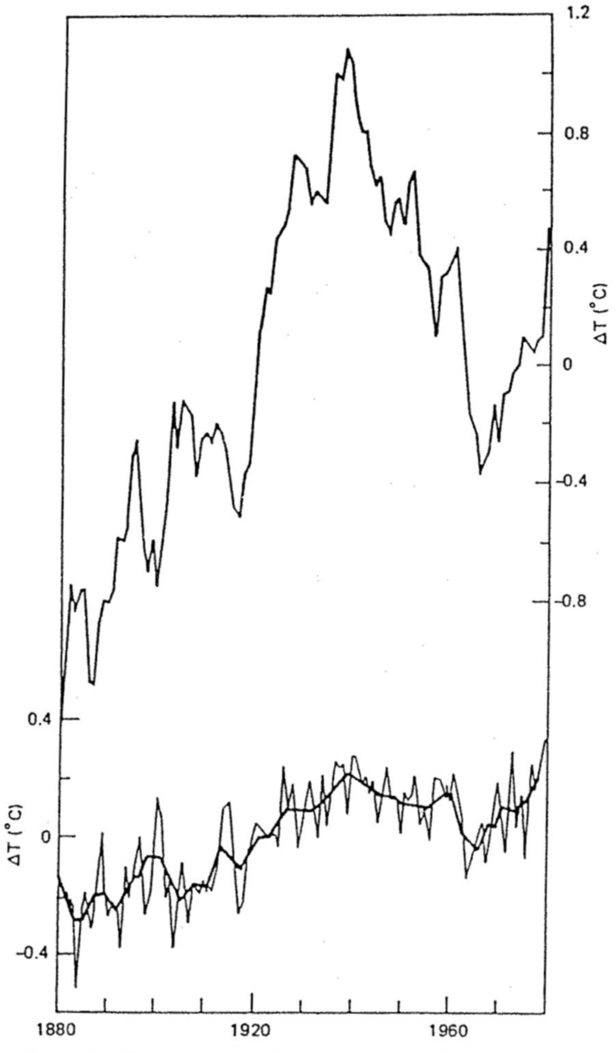

Figure 2. Deviations in air temperature (5 year running means) during 1880-1980 for the globe as a whole (lower curve) and north of 64°N (upper curve). From Stefánsson 1991 (based on Hansen *et al.* 1983).

Causes of climatic changes

A number of causes have been specified to explain changes in climate and consequently in sea temperature. The following main causes have been suggested:

1) Variations in radiation levels of solar energy due to sun spots or other reasons.
2) Variations in solar radiation reaching earth due to the variable distance of the earth from the sun.
3) Changes in the direction of the earth's axis of rotation. Measurements of permanent magnetic fields have shown that the earth's poles have moved in geological times, for example during the last 100 million years. Naturally, this involves a corresponding movement of the climatic zones.
4) Major volcanic eruptions and the impacts of meteorites colliding with the earth, thus increasing dust particles in the atmosphere and consequently reducing solar radiation reaching the earth's surface.
5) Increase in the concentration of certain gases, mainly carbon dioxide, in the earth's atmosphere, raising the mean global temperature by trapping heat emitted from the earth's surface. This is the so-called 'greenhouse effect' without which the average temperature at the earth's surface would be about 33°C lower than it now is, and our planet would be uninhabitable.
6) Large variations in wind direction and speed in certain areas of the globe due to changes in the relative position of high and low pressure areas and the pressure gradients between them.

It is by no means certain which of these causes best explain the climatic changes which have taken place in the past geological history, but with respect to the last 100 years the last two causes mentioned have been most frequently considered.

Greenhouse gases

Through ice core records it has been established that on a geological calendar, climate and greenhouse gases have been closely interactive (Lorius *et al.* 1990). It is now generally accepted that the concentration of anthropogenic greenhouse gases, in particular carbon dioxide but to a lesser extent other gases, such as methane, nitrogen oxides and chlorofluorocarbons, increased significantly in the atmosphere during the last 100-120 years due to human activities. A prime case in point is the ever increasing use of fossil fuels for energy production. Furthermore, the erosion of forests and land has led to reduced photosynthesis and decreasing carbon fixation by terrestrial vegetation. Measurements of radioactive carbon suggest that the concentration of atmospheric CO_2 increased in the period 1880-1980 from 296 to 336 ppm (Broecker and Peng 1982; Moran *et al.* 1986). Theoretically, this could have increased the temperature within the atmosphere by about 0.5°C which is consistent with the results from observations already presented.

It has been established that the continued increase of CO_2 in the atmosphere in 1880-1989 can account for about half of the CO_2 emissions from known sources in this period (Takahashi 1989). However, calculations, carried out by Tans *et al.* (1990), indicated that the difference was only in part accounted for by an increase in oceanic CO_2, and they suggested that while one of the reasons could be an overestimation of deforestation as indicated by recent satellite pictures, a more likely explanation is that vegetation and soil are accumulating carbon at an increased rate in response to an increased CO_2 concentration in the atmosphere. However, as pointed out by Siegentaler and Sarmiento (1993), some estimates of oceanic CO_2 concentrations have been up to twice as high as those reported by Tans *et al.*, and therefore, further research on the CO_2 cycle is obviously needed before it becomes possible to make a reliable prediction of future changes in atmospheric CO_2 and their effect on world climate. The large oceanic data sets to be procured through programmes such as JGOFS and WOCE will hopefully help resolve these questions.

Changes in atmospheric pressure distribution and wind direction

It seems that climatological changes during the present century, especially over the Nordic Seas, may be mainly due to variations in the wind regime. Thus, investigations carried out by Hesselberg and Birkeland (1943) indicated that the increase in temperature in the northern hemisphere during 1910-1935 had been concurrent with an increase in southerly winds. Research carried out in later years (Stefánsson 1962, 1969, 1985; Dickson and Lamb 1972; Dickson *et al.* 1975; Rodewald 1972) have revealed that after 1950, but especially in the decade 1960-1970, there was a large increase in the intensity of northerly winds over the Iceland and Greenland Seas. This was associated with an anomalous increase in air pressure of the Greenland high and a displacement of the track of the Iceland low to the south and east. This led to a widening of the ice belt and intrusion of polar water from the East-Greenland Current into the North Icelandic shelf area. The marked cooling of the sea area north of Iceland from 1965 to 1970 was in close accord with these changes and the same applies to the subsequent period after the early 1970s when warm and cold years have alternated (Dickson *et al.* 1975, 1988; Stefánsson and Jakobsson 1989; Malmberg and Kristmannsson 1992).

The trigger mechanisms of the observed variations in wind direction and intensity are not clear, but it has been pointed out that they may, at least in some instances, be connected with climatological events, involving ocean/air interactions, which have taken place in or near the equatorial parts of the ocean (Gordon *et al.* 1992).

Variations of sea temperatures in the last 100 years have been paricularly prominent near the oceanic polar front where horizontal changes in temperature are largest. This was demonstrated by the Danish oceanographer Jens Smed (1965) who showed that while sea temperature had increased in all of the North Atlantic area between 50°N and 68°N, the increase was appreciably larger in the northern part of the area than in the southern part. A comparison between air and sea temperature in the Icelandic area (Eythórsson 1949; Stefánsson 1954) revealed a close correlation and the same is true for the frequency of drift ice at Iceland and sea temperature in the shelf area north of Iceland (Stefánsson 1969). The available data on temperature variations in the deeper layers show that the intense cooling of the near surface waters north and northeast of Iceland between 1965 and 1970 reached down to 200 m depth east of Langanes (Stefánsson 1969) and to at least 100-150 m in the oceanic area between Langanes and Jan Mayen (Malmberg 1979). At the same time, however, there were little changes of temperature in the Atlantic water south and west of Iceland.

It is common knowledge that variations in temperature may change the ecology of the oceans. Such changes are at times quite obvious but on other occasions less so and even obscured almost completely by variations brought about by human or inter/intra-specific activities. In areas of large temperature gradients, of which Icelandic and Greenland waters are a prime example, the most obvious examples of the effects of temperature on the marine communities are variations in the distribution of species.

Examples of the effect of climatic changes on marine ecological conditions

Icelandic waters in 1900-1950

The Icelandic biologist Bjarni Sæmundsson (1934) described the many changes in the distribution of fish species which had recently taken place in the Icelandic area and were associated with the substantial warming up in the 1920s and the early 1930s (Fig. 3). One of his most striking examples of the effects of climatic warming was the mass spawning of cod off North and East Iceland in addition to the usual spawning off the south and west coasts and the drift of cod larvae across the northern Irminger Sea to Greenland observed by Danish expeditions on r/v Dana in 1931 and 1932 (Fig. 4). Secondly, Sæmundson stated that since 1928 capelin had become practically absent from their usual spawning grounds off South and West Iceland and spawned instead in large numbers at the north and east coasts as well as in the lagoon of Hornafjörður at Southeast Iceland (Fig. 5). Furthermore, Sæmundsson stated that in these years the cod had become much leaner than usual and attributed this to capelin not being available in the southern area in winter. While there is no reason to doubt Sæmundsson's observation of the poor condition of the Icelandic cod, such a situation could naturally have been brought about by low capelin abundance in general, high abundance of cod or both. Schopka (1993) has shown that the cod were abundant in the late 1920's. As will be discussed presently, the abundance of capelin at that time is difficult to quantify, even in relative terms. Other observational results, which Sæmundsson attributed to the rise in temperature, concern the apparent extension of the local herring spawning grounds, the occasional and sometimes frequent appearance of such marine fish species as the tunny, mackerel, saury pike and sunfish which previously had been rare or absent altogether.

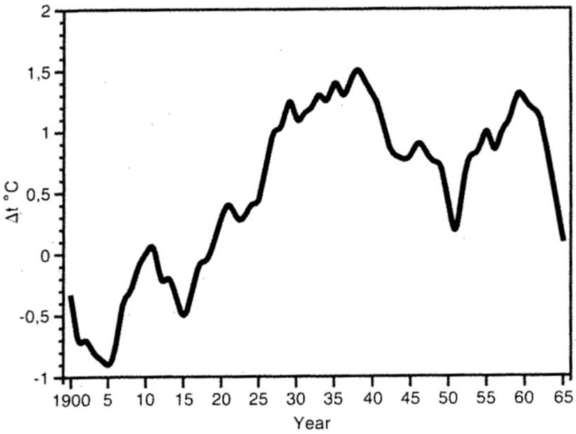

Figure 3. Sea temperature deviations (°C) at Grímsey, North Iceland. Five year running averages 1900-1965. Redrawn after Stefánsson 1969.

In 1948 another Icelandic biologist, Árni Friðriksson, gave an overview of what he termed boreo-tended changes in the marine vertebrate fauna of Iceland in the preceding 25 years. His studies confirmed the initial findings of Bjarni Sæmundsson and showed quite clearly how both the feeding and spawning grounds of cod and herring had increased and extended to the north and east of Iceland during the warm period. Friðriksson further described how the yield of the traditional north coast herring fishery diminished greatly late in this period concurrent with the displacement of the feeding area to the east which he related to unusually high temperatures in the area north of Iceland. At the same time the two local and previously

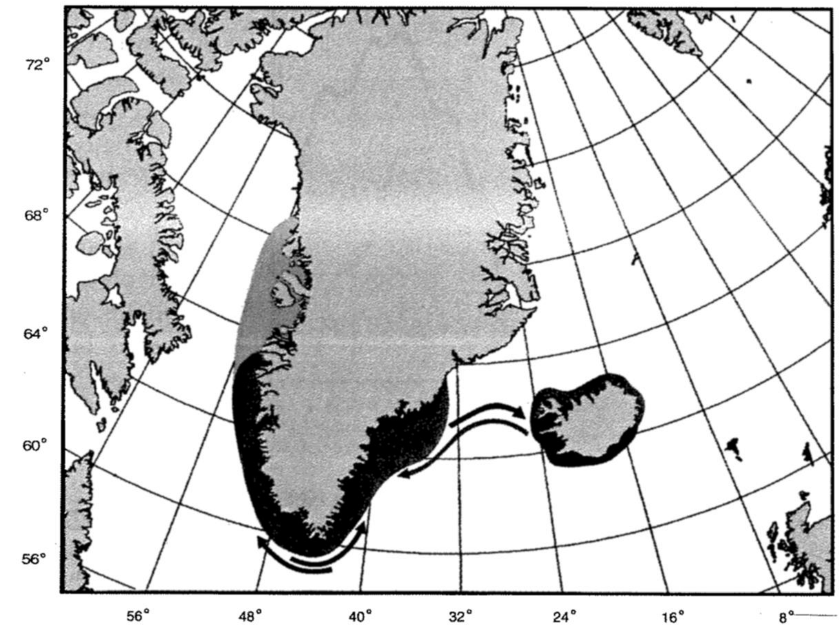

Figure 4. Extension of cod spawning grounds at Iceland (green area) following the climatic improvement of the 1920s and the observed drift of cod larvae (green arrow) across the northern Irminger Sea to Greenland. The figure also shows the increased distribution of cod at Greenland during the first decades of the present century: Before 1917 (red areas), 1918-1920 (green area), 1921-1927 (dark blue area) and after 1927 (light blue and pink areas). The red arrows indicate cod migrations. Based on Sæmundsson 1934; Hansen *et al.* 1935; Jensen 1939; Friðriksson 1948.

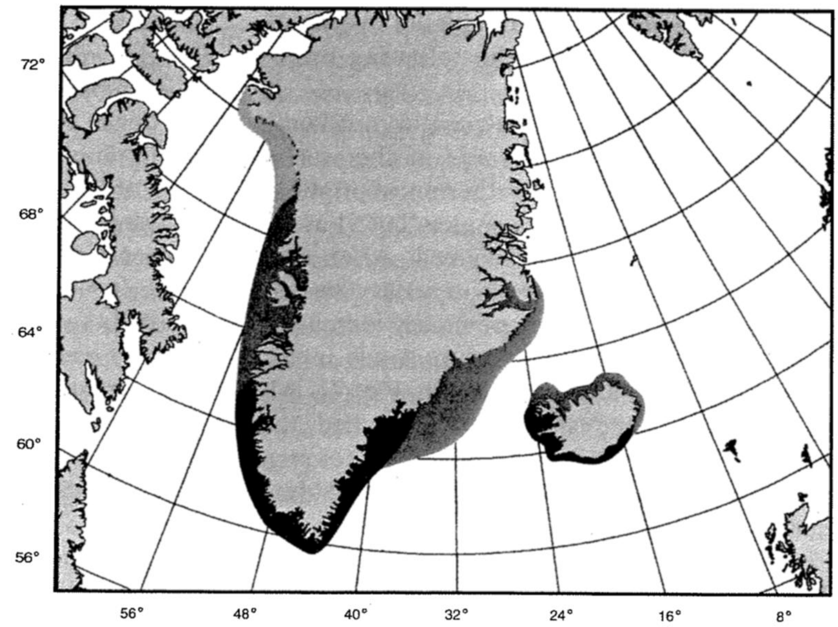

Figure 5. The changes of capelin spawning grounds at Iceland in the late 1920s and the 1930s. The red colour indicates the situation before 1920 and dark blue colour that during the height of the warm period. The figure also shows capelin distribution at Greenland before 1920 (red colour), the northward shift in distribution during the 1920s and 1930s (dark blue areas) and the northernmost records of capelin in the 1930s (light blue area). Based on Sæmundsson 1934; Jensen 1939; Friðriksson 1948.

small spring and summer spawning herring stocks proliferated and gave rise to a new autumn/winter fishery off the southwest coast. Furthermore, Friðriksson (1948) reported the appearance of five Atlantic species not previously recorded at Iceland, *i.e.* swordfish, spotted dragon, pollack, twaite shad and ray. Other fish which were rare during the cold period became quite common. Friðriksson listed no less than 14 species in this category, of which the mackerel and the tunny were typical.

Greenland waters in 1900-1950

The onset of climatic warming in the 1920s (Fig. 6) resulted in even more dramatic changes

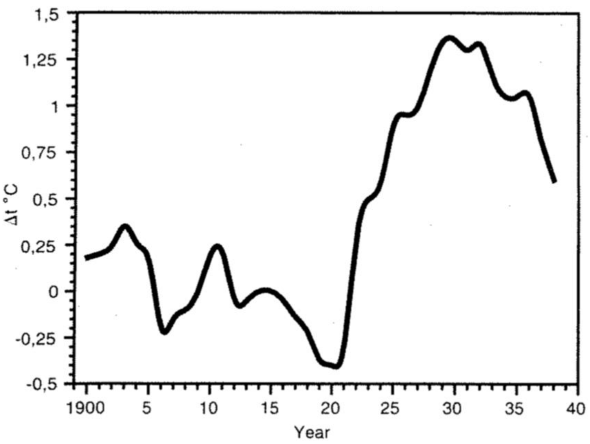

Figure 6. Sea temperature deviations at West-Greenland 1900-1938. From Anon. 1996, based on Smed 1965.

in the fish fauna of Greenland than in that of Iceland. A detailed overview of these changes was given by Professor Ad. S. Jensen (1939) which was summarized and updated by Tåning (1948) and includes *e.g.* the following examples.

In the last years of the 19th century, cod only occurred in scattered numbers in the waters near Cape Farewell, the southernmost promontory of Greenland (approximately 60°N) as indicated by red colour in Figure 4. After 1917 the cod gradually appeared over wider areas, as shown in Figure 4, and in obviously increasing numbers, as reflected in the rapid rise in the catch of cod in the late 1920s (cf. Fig. 7). Already in 1919 the species had reached the Godthaab fjord (64°N, Fig. 4, green colour), Holsteinsborg (67°N) in 1927 (Fig. 4, dark blue) and Disko Bay as well as the Umanak district (70°N) in 1928-1931 (Fig. 4, light blue). Finally, Jensen stated that the northernmost records of cod at West-Greenland were from Upernavik (72°45′N) as indicated by pink colour in Figure 4. In other words, the cod extended their distribution northward along the west coast of Greenland by some 600-800 naut. miles in the 20 years period between 1919 and 1939.

At East-Greenland cod were first noticed in the Ammasalik area in 1912 (Fig. 4, red colour) and began to appear in small schools about 1920. From 1923 cod were fairly common in this area and around 1930 they occurred everywhere along this part of the coast of Greenland (Schmidt 1931). This is indicated by green colour in Figure 4. There is little doubt that initially the cod drifted to Greenland as fry from Icelandic spawning grounds and migrated back to Icelandic waters as adult fish for spawning in winter (Fig. 4, red and green arrows respectively). However, it is equally clear that in the 1920s and especially in the 1930s, the cod migrated back and forth between East- and West-Greenland (Fig. 4, red arrows). During this period, cod were also able to reproduce in Greenlandic waters and did so in large numbers (Jensen 1926, 1939; Hansen 1949; Hansen *et al.* 1935; Tåning 1937).

Furthermore, Jensen (1939) reported that other members of the cod family, such as coalfish, haddock, tusk and ling, that previously had been rare or absent, also made their appearance at Greenland in the 1920s and 1930s. He also described how herring appeared in large numbers at West-Greenland in the 1930s and began to spawn and grow up there in the period July-September, mainly in the area south of 65°N. It is of interest that these herring spawned practically on the beach in the same manner as capelin in these waters. Presumably, the reason for this is that sufficiently high temperatures for spawning and larval development are only available in the near surface layer of West-Greenland coastal waters in summer. In 1937 the northernmost distribution of adult herring reached 72°N.

In the early 1900s the capelin were very common at West-Greenland between Cape Farewell and Disko Bay (Fig. 5, red colour), north of which they were unknown at the time according to Jensen (1939). In the 1920s and 1930s the centre of the capelin distribution gradually shifted northward, the species becoming sparse or altogether absent in its previous main area of distribution. By the 1930s the main spawning seems to have shifted north by some 400 naut. miles to the Disko Bay region (Fig. 5, dark blue colour), the northernmost record of mature capelin being from Thule (76°30′N) in 1935 and 1936 (Fig. 5, light blue colour) where

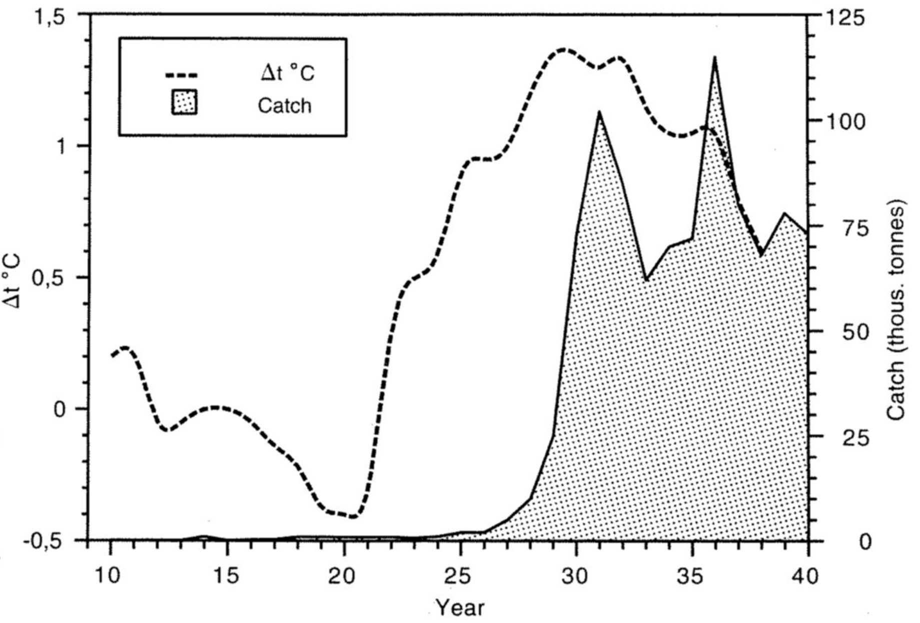

Figure 7. The catch of cod at Greenland 1910-1940 with sea temperature changes at West-Greenland superimposed. Based on Anon. 1996, 1996a.

the inhabitants did not recognize this strange fish (Jensen 1939). At East Greenland capelin gradually extended their distribution to the north as indicated by the blue colour in Figure 5 (Jensen 1939).

In summary, it is obvious that the dramatic improvement in climatic conditions in Icelandic and Greenland waters, that took place in the first half of the present century, brought about some of the most radical changes in quantity, distribution and reproduction of the fish fauna of these areas ever witnessed or documented. Needless to say, these changes had a very strong socio-economic impact in Iceland and Greenland, especially on account of the increased abundance and availability of the all important cod. A prime example is found in the increase of the cod catch at Greenland during the first half of the century (Fig. 7).

Greenland/Iceland in 1950-1996

The drift of 0-group cod from Iceland to Greenland continued intermittently in the 1950s and the first half of the 1960s, although on a much smaller scale than in the case of the super year classes of 1922, 1924 and 1945. The sudden and unexpected deterioration of climatic conditions in the Nordic Seas in the mid-1960s was keenly felt in Greenland. An example of this are the temperature changes in the Fylla Bank area shown in Figure 8 (Buch and Hansen 1988; Anon. 1996). At the same time, the drift of 0-group cod from Iceland to Greenland ceased completely for a number of years and has since then only been registered twice, *i.e.* in 1973 and 1984 (Vilhjálmsson and Friðgeirsson 1976; Vilhjálmsson and Magnússon 1984; Schopka 1993).

Another result of the deterioration of the marine climate in the 1960s was the large reduction in the total cod catch in Greenland waters from about 240,000- 470,000 tonnes annually in the period 1952-1968 to 75,000 tonnes in 1973 (Fig. 8). From 1973 to 1993 the average annual catch of cod in Greenland waters was about 55,000 tonnes with peaks just exceeding 100,000 tonnes around 1980 and 1990. These peaks were generated by the year classes of 1973 and 1984, the young of which drifted in large numbers from Iceland to Greenland. Prior to these year classes entering the fishery at Greenland, there were very few cod in these waters, particularly in the latter case. As shown in Figure 9 there are practically no cod at East- or West-Greenland at present (Anon. 1996a). It seems, therefore, that in spite of some improvements of climate after the decline of the late 1960s and

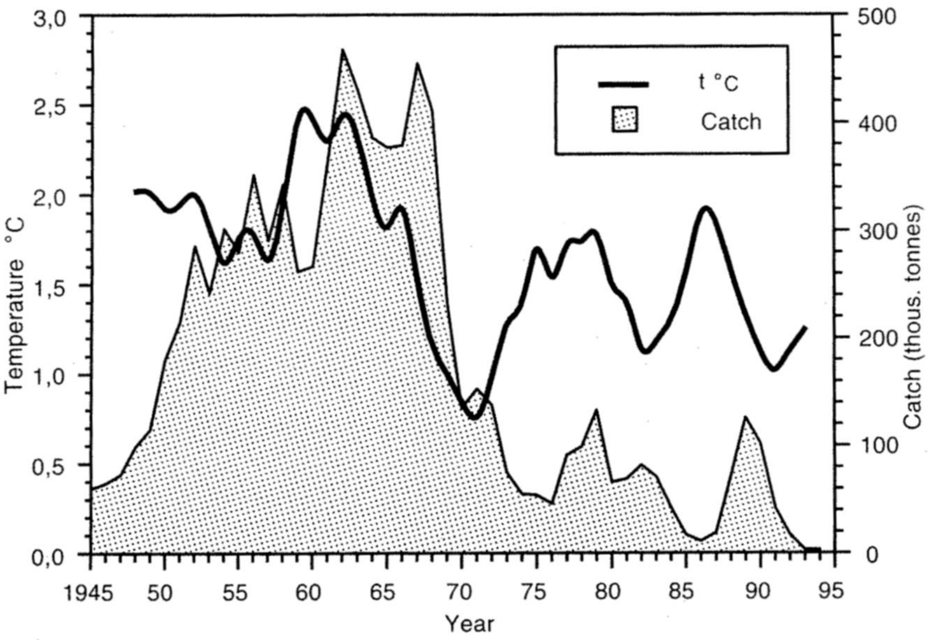

Figure 8. The catch of cod at Greenland and temperature changes on the Fylla Bank as 5 year running means 1945-1995. Based on Anon. 1996, 1996a.

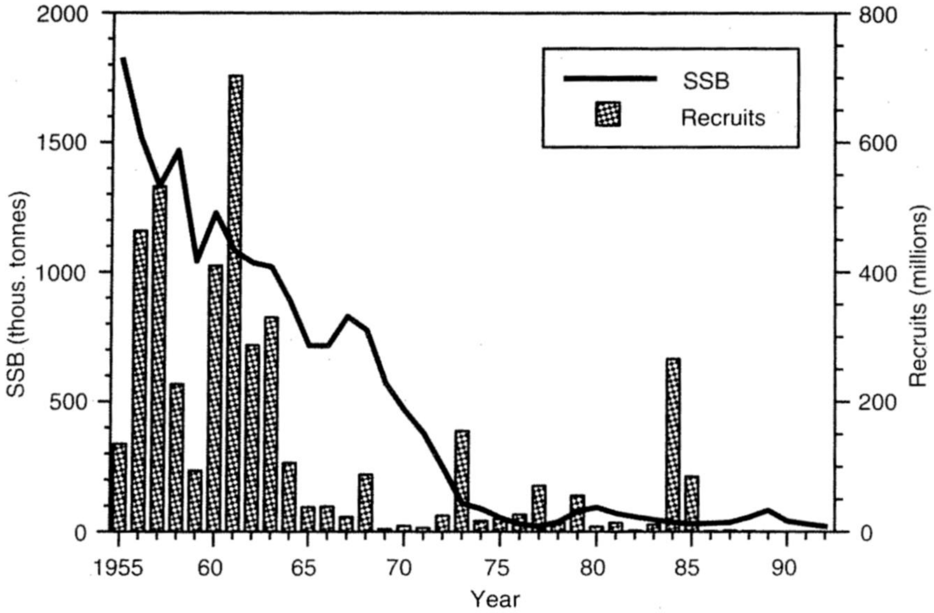

Figure 9. The changes in spawning stock abundance (SSB) of cod and recruitment at Greenland 1955-1992. From Anon. 1996a.

the early 1970s, the cod have generally not been able to reproduce in Greenland waters, and certainly not in the last decade.

At Iceland the climatic deterioration in the latter half of the 1960s was reflected in increasing drift ice, low air temperature and a marked drop in temperature and salinity in the north Icelandic area. The changes in temperature and salinity in spring in the area off the central north coast of Iceland since 1952 (Anon. 1997) are shown as 5 year running averages in Figure 10. The substantial drop in temperature and salinity had wide ranging repercussions on the ecology of these waters. Thus, the increased distribution of cold, low-salinity polar water prevented vertical mixing and renewal of nutrients and led to a large reduction of primary production (Thórdardóttir 1976, 1977, 1984).

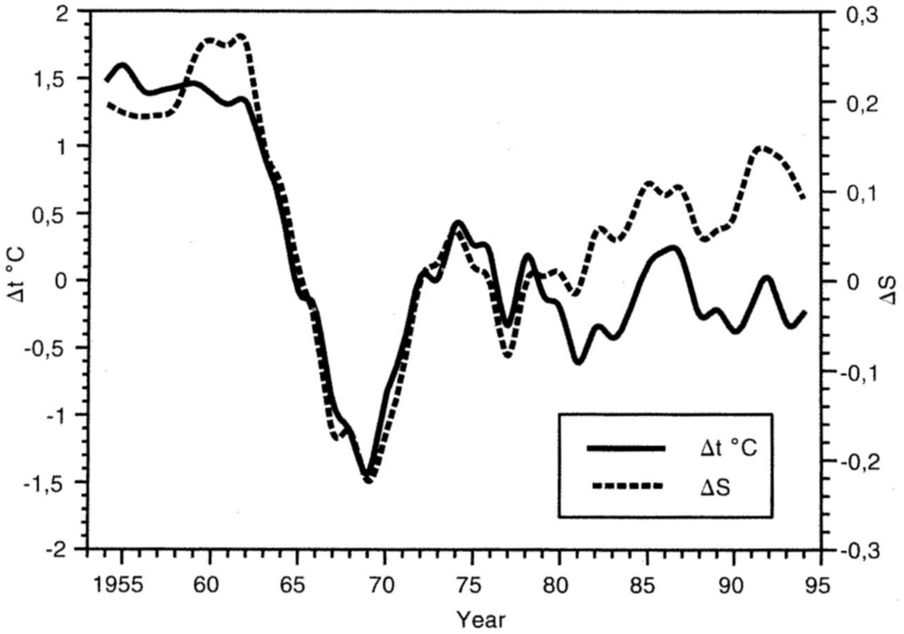

Figure 10. Deviations in temperature and salinity off the central north coast of Iceland. Five year running means 1952-1996. Based on Anon. 1997.

This in turn greatly reduced the zooplankton community which furthermore changed in species composition from boreal to arctic nature (Jakobsson 1978; Astthorsson *et al.* 1983). With regard to the Atlantic copepod species *Calanus finmarchicus,* one of the most important food items of herring in the Nordic Seas, the north Icelandic area in fact became a veritable desert during the latter half of the 1960s. Indeed it seems that in spite of a somewhat improved climate after the early 1970s, of which salinity is probably a better indicator than temperature since it is less sensitive to the effects of variations in observation time during surveys conducted in late May and June (Ólafsson pers. comm.), the *Calanus finmarchicus* community of the north Icelandic area may not yet have recovered completely.

In the Icelandic area herring was undoubtedly the fish species which was most affected by the environmental adversities (*e.g.* Jakobsson 1978, 1980; Dragesund *et al.* 1980). This is not surprising since herring are plankton feeders and in Icelandic waters near their limit of distribution. Thus, the traditional feeding migrations of the Norwegian spring spawning herring stock to the north Icelandic area (Fig. 12a) stopped completely when the Atlantic plankton community collapsed. In 1965-1966 the oldest herring were instead forced to search for their food in the Norwegian Sea near the eastern boundary of the East Icelandic Current, *i.e.* some 150-200 naut. miles farther east than in the years before (Fig. 12b). In 1967-1968 the stock migrated all the way to Spitzbergen during summer (Fig. 12c). The same was true for 1969 when the overwintering grounds also shifted from 40-80 naut. miles east of Iceland to the west coast of Norway (Fig 12d). The Norwegian spring spawning herring stock collapsed in the latter half of the 1960s (Dragesund *et al.* 1980) and the feeding migrations to the west into the Norwegian Sea stopped altogether (Fig. 12e).

As shown in Figure 11 (Anon. 1996b), the abundance of the Norwegian spring spawning herring stock has increased dramatically in the last few years. This process has, however, taken about a quarter of a century despite a ban on commercial fishing for two decades. And it is only in the present decade that these herring have resumed some semblance to their previous feeding pattern (Fig. 12f). At the moment the Norwegian spring spawning herring still overwinter in two fjords in the Lofoten area (Fig. 12f). When and if they revert completely

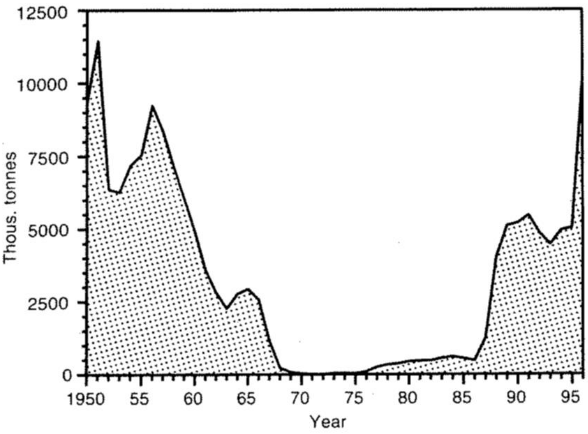

Figure 11. Changes in stock abundance of Norwegian spring spawning herring 1950-1996. From Anon. 1996b.

to the traditional distribution and migration pattern, is anybody's guess.

Little can be said about changes in the migrations of the two local herring stocks. However, like the Norwegian herring, the Icelandic spring and summer spawning herring stocks both collapsed in the late 1960s in tune with the adverse environmental conditions of the area (Jakobsson 1980). Whether this relationship is causal directly or indirectly is, on the other hand, open to question due to the very large fishing pressure which all of these stocks were subjected to. The fact remains, however, that the Icelandic summer spawning herring made a slow but complete recovery beginning with a slight climatic improvement in the early 1970s and continuing since then in spite of more variable climatic conditions than in the period prior to the late 1960s. After the stock recovered, it has produced some very large year classes, two of which in the relatively cold years of 1988 and 1989 (Jakobsson *et al.* 1993). On the other hand, the Icelandic spring spawning herring stock has not recovered yet and is *de facto* no longer present in Icelandic waters. It seems reasonable to agree with Jakobsson (1980) that the conditions of the Icelandic marine environment are marginal for the self-propagation of a spring spawning herring stock, and that this stock would probably have collapsed or declined to a very low level in the late 1960s, even without a fishery.

Due to the comparatively short series of regular observations, there is not much that can be said about the the reactions of capelin, the other main plankton feeding species of the Icelandic area, to climatic changes since the 1950s. It has been related how capelin no longer migrated to their previous spawning grounds at South and West Iceland in the 1930s and the first half of the 1940s (Sæmundsson 1934; Friðriksson 1948). After that, however, capelin reappeared to spawn in these locations and since then have done so in most although not all years. The observed variations seem to coincide with low spawning stock abundance and, possibly, with variations in current velocities off the south coast of Iceland brought about by weather conditions (Vilhjálmsson 1994).

About 20 years ago, an attempt was made to gather information in order to discover whether capelin spawning migrations during the warm period had been different from those after the climatic deterioration in the mid-1960s (Vilhjálmsson, unpublished material). For this purpose, a large number of small craft fishermen, operating from ports on the west and north coasts of Iceland, were interviewed and asked about the timing and magnitude of capelin spawning migrations in their respective localities in the period 1935-1970. The idea was to compare such information with hydrographic data as well as data on wind direction and wind stress which, as well known, will affect the speed of the coastal current running in a clockwise direction around Iceland. While it was fairly obvious from the answers that capelin migrations had been quite variable in abundance and timing, both in the western and northern areas, it was equally clear that these variations could not be sensibly quantified and only be dated on occasions when such variations could be referred to other occurrences, *e.g.* some important sociological event.

While the growth rate of capelin has shown a strong correlation with temperature and salinity variations in the north Icelandic area in the past 25 years (Fig. 13), this relationship probably describes feeding conditions rather than the direct effect of temperature or salinity (Vilhjálmsson

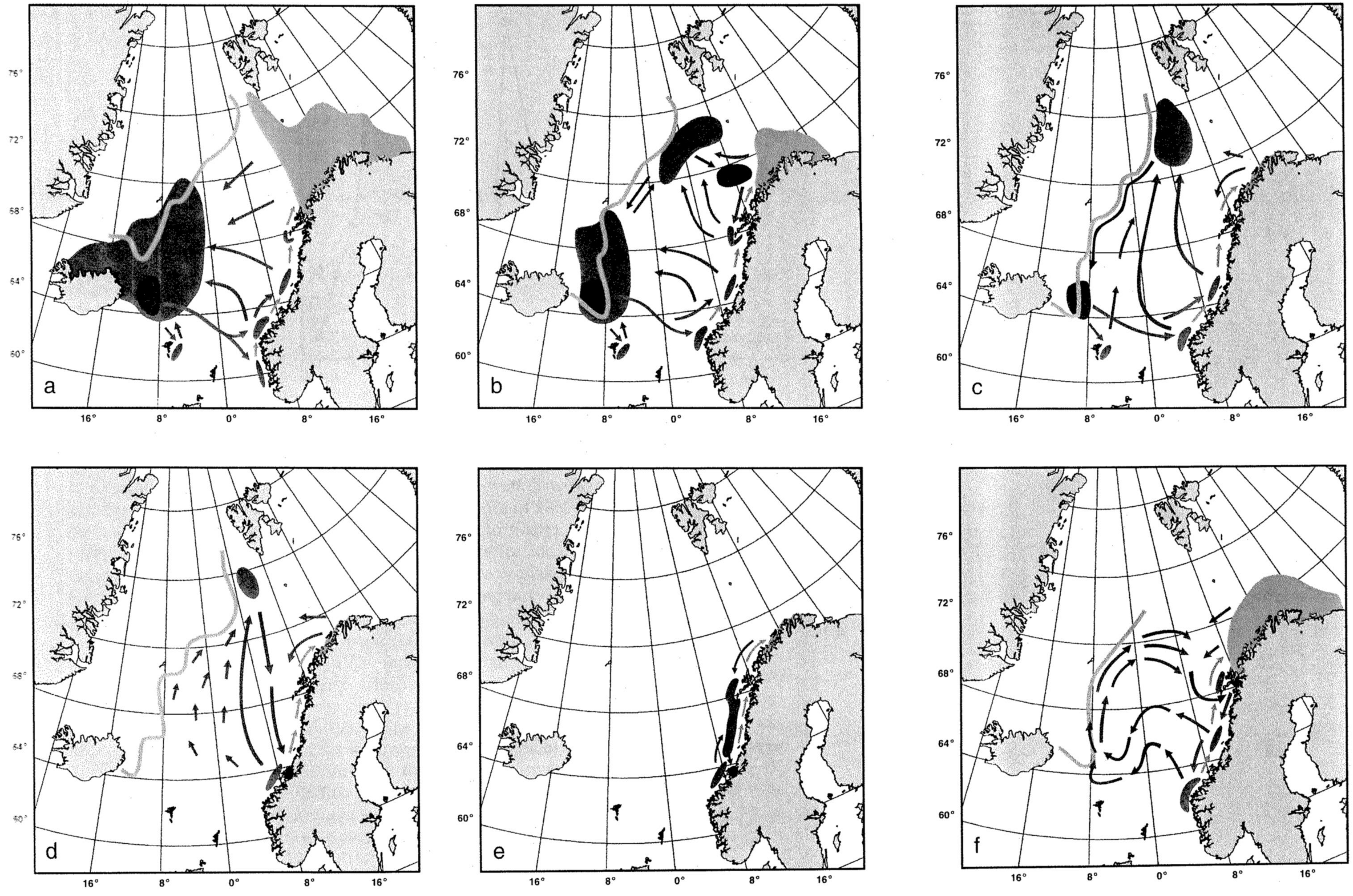

Figure 12. Migration patterns of Norwegian spring spawning herring. a) traditional; b) 1965-1966; c) 1967-1968; d) 1969; e) 1972-1986; f) 1995. Modified after Anon. 1970, 1995a; Røttingen 1990. Dark blue: spawning areas; light blue: nursing area; green: feeding area; red: wintering area. Green arrows feeding migrations; red arrows: migrations to wintering areas; dark blue arrows: spawning migrations; light blue arrows: larval drift. Continuous light blue line: the 2° isotherm at 50 m depth, indicating the approximate boundary af arctic water.

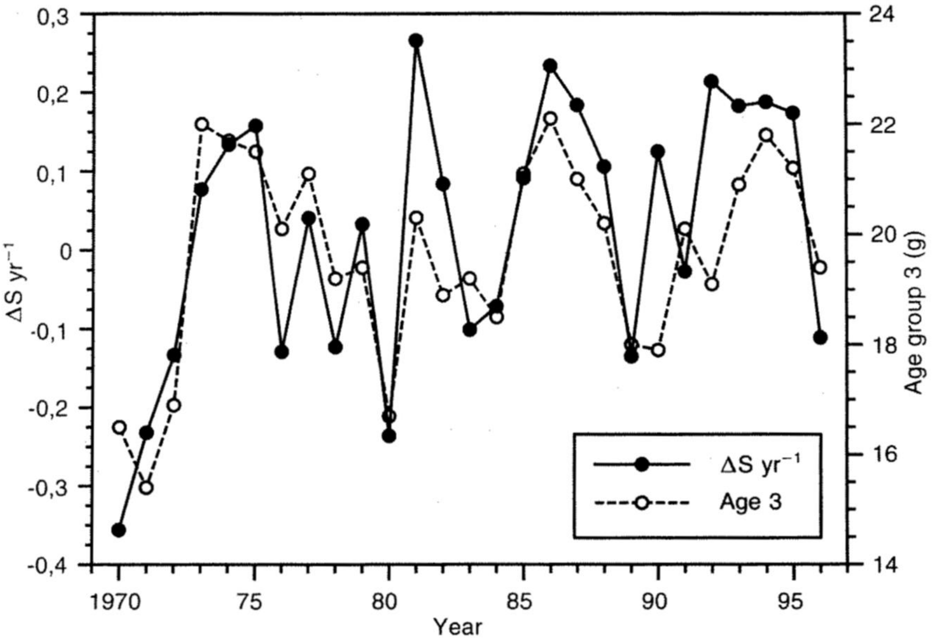

Figure 13. Mean weight of 3 years old capelin in January and salinity deviations off the central north coast of Iceland in spring of the previous year. From Vilhjálmsson 1994.

1994). However, the results of attempts to relate recruitment of the Icelandic capelin stock to physical and biological variables, such as salinity, temperature and zooplankton abundance, have been ambiguous.

The Icelandic stock of cod has been much in the limelight in recent years due to its low abundance and restrictions of the allowable catch (Anon. 1996c). Recently, the abundance of and recruitment to this cod stock has been retrospectively assessed as far back as 1926, including fish migrating from Greenland which, at least in the 1920s and in later years, were probably of Icelandic origin (Schopka 1993). The results are illuminating in view of the large variability in climate and fishing pressure that took place during this period. In the first half of the period the spawning and consequently the fishable stock was very large, the spawning stock fluctuating between about 1.0 and 1.7 million tonnes. Beginning in the late 1950s, there followed a rapid decline in recruitment and stock abundance, reaching an all time low in the last decade since no large year classes have been produced for 12 consecutive years. Concurrent with the environmental adversities of the late 1960s and again in the late 1970s there was a reduced recruitment followed by fairly good year classes, while no good year classes have been produced since then in spite of greatly improved climatic conditions in comparison with those of 1966-1971 and 1979.

In Figure 14 the spawning stock biomass of the Icelandic cod and the resulting recruitment are presented as 5 year running averages beginning in 1930 and ending in 1995. Even with this smoothing the highly variable recruitment is clearly distinguishable as is the effect of single large year classes or adjoining groups of good year classes on the spawning stock 7-10 years later. However, of special interest is, on the one hand, the apparent irregularity of recruitment fluctuations in the first half of this period when the stock was very large, and on the other, the regular peaks at about 10 years intervals in the latter half of the period when the spawning stock biomass was much lower. Although the first two peaks and troughs in the cod recruitment at Iceland since the 1960s are in phase with variations of temperature and salinity in the north Icelandic area in spring, recruitment variability during the last 15 years is not, except to a very small degree, directly correlated to such environmental variables. In view of the gradually improving climatic conditions in the last one and a half decade, the historic recruit-

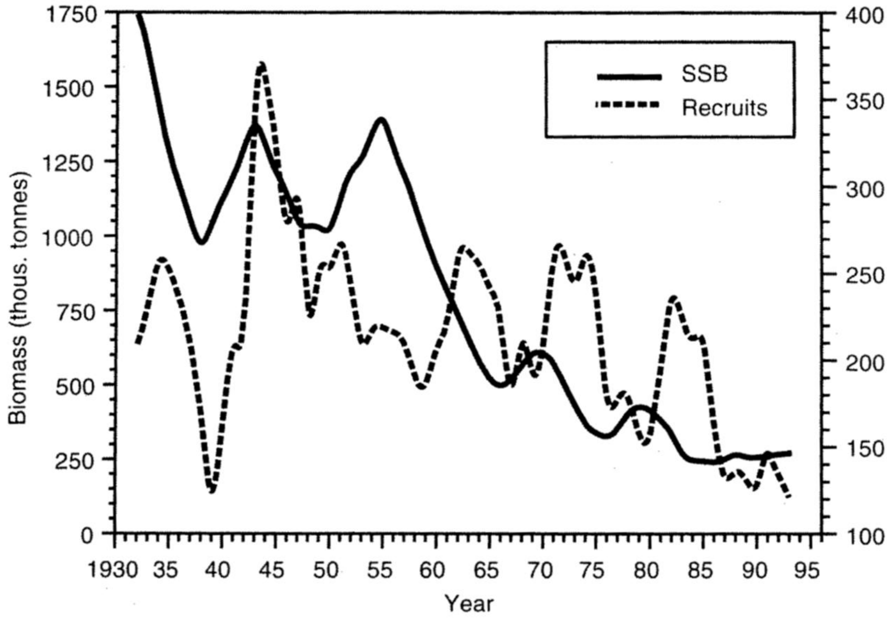

Figure 14. Five year running averages of spawning stock biomass (SSB) and recruitment of the Icelandic cod stock during 1930-1995. Based on Schopka 1993, 1994; Anon. 1996c.

ment series, as well as the fact that a small parent stock, has been known to produce good year classes, one would have expected better recruitment than that which actually materialized.

As mentioned earlier, the Icelandic summer spawning herring stock collapsed in the 1960s. The collapse was without doubt caused by excessive fishing pressure in times of adverse environmental conditions. Although the herring and cod stocks at Iceland have quite differrent life cycles and are at different levels in the food chain, they are both relatively long-lived species with variable recruitment. It is therefore of interest to compare the developments of these two stocks during the last few decades. As shown in Figure 15, herring abundance increased in the 1950s and early 1960s as a result of some large incoming year classes. In the latter half of this period the fishing mortality skyrocketed and the stock was reduced to an extremely low level, 10,000-20,000 tonnes at most. Concurrent with improved climatic conditions, the small spawning stock produced two fairly good year classes in the early 1970s and the stock began to recover. Since then, the Icelandic summer spawning herring stock has grown beyond its recorded historic maximum size and is still on the increase. At the same time, recruitment has increased dramatically, good year classes having become more frequent and larger than previously.

What then is the most likely reason for the failure of the recruitment to the cod stock and the success of the summer spawning herring? Figure 16 shows the fishing mortality of these two stocks in past decades. The two graphs are indeed very different. After World War II, the fishing mortality of the cod stock increased steadily until in the early 1970s. At that time, Iceland finally won the so-called 'cod war' and foreign fishing stopped almost overnight. There was a subsequent large drop in fishing mortality which unfortunately could not be maintained at the new and much lower level as compared to previous years. New and more advanced fishing vessels were built and in a few years fishing mortality increased to the previous high level and beyond it. After the collapse of the herring stock, on the other hand, fishing mortalities have consistently been kept at a low level.

The stock/recruitment relationship in the Icelandic cod over the last 4 decades is statistically quite vague due to the large variability of the data. However, Stefánsson (1992) has pointed out, that although the stock/recruitment plot looks like a random scatter of points the fact remains that the probability of poor

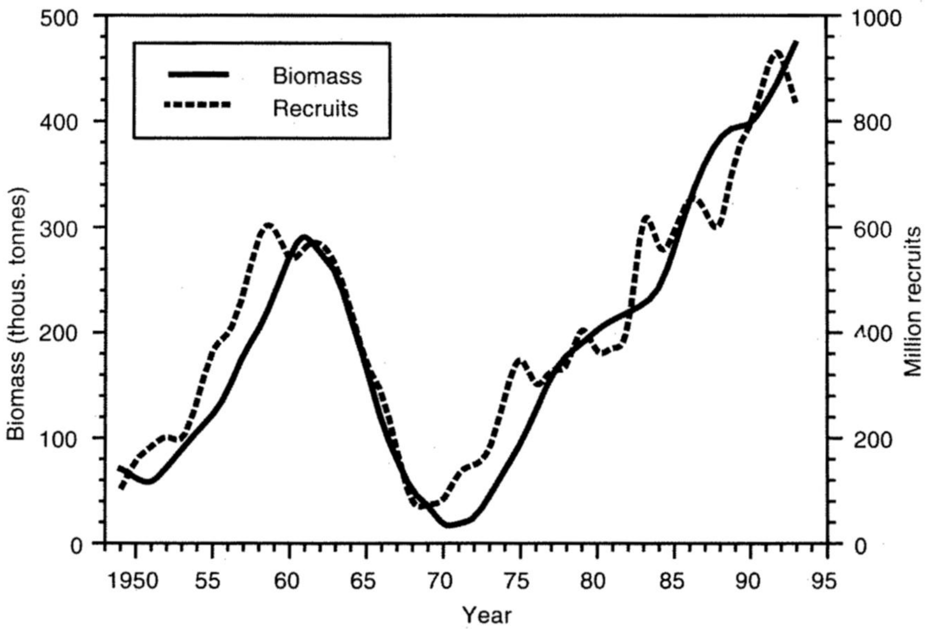

Figure 15. Five year running averages of adult stock biomass and recruitment of the Icelandic summer spawning herring 1950-1995. Based on Anon. 1996b; 1996c.

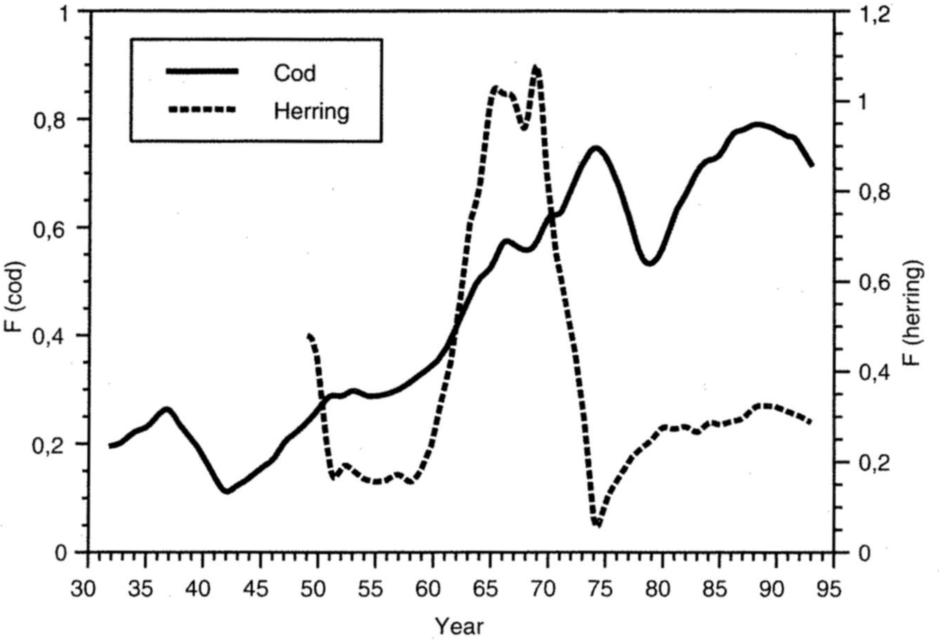

Figure 16. Five year running averages of of fishing mortalities (FS) of Icelandic cod and summer spawning herring 1930-1995. Based on Anon. 1996a; 1996b.

(below 150 million) recruitment is 45% when the spawning stock is below 500 thous. tonnes but decreases to 17% at larger spawning stock size. He concludes that, since this comparison is statistically significant ($\chi^2 = 6.4$, $p = 0.01$), the data contain indications of increased likelihood of poor recruitment at lower levels of spawning stock abundance than when the stock is large. However, as Stefánsson also points out, it is possible that environmental changes in the last part of this period have had the effect of reducing both spawning stock biomass and recruitment. But in view of the improved climate after 1970 and the large increase of fishing mortality (F) during the period 1950-1990 from about 0.3 to 0.8 (Fig. 16), the latter explanation does not seem very convincing.

It has long been suspected that year class size may not simply depend on the quantity of spawners but to a degree also on their quality as well as the spatial and temporal distribution of the spawning. Recently, studies have been carried out of the possible influence of the age structure of the mature part of the Icelandic cod on recruitment. This was done by conducting experiments on larval survival from different age and size groups of parents (Marteinsdóttir 1994) and by an analysis of existing historic data on variations of the age structure of the spawning stock and the resulting recruitment (Marteinsdóttir and Steinarsson 1996). The tentative findings of these studies appear to support the theory that a fairly broad age structure of the cod spawning stock enhances its possibilities for producing large year classes for any given condition of the environment. The spawning products of the older fish are indeed of higher quality than those of younger and smaller individuals and a wider spread of spawning in space and time results when many age and size groups are present in the stock.

In view of Marteinsdóttir's findings, the failure of the Icelandic cod stock to produce year class above average in the last 12 years is perhaps not so surprising. On the graph in Figure 14 it is seen how the recruitment peaks are generally reflected in the spawning stock biomass some 7-10 years later. However, the last recruitment peak, due mainly to the rich year classes of 1983 and 1984, did not produce a noticeable increase in the 5 year running means of the spawning stock biomass. This indicates that the fishery had taken most of these fish before they could mature and spawn even once, let alone many times. This is in accordance with changes in the mean age of this cod stock which has dropped to an all time low in the last dedade. In other words, it seems that regular peaks of recruitment, generated by the last large year class or group of year classes, appear when the spawning stock is reduced to below some 500,000 tonnes. Under the large fishing pressure at the presently low spawning stock abundance of about 200,000-250,000 tonnes, this self-generating effect is lost due to the scarcity or lack of older age groups at unnaturally low stock abundance and the production of a large year class becomes something of a chance occurrence, even under favourable environmental conditions. On the other hand, due to the much lower fishing pressure on the herring, the stock increased and consequently a much larger part of herring year classes have been allowed to reach high age. Therefore, the spawning stock of the Icelandic summer spawning herring has consisted of many age groups in the past 10-15 years.

Concluding remarks

There is no doubt that variations of the marine climate can have large, long-lasting and far-ranging effects on the ecology of the seas. As described above these effects are naturally largest in border areas where species are near their limit of of distribution. In such cases, both distribution and reproductive success/abundance may be radically changed.

Some of the changes in the ecology of the sea area around Iceland and Greenland are obviously beyond human control and would have been felt and observed in one way or another irrespective of whether or not a fishery had been conducted at the time. Special cases in point are changes in the migrations of the Norwegian spring spawning herring and the state of the cod stock(s) at Greenland.

It is also noted that the Norwegian spring spawning herring did not resume their westward feeding migrations to the Norwegian Sea for a quarter of a century in spite of the fact that hydrographic conditions improved again in the 1970s. The reason for this is the stock collapse which was brought about by overfishing, both of adult but in particular of juvenile small and fat herring. There was simply so little herring in the 1970s and 1980s that they did not need to undertake large migrations to sustain the stock.

However, there are other cases of which the Icelandic cod and summer spawning herring stocks are typical examples. Through excessive fishing the former stock has been reduced to such a low level that it probably has been unable to respond to the improved climatic conditions after the environmental adversities of the period 1966-1971. The summer spawning herring, on the other hand, has been harvested at a modest rate since the stock collapse in the late 1960s and early 1970s, and for that reason, been able to make use of the improved conditions in the years that followed.

Finally, we may ponder the case of the 'northern cod' of Labrador and Newfoundland waters. This huge stock, which in its heydays must have counted millions of tonnes, has in recent years been reduced to practically zero. Indeed, a complete fishing ban, imposed in 1992, has not significantly improved the situation and the expected increase in abundance has not materialized (Fig. 17). There are two main reasons for the collapse of this cod stock. One is the uncontrolled and excessive fishing during the 1960s and the first half of the 1970s, resulting in skyrocketing catches. The other reason relates to the fact that after Canada extended its jurisdiction to 200 miles and reduced fishing effort in the late 1970s, recruitment proved to be much below expectations. The Canadian scientists did not realise what had happened until

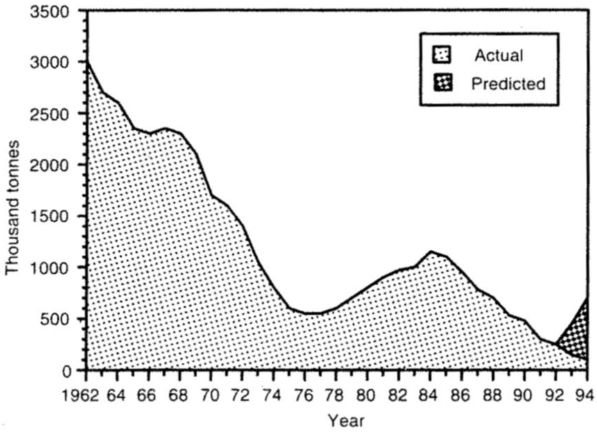

Figure 17. The abundance of adult northern cod 1962-1994. The dark area indicates the expected increase of stock abundance following the fishing ban enforced in 1992. It did not materialise. After Harris *et al.* 1990; Anon. 1995.

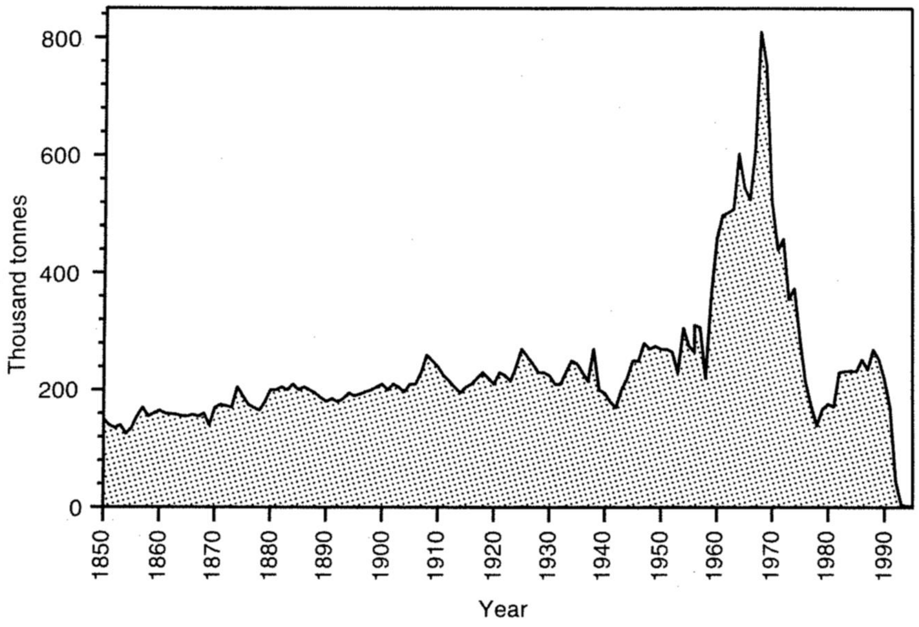

Figure 18. The catch of northern cod off Newfoundland and Labrador during 1850-1994. After Harris *et al.* 1990; Anon. 1995.

around 1990, by which time it was too late (Harris *et al.* 1990; Anon. 1995; Shelton *et al.* 1996).

It is illuminating to look at the catch series for the 'northern cod', dating back to 1850 (Fig. 18), and ponder why annual catches to the tune of 150-350 tonnes for more than a century do not seem to have affected the propagation of the stock, even during the very adverse environmental conditions during the last decades of the 1800s and the first two decades of the present century. In all probability the 'northern cod' reacted simply by shifts in distribution to the south and west during exceptionally cold periods, repopulating its previous distribution areas as conditions improved again. Due to the extremely low stock abundance it is unable to do so with sucess at the preaent time.

Therefore, our lesson must be that unless mother nature has the necessary material to work with, she may be unable to respond to and repair the damage inflicted by herself or by human activities.

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Interactions between capelin *(Mallotus villosus)* and other species and the significance of such interactions for the management and harvesting of marine ecosystems in the northern North Atlantic

Introduction

In the not too distant past the management of living marine resources was usually based on single species models where the key input parameters were overall stock abundance in number and weight at age, the biomass of the spawning stock, estimates of recruitment and natural as well as fishing mortalities. Furthermore, some account of likely changes in the physical marine environment in the immediate future, usually in terms of temperature and salinity variations, were considered on the assumption that in arctic and subarctic regions a warmer climate would favour the stock through increased bioproduction in general, while a cooler climate would have the reverse effect.

Technical innovations in the fields of fish finding and catching in the last 30 years or so brought about a large increase in fishing mortality with regard to most if not all commercial species in the North Atlantic. On numerous occasions, we have witnessed the collapse of stocks, related to excess fishing, environmental variability or both.

However, these catastrophes and their far-reaching biological and economic effects, deplorable as they are, have not entirely been without benefaction. Thus, the collapse of commercial stocks, in particular of cod, herring and capelin, has resulted in intense research activities at various marine institutes on both sides of the Atlantic. Fairly quickly these studies led to the conclusion that the previous single species management approach was inadequate, and that each ecosystem would have to be considered more or less as a whole. This in turn led to the concept of the multispecies approach to fisheries management by which most of the work of present-day researchers is conducted. As a result, biological studies have proliferated and today's marine biologists are now busy continuing and improving the work of their predecessors which has been conducted at the single species level far too long.

In its simplest terms, the marine food chain is composed of plants, herbivorous zooplankton, plankton-feeding and usually pelagic fish, which in turn are eaten by other fish, marine mammals and sea birds. A representation of a common food chain with capelin as the focal point is given in Figure 1. The balance of the marine food chain is delicate and often disturbed by natural events over which we have no control. Of no less importance, however, is human intervention which frequently has wreaked havoc among the upper echelons of the food chain, not to mention in the domain of pelagic fish.

The capelin is a typical example of a plankton-feeding pelagic species, easily caught and highly important in the diet of major fish species like the cod and in the diet of baleen whales, such as minke and humpback, as well as seals and sea birds. All of these predators are known to take large tolls of capelin stocks, and some of them have been unable to find substitute food in times of low capelin abundance. In consequence, human harvesting of the species, without taking account of mortalities caused by predators and the variable recruitment, whether induced by environmental changes or exploitation, will inevitably lead to an imbalance of the marine food chain in areas inhabited by the capelin, sometimes with catastrophic results.

In the following, a simplified overview will be given of three ecosystems in the North Atlantic, *i.e.* the Barents Sea, Icelandic waters and the banks off Newfoundland and Labrador (Fig. 2).

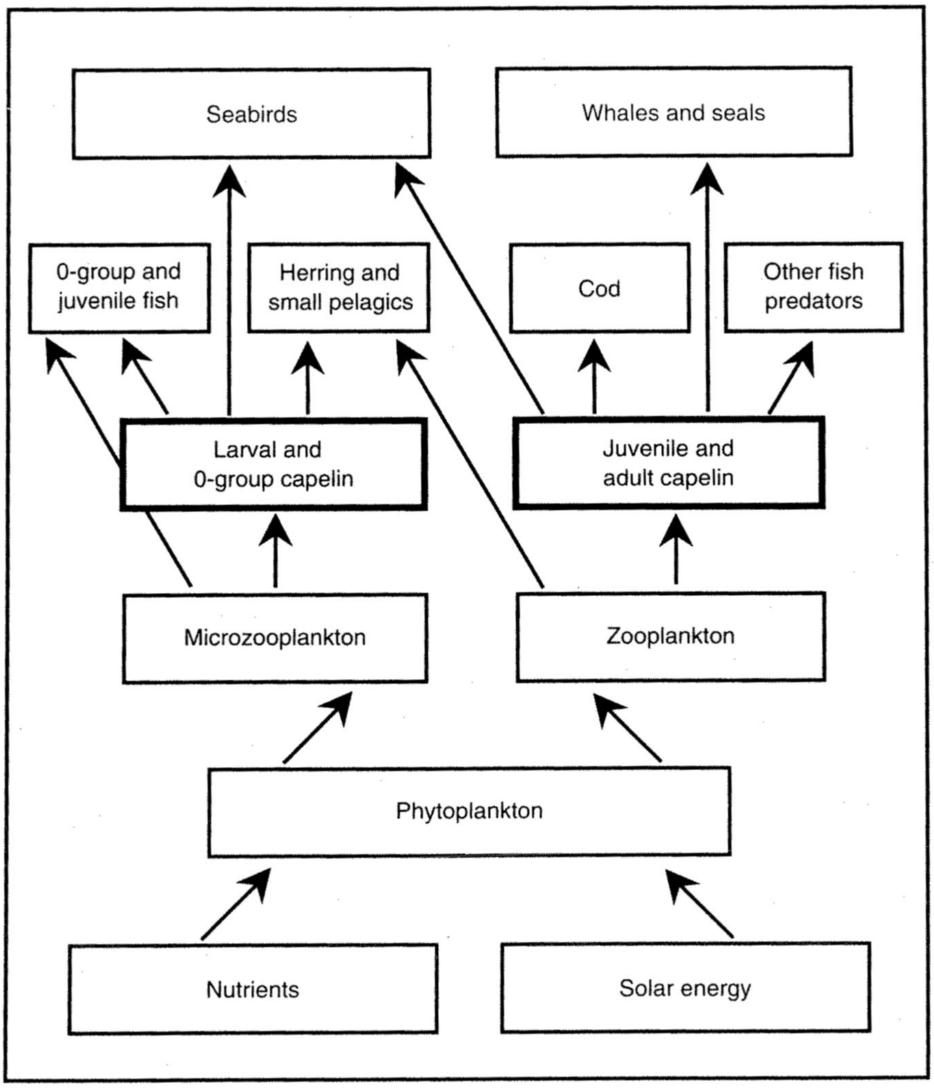

Figure 1. A simplified presentation of the status of capelin in the marine food web of arctic and subarctic regions of the North Atlantic.

While the great importance of the capelin is acknowledged in all of these ecosystems, there are considerable differences between them, both with regard to the physical environment and the direct economic importance of capelin to the fishing and processing sectors and indirect importance through interactions of capelin with other species, exploited or otherwise.

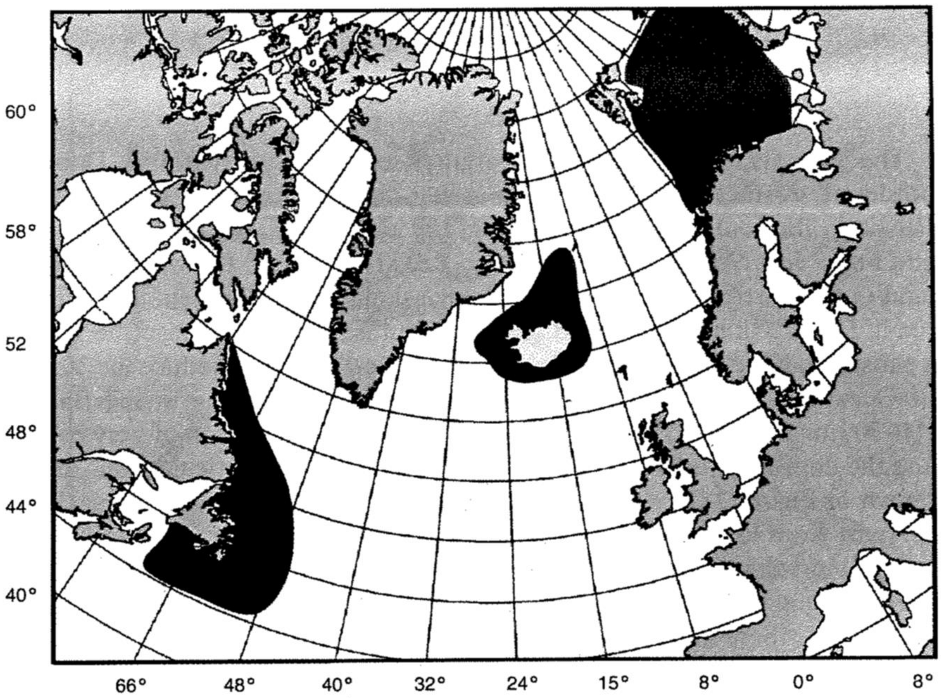

Figure 2. The location of the ecosystems under consideration. Blue: Newfoundland-Labrador; red: Iceland; green: Barents Sea.

The Barents Sea

The Barents Sea is a shallow marginal sea, bordered by the north coast of Norway and Russia in the south, Novaja Zemlya in the east and Franz Josef Land, Spitzbergen and Bear Island in the north and west. This extensive shelf sea is $1.4 \cdot 10^6$ km^2 in area and thus constitutes a substantial part of the shelf region of the Arctic Ocean. Most of the Barents Sea is less than 200-300 m in depth. The main water currents and the depth contours for 200 m and 500 m are shown in Figure 3.

Apart from low salinity coastal water, driven by the Norwegian and Murman Currents eastwards along the north coast of Norway and Murmansk, there are two main current systems which determine the oceanographic conditions of the Barents Sea (Fig. 3). The first is the north and east flowing Norwegian Atlantic Current (red arrows), which is a part of the North Atlantic Drift and enters the Barents Sea from the southwest, through the Bear Island Channel between the Tromsø Bank and the Bear Island. The second consists of cold arctic currents flowing south and southwest, *i.e.* the East Spitsbergen Current from the north and the Persey Current from the east and northeast between Franz Josef Land and Novaja Zemlya (dark blue arrows).

Over the years, it has been shown that large variations exist in oceanographic conditions and distribution of drift ice in the Barents Sea, both seasonally and from year to year. The ice reaches a maximum in March, when it covers most of the Barents Sea except for the southwestern part, while in September it reaches a minimum when the whole region south of 80°N is practically ice free.

Transport of Atlantic water into the Barents Sea normally reaches a maximum in late autumn (October-December), but a minimum in late spring (April-June). There are, however, marked inter-annual variations, depending upon the wind conditions between Norway and Spitsbergen, in such a way that winds from the west increase the Atlantic influx while easterly winds reduce it. An important phenomenon, occurring in the Barents Sea in winter, is the formation of very cold and saline bottom water, in particular on the banks between Novaja Zemlya and Franz Josef Land, but also on the Spitsbergen Bank. This heavy bottom water is mainly formed by intense cooling and increase in salinity due to rejection of brine during the freezing process. The bottom water eventually flows down the continental slope into the Arctic Ocean Basin as well as into the Norwegian Sea. To compensate for this, there will be an equivalent inflow of Atlantic water into the Barents Sea from the west. Thus, following a strong outflow of bottom water between 1982 and 1983 as well as in 1989 and 1990, an increased influx of Atlantic water and higher temperatures were observed (Mittun 1985; Loeng 1989, 1991).

Naturally, these changes affect the lower echelons of the ecosystem of this shallow area, causing shifts in the distribution of several indigenous fish stocks and influencing the success of their larval cohorts as well as the abundance of food for juveniles and adults of plankton feeding species (Loeng *et al.* 1983; Loeng *et al.* 1992; Loeng and Mittun 1984; Loeng 1989a; Skjoldal *et al.* 1992).

Potentially, the largest and probably the most intensively studied capelin stock in the world inhabits the Barents Sea and adjacent waters (Fig. 4). These capelin spawn off northern Norway and Russia in April. The larvae drift to the southern and eastern Barents Sea where the

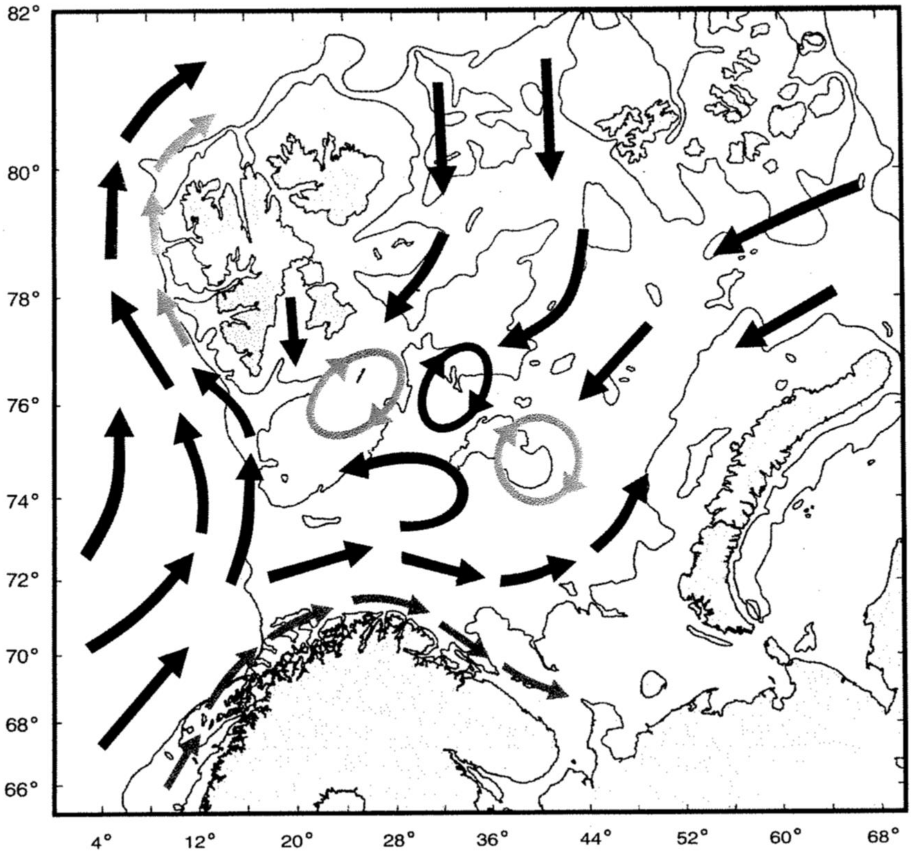

Figure 3. The main ocean currents of the Barents Sea. Dark blue arrows denote polar currents, red arrows Atlantic currents, light blue arrows mixed water and brown arrows coastal current. (Modified after Loeng 1989, with depth contours added for the 200 m and 500 m isobaths).

young capelin spend the first 2-3 years of their life. The adult stock feeds in the zooplankton rich areas south of the receding ice border in summer and it retraces its migration route towards the spawning grounds in the south in late autumn and winter. The growth rate may vary considerably in tune with environmental conditions (Gjøsæter and Loeng 1987) and, furthermore, as shown in Figure 5 there may be large east-west variations in the spatial distribution of the feeding concentrations of capelin in summer as well as in the location of the spawning grounds depending on hydrographic conditions (Prokhorov 1967; Loeng *et al.* 1983; Ozhigin and Luka 1985; Dragesund and Gjøsæter 1988; Loeng 1989a; Røttingen 1990).

Another major plankton feeding fish stock inhabits the Barents Sea. This is the Norwegian spring spawning herring, the potentially largest herring stock in the world (Fig. 6). These herring spawn along the west coast of Norway in March. The larvae drift with the coastal current north along the coast to the fjords of northern Norway and, especially in the case of large year classes, into the southern and sometimes eastern Barents Sea. The herring spend the first

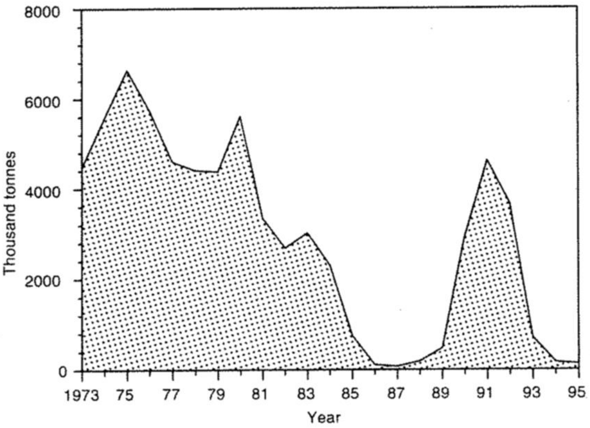

Figure 4. The estimated total stock biomass of Barents Sea capelin 1973-1995. From Anon. 1996.

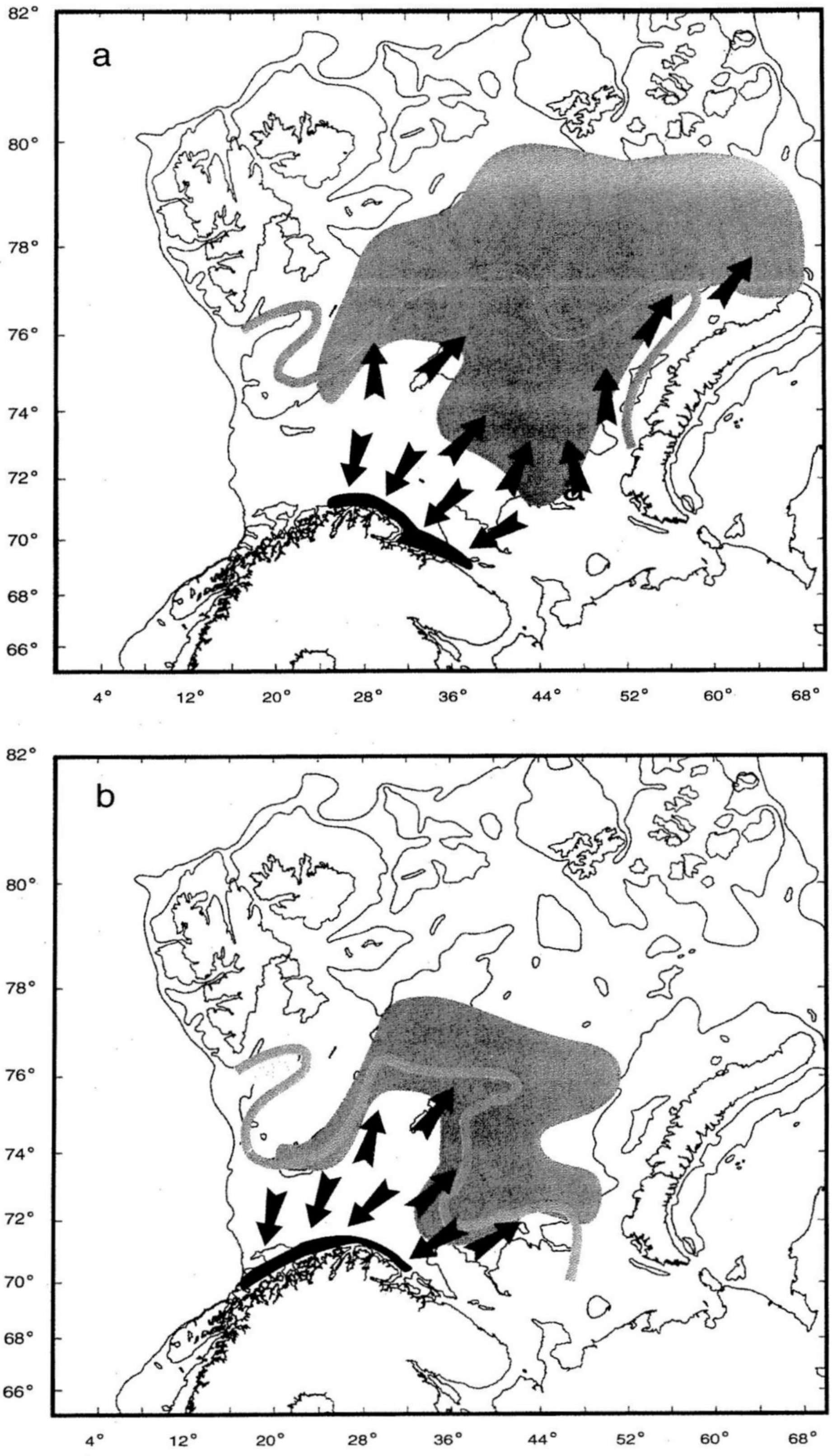

Figure 5. Feeding areas (green) and spawning grounds (red) of adult Barents Sea capelin; in a) warm years and b) cold years. Green arrows indicate feeding migrations and red arrows spawning migrations. The light blue line denotes the position of the polar front in summer (Modified after Loeng 1989).

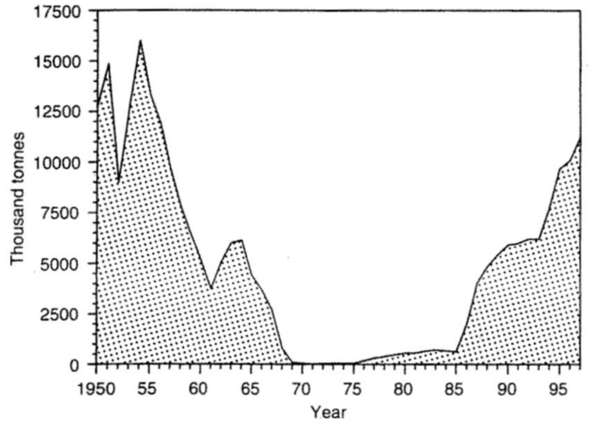

Figure 6. The estimated total stock biomass of Norwegian spring spawning herring 1950-1997. From Anon. 1996.

years of their life there, but leave the Barents Sea ecosystem on approaching maturity, generally at the age of 3-4 years, to feed in the open waters of the Norwegian Sea as well as in the area between Iceland and Jan Mayen and north of Iceland (Friðriksson 1944; Jakobsson 1978; Dragesund *et al.* 1980). The distribution area of juvenile herring and capelin in the Barents Sea may, therefore, overlap for a period of 2-3 years at least. It has been suggested that when such a situation occurs, the young herring may feed heavily on capelin larvae and 0-group and severely reduce capelin cohorts (Øiestad and Moksness 1979; Øiestad 1983; Hamre 1988, 1989, 1990; Huse and Toresen 1994).

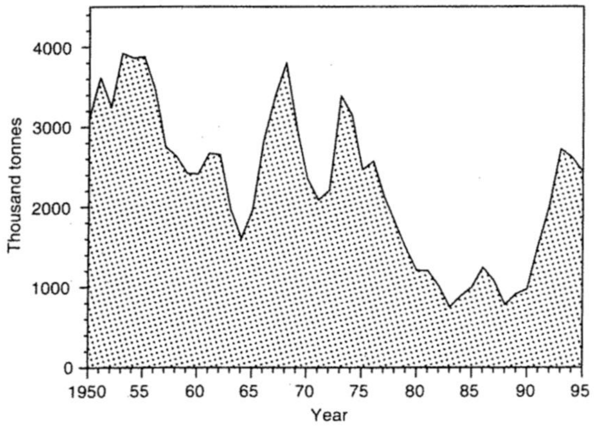

Figure 7. The estimated total abundance of the NE-Arctic cod 1950-1995. From Anon. 1997.

The main predator of adult capelin and young herring in the Barents Sea is the northeast arctic cod (Fig. 7). These cod may feed heavily on the juvenile herring, especially at such times when large year classes of herring are growing up in the southern parts of the Barents Sea. Otherwise, the cod are dependent on adult or adolescent capelin to the extent that in periods of low abundance of young herring and capelin, the cod is unable to find sufficient substitute food for compensation (Mehl 1989, 1991; Mehl and Sunnanå 1991; Bogstad and Mehl 1996).

Harvesting of the Barents Sea capelin stock began in a very modest way in the 1950s. As shown in Figure 8, the catch increased dramaticatically from around 100,000 tonnes in the mid-1960s to about 1.3 million tonnes in 1970. From 1970-1984 the annual Barents Sea capelin catch varied between about 1.1 and 3 million tonnes, the average for this 15 years period being about 1.8 million tonnes (*e.g.* Hamre 1985, 1990; Anon. 1996).

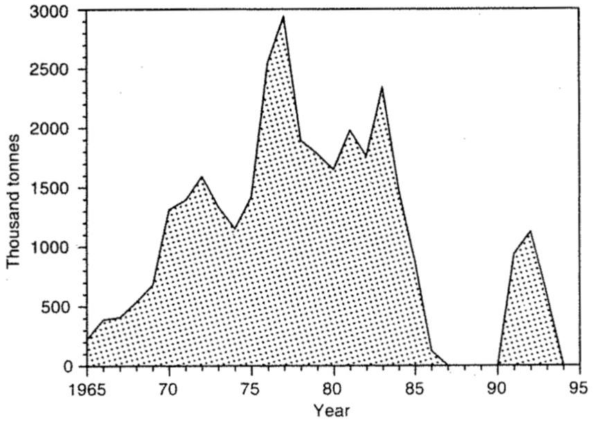

Figure 8. The Barents Sea capelin catch 1965-1995. From Anon. 1996.

In 1983, large year classes of cod and herring were produced (Fig. 9) and entered the Barents Sea ecosystem simultaneously. The effects were enormous. The young herring, it is thought, proceeded to devour capelin larvae drifting into the area and so decimated larval capelin cohorts (Øiestad 1983; Moksnes and Øiestad 1987; Hamre 1990; Huse and Toresen 1994). The

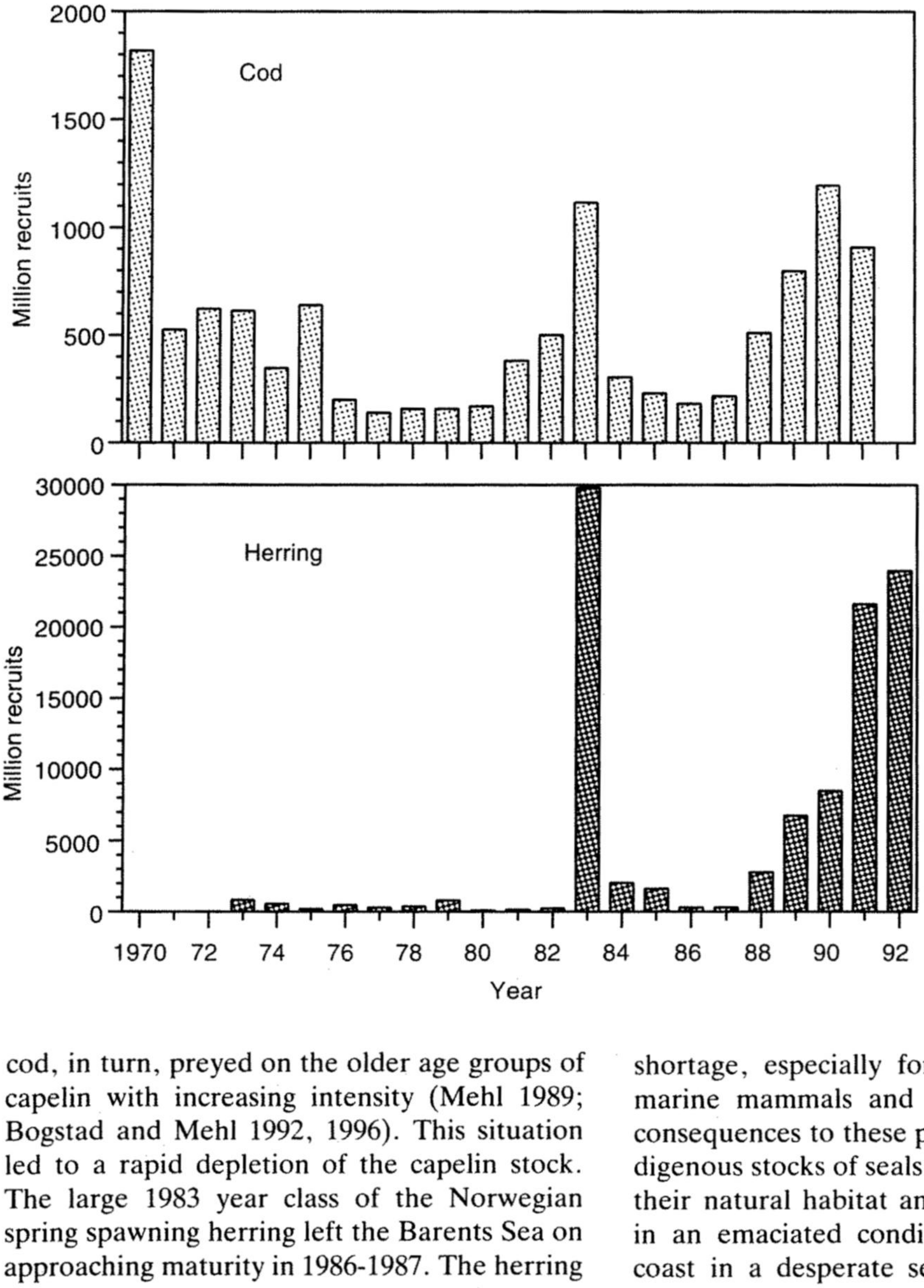

Figure 9. Recruitment of NE-Arctic cod and Norwegian spring spawning herring 1970-1992. From Anon. 1996, 1997.

cod, in turn, preyed on the older age groups of capelin with increasing intensity (Mehl 1989; Bogstad and Mehl 1992, 1996). This situation led to a rapid depletion of the capelin stock. The large 1983 year class of the Norwegian spring spawning herring left the Barents Sea on approaching maturity in 1986-1987. The herring year classes of 1984 and 1985 were as juveniles heavily preyed upon by the cod and consequently did not recruit to the adult stock in the expected numbers (Mehl 1989; Røttingen 1990).

In the mid-1980s the Barents Sea capelin stock collapsed completely and did not recover until 1990 (cf. Fig. 5). Since there were few juvenile herring in the area during the latter half of the 1980s, there arose an extreme food shortage, especially for the cod but also for marine mammals and sea birds, with severe consequences to these predators. The large, indigenous stocks of seals and sea birds starved in their natural habitat and subsequently flocked in an emaciated condition to the Norwegian coast in a desperate search for food (Hamre 1990; Nakken 1994).

As mentioned above, the abundant 1983 year class of northeast arctic cod was unable to find adequate substitute food and turned on its own progeny from the spawnings of the mid- and late-1980s, so reducing the cod year classes of 1984 and 1985 (Mehl 1989; Bogstad and Mehl 1992). Furthermore, the mean weight at age of the north east arctic cod was reduced drastically at the height of this period of famine (Mehl and

Sunnanå 1991; Fig. 10), when only less digestible prey species with lower caloric content (*e.g* amphipods) were available (Bogstad and Mehl 1996). The opinion was even voiced that probably it would be necessary to "fish down" the cod stock in order to enable the ecosystem to regain its natural balance.

Fortunately, this was not done. On the contrary, the research community persuaded management authorities to reduce fishing effort greatly (Fig. 11). Concurrently, a comprehensive research programme was implemented for in-depth investigations of the Barents Sea ecosystem and its functioning (Nakken 1994).

The Barents Sea capelin stock began to recover in the late 1980s with the advent of the 1989 year class, as well as those of 1990 and 1991. The total stock abundance was assessed to be between 2.9 and 4.6 million tonnes in the 1990-1992 period (Anon. 1996; Fig. 5). This

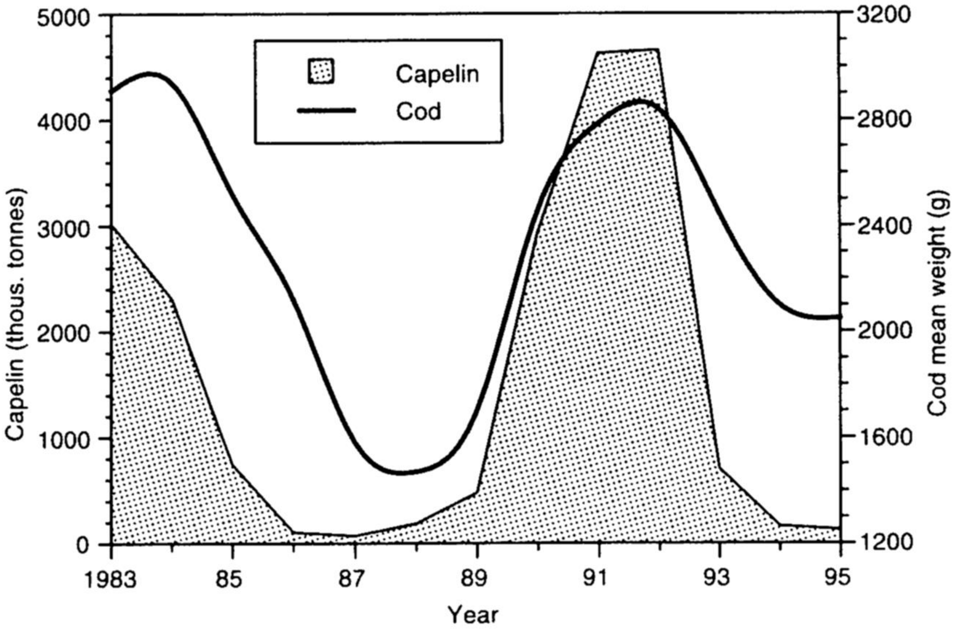

Figure 10. Variations in stock abundance of the Barents Sea capelin and mean weight of age 6 NE-Arctic cod. From Anon. 1996, 1997.

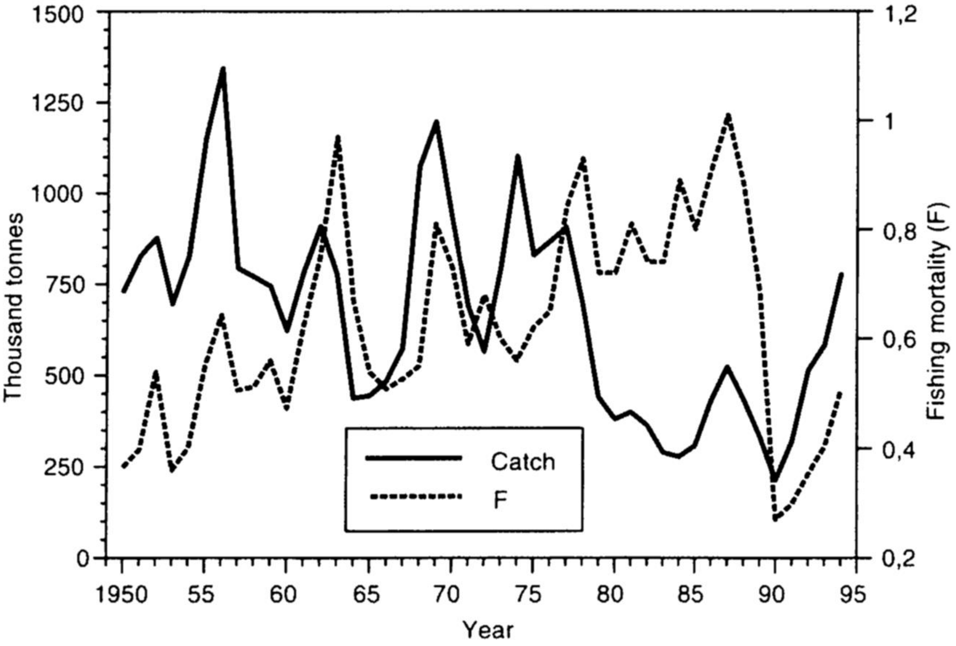

Figure 11. The catch and fishing mortality (F) of NE-Arctic cod 1950-1994. From Anon. 1997.

had an immediate beneficial effect on the cod stock, which despite the previous adversities still counted large numbers of fish of the 1983 year class as well as fish of medium and large year classes from 1988-1991. These cod were able to take advantage of the improved food supply and, as a result, the biomass of cod in the Barents Sea multiplied (*e.g.* Mehl and Sunnanå 1991; Nakken 1994). With the cautious approach to the fishery of capelin after the stock collapsed, all was well – for a while.

As shown in Figures 6 and 9, the increased spawning stock of the Norwegian spring spawning herring produced year classes in 1991 and 1992 which were on a par with that of 1983. In their younger stages these herring year classes, it is believed, took their toll of the incoming larval cohorts of capelin, leading to lower capelin recruitment (Huse and Toresen 1994). The continued presence of large amounts of cod in the Barents Sea soon reduced the adult and juvenile stock of capelin also, and by 1994 the Barents Sea capelin stock had collapsed again (Anon. 1994, 1995, 1996). For a while, the cod may to some extent have been able to substitute herring for capelin in their diet. Such predation could *i.a.* explain the conflicting results of abundance assessments of the 1993 herring year class carried out in 1994 and 1995 (Anon. 1996). The large 1991 and 1992 year classes of herring have now left the Barents Sea and, due to the predatory pressure by the cod, the capelin stock is not expected to recover for another 2-3 years.

Marine mammals and to some extent birds may influence the abundance of fish stocks, either directly by predation or indirectly through competition for food. In the absence of long-term time series, the effects of these predators can not be quantified in detail, but on the whole they are considerable. Recent estimates indicate that the total annual fish consumption by these top predators amounts to between 4 and 8 million tonnes (Nakken 1994).

The Iceland-Greenland-Jan Mayen area

Compared to the Barents Sea, the marine ecosystem around Iceland is much more open. Thus Icelandic waters consist of a relatively narrow shelf, a steep or moderately steep slope region and deep waters beyond. The ocean currents and bottom topography of this area, as described by the 200 m and 500 m depth contours, are shown in Figure 12.

The areas off the south and west coasts of Iceland are bathed by relatively warm and saline Atlantic water of the clockwise flowing Irminger Current (red arrows). Topography plays an important role with respect to the water circulation around Iceland. Thus, at the Iceland-Greenland Ridge the warm Irminger Current splits into two parts. One branch swings to the west and southwest and forms a cyclonic eddy in the Irminger Sea. The other, the North Icelandic Irminger Current, follows the Icelandic shelf area and continues eastwards along the north coast, where it is mixed to a varying degree with colder arctic waters of the East Icelandic Current (light blue arrows) and at times with polar water of the East-Greenland Current proper, which transports cold, low salinity water to the south and crosses the Iceland-Greenland Ridge (dark blue arrows).

The East Icelandic Current, formed by south

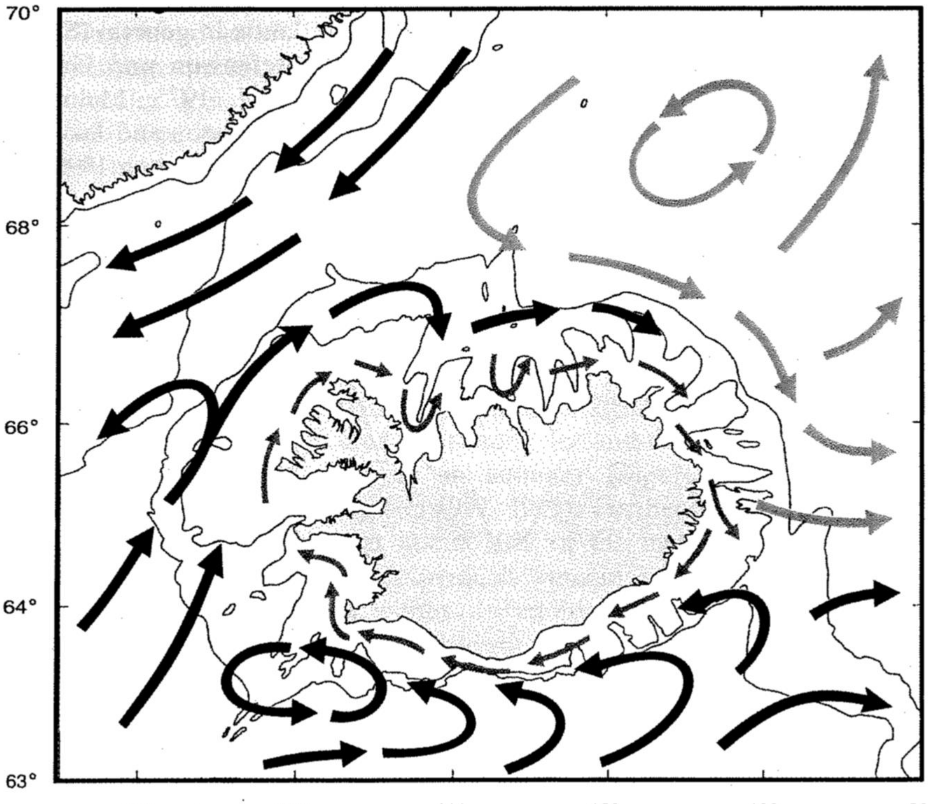

Figure 12. The main ocean currents of Icelandic waters. Dark blue arrows denote polar water, red arrows Atlantic water, light blue arrows arctic or mixed waters and brown arrows the coastal current. (Modified from Stefánsson and Ólafsson 1991, with depth contours added for the 200 m and 500 m isobaths).

flowing arctic water, often mixed to a varying degree with polar water from the East-Greenland Current, continues southwards along the east Icelandic continental slope, but turns to the southeast and east at the Faroe-Iceland Ridge. Thus transport out of the coastal area mainly takes place in two regions, *i.e.* off Látrabjarg on the northwest coast of Iceland and off the southeast coast.

In addition to these two main systems of ocean currents, a lower salinity coastal current, driven by gravity forces, runs in a clockwise direction around Iceland (yellow arrows).

Year to year changes are relatively small in the area south and southwest of Iceland whereas off the north and northeast coasts very large variations are frequent due to changes in the wind regime and the distribution of polar water (Stefánsson 1962, 1969). Such changes have marked effects on primary and secondary productivity and biological conditions in general (*e.g.* Stefánsson and Jakobsson 1989).

In the Icelandic area, most fish stocks spawn in the warm Atlantic waters in the south and west. The young drift with the surface currents to the north and east of Iceland where they spend most of the adolescent part of their life. Under normal circumstances these regions are also the main feeding areas of the adults in summer. Due to the open nature of this ecosystem the young of species such as cod and capelin often drift across to Greenland in fairly large numbers. The area off North and East Iceland is noted for frequent and often large variations in the physical and biological environment (*e.g.* Stefánsson and Jakobsson 1989; Jakobsson 1992; Vilhjálmsson 1994). As expected, these physical variations are correlated with changes in the atmospheric circulation and wind stress in the adjacent areas and the northern North Atlantic in general (Stefánsson 1954, 1962, 1985; Stefánsson and Gudmundsson 1969; Dickson *et al.* 1975; Malmberg and Svansson 1982; Stefánsson and Jakobsson 1989; Malmberg and Kristmannsson 1992).

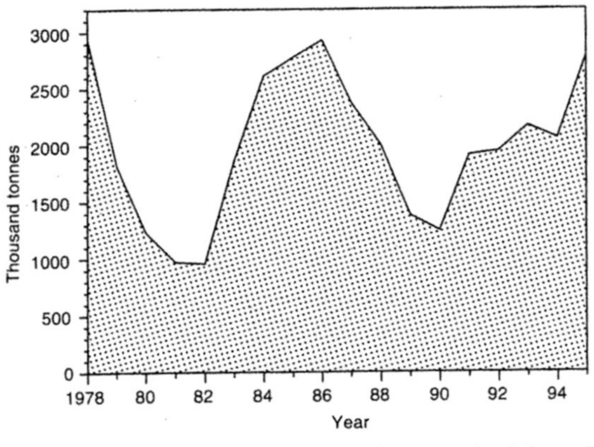

Figure 13. The estimated total biomass of adult and juvenile Icelandic capelin 1978-1995. From Anon. 1996.

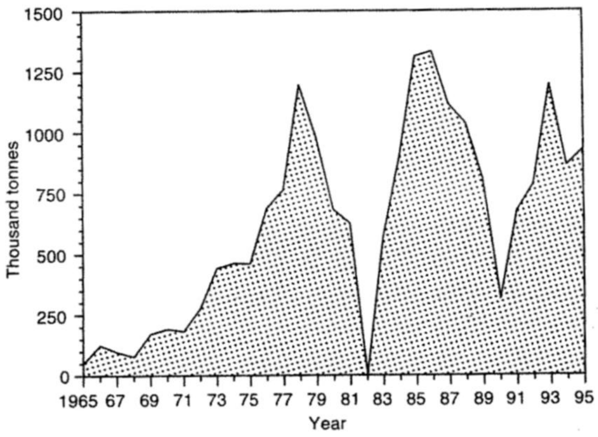

Figure 14. The catch of Icelandic capelin 1965-1995. From Anon. 1996.

A large stock of capelin inhabits the area between Iceland, Greenland and Jan Mayen (Fig. 13). The fishery of these capelin began in the mid-1960s, about a decade later than the first small-scale capelin fishery in the Barents Sea, but thereafter developed along similar lines (Fig. 14). A summer fishery based on feeding concentrations of capelin was begun in 1976, and by 1978 the annual catch had increased from about 400-500 thousand tonnes to more than 1 million tonnes. The adult stock was reduced to a very low level in the early 1980s and was again reduced to a low level in 1989-1990. Recovery was achieved in 1-2 years on both occasions (Vilhjálmsson 1994; Fig. 13).

In the Iceland-Greenland-Jan Mayen area the interactions of capelin with other species are somewhat more simple than in the Barents Sea. The main fish predator is the cod, which may consume large amounts of capelin, especially of individuals from the adult stock (Pálsson 1983, 1994; Magnússon and Pálsson 1989, 1991). The other main fish predators are the Greenland halibut and saithe, but the effect of grazing by these species is less than that by the cod, both because of the smaller stock sizes of the former and also due to a more limited overlap between capelin, Greenland halibut and, in particular, the saithe whose predation is mainly limited to the warmer waters off southern Iceland in winter (Skúladóttir and Jónsson 1991; Jónsson 1996). The distribution area of the Icelandic summer spawning herring does not overlap with that of the capelin, except to a very small degree, and these herring, therefore, have very little if any effect on the success of cohorts of larval capelin in this area.

However, this need not always have been so. Prior to the collapse of the Norwegian spring spawning herring stock in the late 1960s, adult herring belonging to this stock used to migrate across the Norwegian Sea to feed in large numbers north and northeast of Iceland (Friðriksson 1944; Jakobsson 1978; Dragesund *et al.* 1980). These waters also constitute the main feeding area of the much smaller Icelandic spring spawning herring stock. The capelin stock also collapsed in the 1960s but has not recovered (Jakobsson 1980). At times, part of the diet of these spring spawning herring may have consisted of 0-group capelin which by July-August had drifted to the north and northeast of Iceland from the spawning grounds in the south and west (Jespersen 1920; Friðriksson 1944).

Furthermore, in the very warm year of 1960 there was a strong inflow of Atlantic water to the north Icelandic area bringing along huge quantities of 0-group capelin. The concentrations of redfeed (*Calanus finmachicus*), usually occupying these waters at that time of year, were displaced to the north and northeast. Consequently, when the herring arrived in their usual summer feeding area they found mainly 0-group capelin. On approaching the surface, the schools, therefore, dispersed and the herring were very difficult to catch. This phenomenon was referred to as "rock-herring" in the honour of Bill Haley and his Comets – who are credited with introducing the so-called rock and roll music which resulted in most spectacular gymnastics.

The effect of grazing on capelin larvae by the spring spawning herring was never quantified. The available evidence suggests that in the Icelandic area the preying by herring on capelin larvae has occurred only sporadically in areas where the supply of calanoid copepods and euphausiids was low. Naturally, there are no estimates of capelin abundance available from those years for comparison. It will be interesting to follow developments of the migratory pattern of the Norwegian spring spawning herring as the stock abundance increases in the coming years. Already, there are signs of extended westward migrations in the Norwegian Sea (Anon. 1995a, 1996a) which might eventually lead to a resumption of the earlier migration pattern of feeding in the waters north of Iceland, the main distribution area of 0-group capelin.

Much of the adult Icelandic capelin normally migrate north to feed in the deep waters of the Iceland Sea during the months of July-September (Vilhjálmsson 1994; Fig. 15). This area is completely free of fish predators but is visited by plankton eating whales, especially minkes and humpbacks. The humpback has been protected since the 1950s and the stock has increased greatly from its previously low abundance. The same is true for the minke whale which has not been hunted since 1985. It is estimated that in the late 1980s about 10,000 minke whales and 1,800 humpbacks were in the area between Iceland-Greenland and Jan Mayen in summer (Sigurjónsson and Víkingsson 1992, 1995). Furthermore, it is believed that about 10% of the humpbacks, or nearly 200 individuals, remain within Icelandic waters in winter. In addition to krill and copepods, these whale species feed on capelin when available. In the absence of concrete data on stomach contents it is difficult to quantify the amount of capelin taken by whales. Recent estimates (Sigurjónsson and Víkingsson 1995) indicate that together these whale species con-

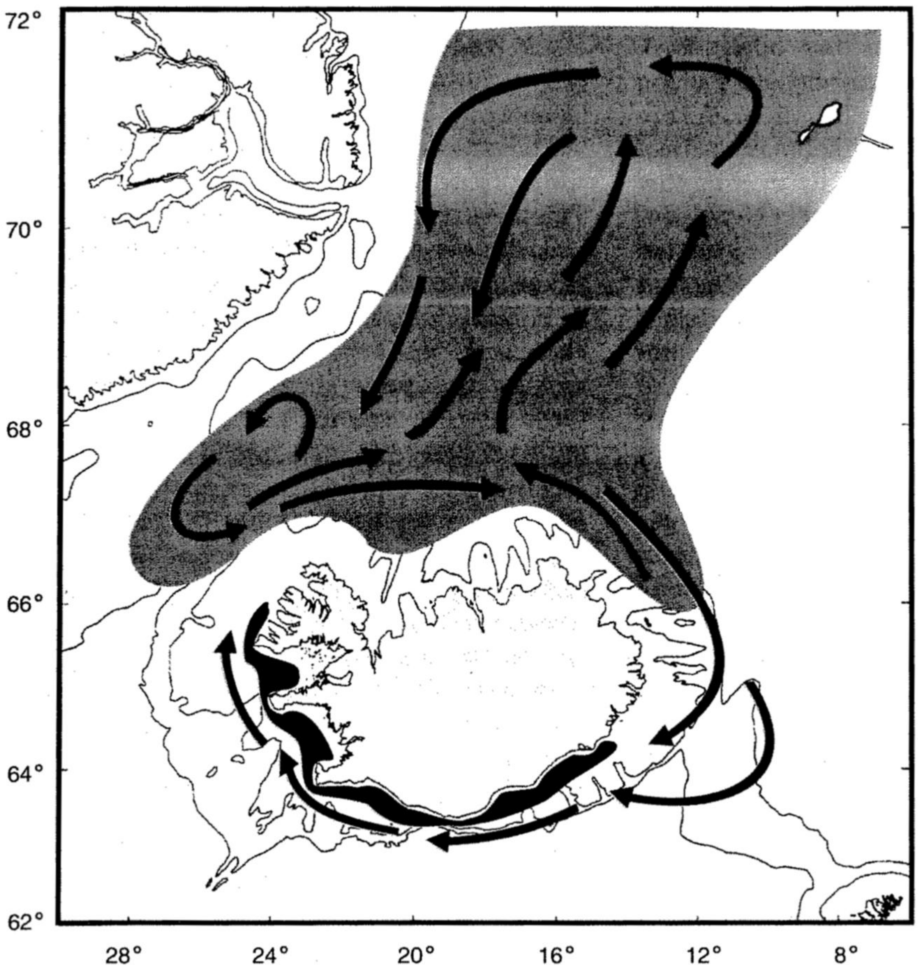

Figure 15. The feeding areas (green) and spawning grounds (red) of adult Icelandic capelin. Green arrows indicate feeding migrations, blue arrows autumn return migrations and red arrows spawning migrations. (Modified from Vilhjálmsson 1994).

sume about 350,000 tonnes of fin-fish annually in the Icelandic area and adjacent waters, most of which is probably capelin. Considerable quantities of juvenile and adult capelin are also taken by sea birds. Seals have only a minor effect on capelin abundance in Icelandic waters (Hauksson 1989).

As stated above, the adult capelin are out of reach of cod while feeding in the northern region as well as in the cold waters between Northwest Iceland and Greenland. This situation changes with the return of the capelin to the shelf area north of Iceland in October-November (Vilhjálmsson 1994; Fig. 15). From then on until spawning off South and West Iceland in March, the adult capelin are available to the cod stock and indeed eaten by the cod in large quantities, especially on and near the spawning grounds at Southwest and West Iceland (Magnússon and Pálsson 1989, 1991). Large quantities are also taken both north and east of Iceland, but hitherto insufficient effort to assess capelin abundance and cod stomach contents concurrently, has been devoted to these areas at other times of the year (Vilhjálmsson 1994).

However, there is no doubt of the importance of capelin to the well-being of the Icelandic cod stock. Thus, it was found that during the near-collapse of the Icelandic capelin stock in the early 1980s the weight at age of the cod stock, in particular among age groups 4-8, decreased by about 25% (Anon. 1996; 1996b; Fig. 16). The condition of the cod improved again following the quick recovery of the capelin in 1983 and 1984, declined again with reduced

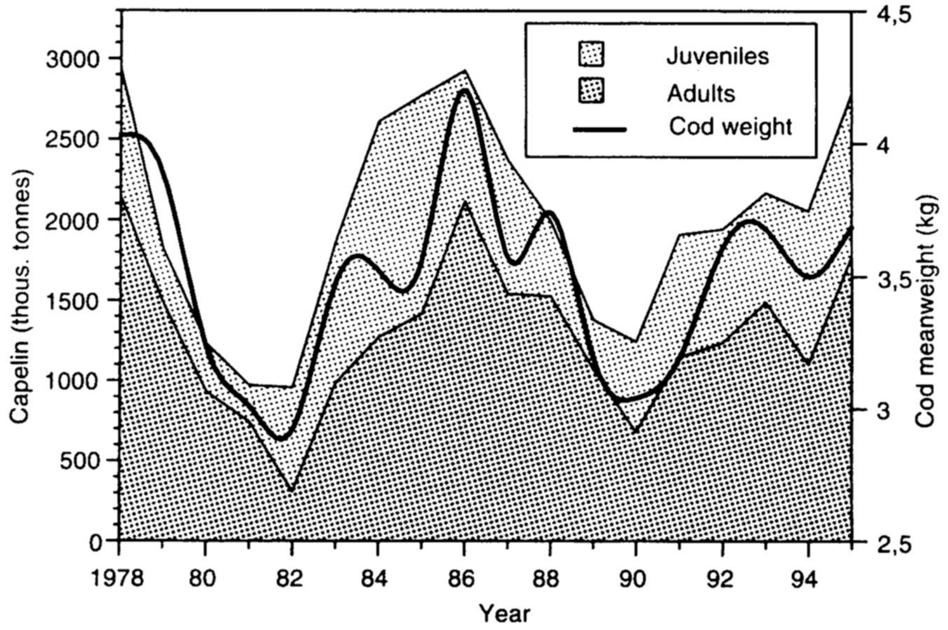

Figure 16. Changes in capelin biomass (adult and juvenile) and weight at age 6 of Icelandic cod 1978-1995. From Anon. 1996, 1996b.

capelin abundance in 1989-90 but improved after that in tune with increased capelin abundance.

Although young cod will eat juvenile capelin (Pálsson 1980), this does not seem to apply to the same extent to the older year classes of cod, at least not in the Icelandic area (cf. Fig. 16). The reason for this is probably the low energy content of juvenile capelin, in particular the 0- and 1-group, which do not build up fat reserves as do the maturing fish (Vilhjálmsson 1994). When adult capelin are not available, cod will turn to other food, mostly krill and shrimp, which as a rule are abundant in various parts of the main feeding area of the cod off the northern part of Iceland. However, it is quite clear that these and other available prey species can not fully substitute for the loss of the capelin from the diet of cod in the Icelandic area.

The Newfoundland- Labrador region

The bottom topography of the extensive continental shelf off Labrador and Newfoundland (200 m and 500 m depth contours), together with the main ocean currents, is shown in Figure 17. The ecosystem of these waters is unique among the three areas under consideration in that it is dominated by the cold water of the south-going Labrador Current (dark blue arrows), with warm water of Atlantic origin (red arrows) playing a much smaller role than in the other two areas (Fig. 17). In fact, primary production of algae as well as of zooplankton on the Newfoundland and Labrador banks depends to a large degree on their relatively low geographic latitudes (approximately 45-55°N) which favour the early establishment of a thermocline in these cold waters, while nutrient renewal by mixing can occur during storm events

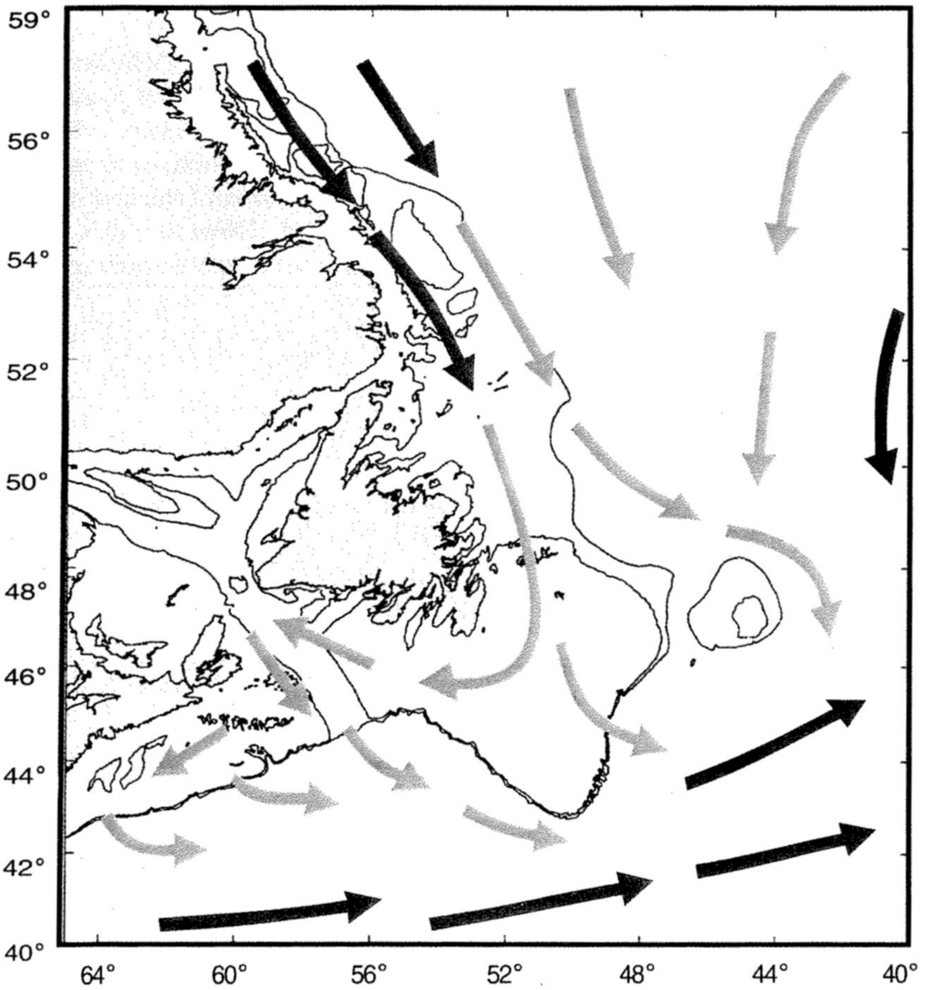

Figure 17. The main ocean currents of the Newfoundland-Labrador area. Blue arrows denote polar water, red arrows Atlantic water and light blue arrows arctic and/or mixed waters. (Modified from Carscadden *et al.* 1989, with depth contours added for the 200 m and 500 m isobaths).

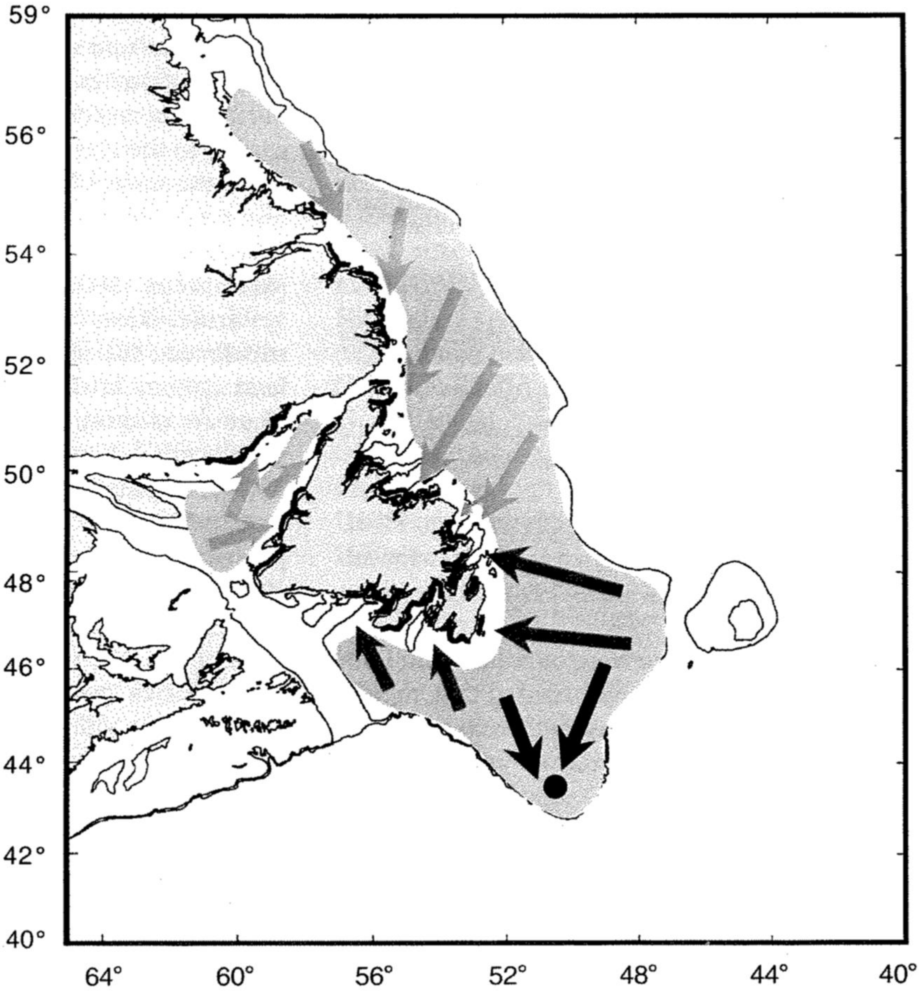

Figure 18. Major capelin stocks and spawning grounds in the Newfoundland-Labrador area. Light blue arrows: Labrador/ northeast Newfoundland stock, dark blue arrows: northern Grand Bank/ Avalon stock, red arrows: southern Grand Bank stock, green arrows: St. Pierre Bank stock and light brown arrows: Gulf of St. Lawrence stocks. (Modified from Carscadden 1982).

in the shallower parts of this area (Frank and Leggett 1981; Frank and Carscadden 1989) and by upwelling near the shelf break as well as where deep troughs cut across the shelf at right angles to the flow of the all important Labrador Current. Furthermore, the rapid warming of the surface layers in May and June, from the sub-zero temperatures of the winter period, enables the capelin to spawn early enough in the year to allow survival through the winter and populate a much larger part of these waters than otherwise possible.

There appear to be several stocks of capelin inhabiting the waters of the banks off Labrador and Newfoundland with spawning grounds as indicated in Figure 18 (Carscadden and Misra 1980; Carscadden 1982, 1984). Prior to the 1950s, some 20-25 thousand tonnes of capelin were taken in Newfoundland annually for various purposes during the spawning season, but during the following two decades the inshore capelin fishery declined to very low levels. There was a renewed interest in the fishing of Newfoundland-Labrador capelin in the 1970s, in offshore areas during the first half of the decade, but in inshore waters in the late 1970s. In 1972 the first offshore catches of about 70 thousand tonnes were reported. The offshore catch increased rapidly, peaking in 1976 at about 360 thous. tonnes. After that the offshore catch declined sharply with reduced stock abundance. Since 1979 the Newfoundland-Labrador capelin have only been fished during the spawning season for the processing of frozen females

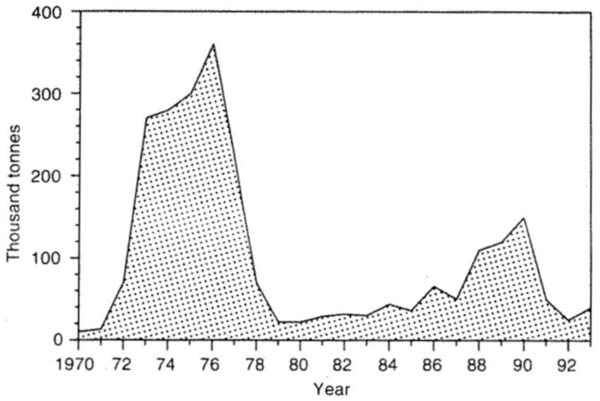

Figure 19. The capelin catch in Newfoundland-Labrador waters 1970-1993. From Anon. 1989, 1989a, 1995b.

for the Japanese market (Carscadden *et al.* 1994). The total capelin catch in the Newfoundland-Labrador region 1973-1994 is shown in Figure 19.

For the region of the Newfoundland and Labrador shelves it has been estimated that capelin comprise over 90% of the diet of cod in these waters during the capelin spawning season in June and July and 30-55% on an annual basis. However, Lilly (1989) has shown that over the period 1978-1986 the contribution of capelin to the diet of the northern cod varied considerably between years in the various parts of this area. He attributed these differences to variations in capelin abundance and noted that the cod did not seem to find substitute prey in times of low capelin abundance. Nevertheless, similar reductions in mean weight at age, as were recorded in the cod stocks of the Barents Sea and Icelandic waters in the 1980's, have not been observed among the northern cod of Newfoundland and Labrador as shown in Figure 20 (Millar *et al.* 1990; Anon. 1989, 1989a; 1995b).

Furthermore, the Newfoundland-Labrador capelin are the mainstay of the diet of Greenland halibut in the length range of 20-80 cm. They are also the main prey species of Atlantic salmon as well as of American plaice. Large pelagic fish such as bluefin tuna may also feed on capelin in the Newfoundland area and small pelagics also feed on capelin larvae and juveniles (Pitt 1973; Winters and Carscadden 1978; Bowering and Lilly 1992).

Mitchell (1975) found capelin to be the dominant species preyed on by 90% of the fin whales taken off north-eastern Newfoundland in 1947-1951 and was almost the exclusive food of fin whales in 1967-71. Sergeant (1963) reported that capelin were found in 85% of the stomachs of minke whales caught commercially in Newfoundland waters and furthermore that other less abundant whales, such as the sei whale, also eat substantial quantities of

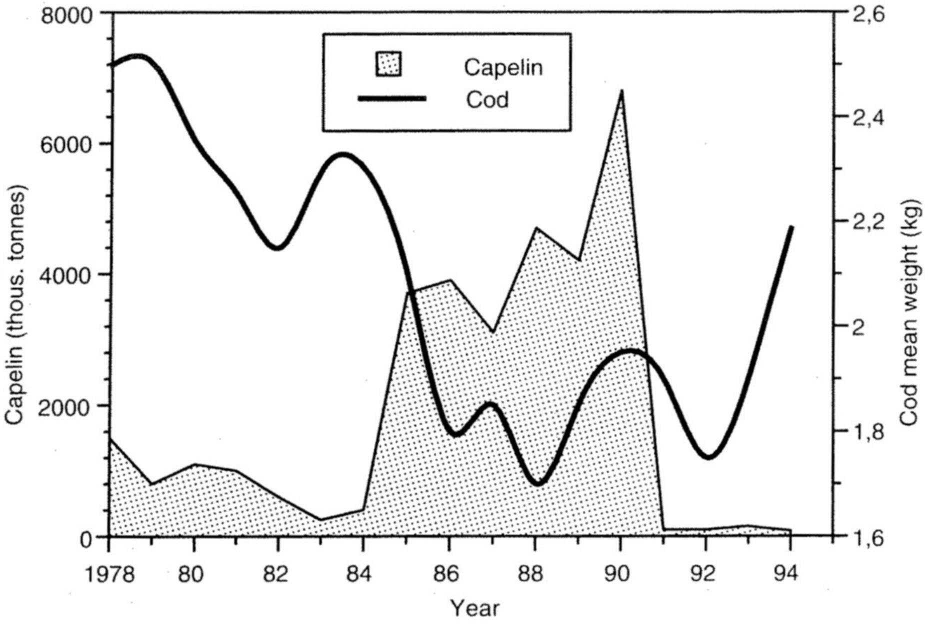

Figure 20. Changes in adult capelin biomass and weight at age 6 of the 'northern cod' 1978-1994. Anon. 1989, 1989a, 1995b; Millar *et al.* 1990.

capelin. Furthermore, Whitehead and Carscadden (1985) found that the inshore abundance of humpback and finback whales could be predicted from knowledge of adult capelin abundance while minke whale migrations were related to the distribution and abundance of juvenile capelin.

An estimation of the removal of capelin by some of the major predator species was attempted by Winters and Carscadden (1978). They estimated that in the years 1947-1951 the northern cod had consumed about 4 million tonnes of capelin annually, the consumption shrinking to about 3 million tonnes in the mid-1970s due to the large reduction in the size of this cod stock. The same authors estimated that the harp seal population of about 1.3 million animals, which breed off Labrador and northeast Newfoundland, would remove annually about 300 thousand tonnes of capelin from the Newfoundland-Labrador area. Furthermore, it was estimated that about 250 thousand tonnes were removed by fin whales and some 35 thousand tonnes by minkes.

Finally, the large numbers of sea birds in the Newfoundland-Labrador area depend for the most part on capelin for food. Thus, Brown and Nettleship (1984) estimated that the total annual capelin consumption by all seabirds in the Newfoundland-Labrador area, including the Grand Banks, was on the order of some 250 thousand tonnes or of a similar magnitude as the consumption by whales and seals but about 1/10th of the capelin consumption by cod in the 1970s.

Discussion

What then can we conclude from our existing knowledge of the interaction between capelin and other species with regard to management and harvesting of marine ecosystems in the North Atlantic?

It is true to say that both researchers and managers of all ecosystems in the North Atlantic recognize the highly important role played by the capelin wherever it occurs. The importance of capelin has in particular been brought home in the Barents Sea and in Icelandic waters through the large negative deviations in weight at age of the dominant predator, the all important cod, in times of low capelin abundance (Mehl and Sunnanå 1991; Bogstad and Mehl 1996; Anon. 1996; Steinarsson and Stefánsson 1991). Although negative deviations in weight at age of this predator species have not been observed with respect to the northern cod stock of Newfoundland and Labrador following periods of low capelin abundance (Millar *et al.* 1990; Anon. 1996), this does not necessarily mean that such a relationship does not exist in these waters. In the 1990s, the marine environment off Newfoundland and Labrador has been subjected to a marked cooling as compared to the previous decade. This is believed to have caused anomalous shifts of the distribution of capelin, in particular those stocks occupying the more eastern and northern parts of the area. Therefore, the standard hydroacoustic surveys of capelin abundance may have missed large parts of the stock, resulting in conflicting assessments of stock status (Anon. 1995b). Furthermore, the northern cod has been in an extremely depleted state since the late 1980s (Fig. 21), which in all probability is mainly due to excessive fishing but also general environmental adversities (Harris *et al.* 1990; Bishop *et al.* 1993; Anon. 1996c). For these reasons it is likely that the cod/capelin relationship can not be detected in the existing data. However, the harvesting of capelin from all of the three ecosystems is approached in a more cautious manner nowadays than it was in the 1970s and 1980s.

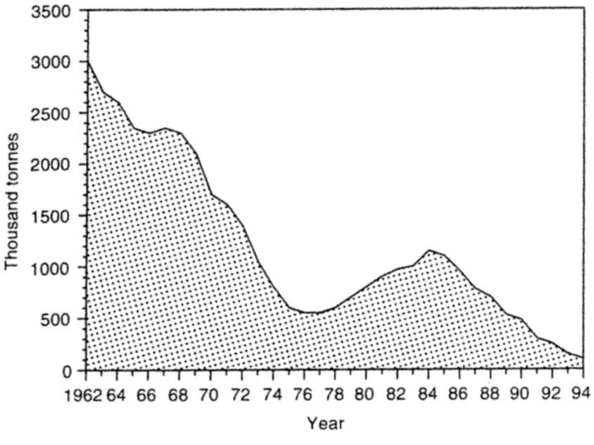

Figure 21. Stock abundance of the 'northern cod' 1962-1994. From Harris *et al.* 1990; Anon. 1995b.

It has been suggested that the capelin fishery of the 1980s had very little to do with the collapse of the capelin stock in the Barents Sea. Thus, Hamre (1990) argues, on the basis of a comparison of indices of the abundance of larval, 0- and 1-group capelin, that the capelin year classes of 1983-1985 were grazed down, first by herring and then by cod of the 1983 year class and, therefore, never had a chance. Furthermore, Olsen (1968) pointed out that capelin abundance seemed to have been low in the years following the appearance of the large herring year classes of 1950 and 1959. The grounds for Hamre's argument for the adverse effect of the 1983 year class of herring and cod are illustrated in Figure 22 which further shows that, following the appearance of the large herring

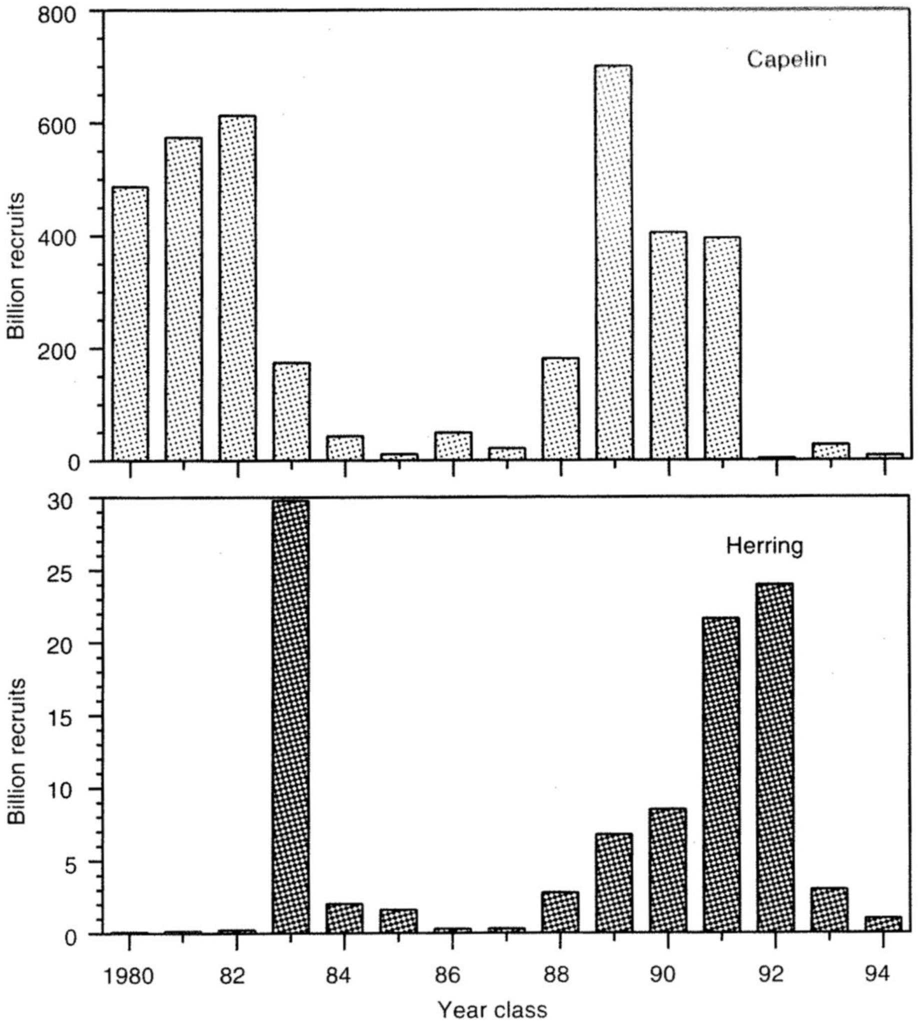

Figure 22. Recruitment of capelin and herring in the Barents Sea 1980-1994. From Anon. 1996.

year classes of 1991 and 1992, the abundance of 0- and 1-group capelin has remained very low after 1992. The very low abundance of capelin larvae in 1994 and 1995, on the other hand, probably reflects the depleted state of the capelin spawning stock.

Other researchers have argued that the intense capelin fishery in the latter half of the 1970s must have accelerated the alarming decline of the stock, observed from about 1976 onwards (*e.g.* Nilsen and Hopkins 1992). Apart from the rapid decline of capelin stock abundance, the main argument in this case was that the intense fishery accelerated the observed large increase in growth and maturing rates, which obviously were density dependent, and thus largely reduced the numbers of 4 and 5 year old fish in the spawning stock and even obliterated the latter component. These basic trends would then have resulted in a greater proportion of the maturing fish being taken for a given unit weight of total allowable catch (TAC) and, therefore, in an increased relative exploitation of the maturing stock (cf. Fig. 23). Furthermore, the spawning stocks of 1980 and 1982-1986 were reduced very much beyond the targeted minimum of 400-500 thousand tonnes (Anon. 1996). However, it is only fair to state that the 1986 winter fishery must be written on the management's account and not on that of the advisors.

Since the stock collapse in the mid-1980s, the management of the Barents Sea capelin has been approached in a multi-species context and

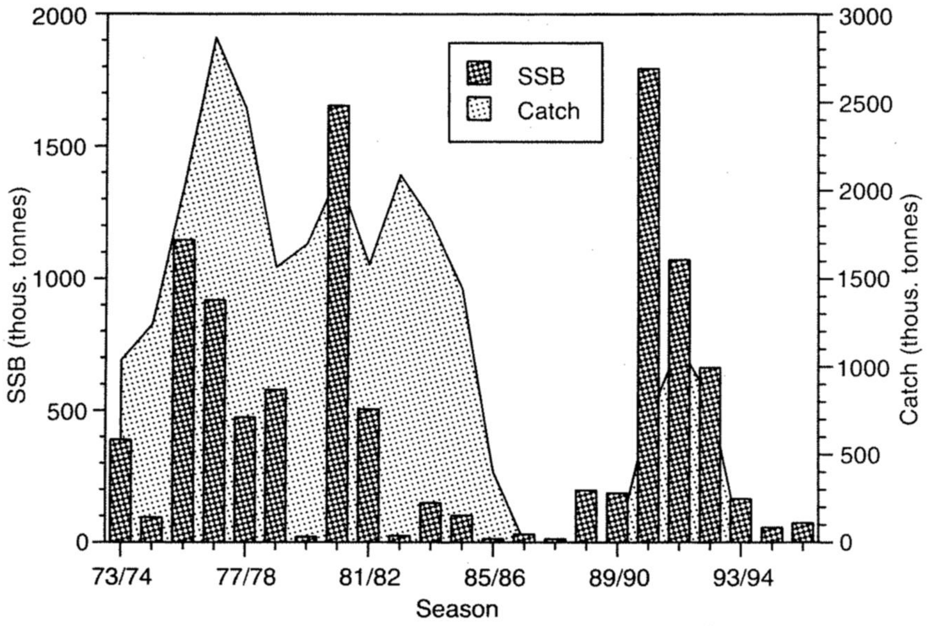

Figure 23. The catch of Barents sea capelin and the remaining spawning stock biomass (SSB) in the 1973/74-1995/96 seasons. From Anon. 1996.

in a very conservative manner as compared to earlier times (Gjøsæter 1991; Anon. 1990-1996; Bogstad and Mehl 1996). Thus, the needs of the main predators, of which the arctic cod takes top priority, are the primary concern, with the direct harvesting of capelin in second place. To attain this objective and giving non-human predators first choice, no summer and autumn fishery was allowed in 1990 in spite of an acoustic assessment of about 2.9 million tonnes of adult capelin on 1 August of that year and only very moderate catches were taken in the autumn of 1991 and 1992. The winter catch in 1991-1993 was kept at a comparatively low level as well (Anon. 1992, 1993, 1994). Thus, the Barents Sea capelin were allowed to utilize their growth potential during the feeding season almost in full and the uneconomical harvesting of immatures in the mixed summer-autumn fishery was for the most part averted.

In spite of these severe restrictions on the harvesting of the Barents Sea capelin, the stock collapsed once again, possibly starting a train of events leading to destabilization of the ecosystem similar to those of the mid-1980s. This time the capelin fishery is certainly not to blame. The reasons are probably a combination of environmental and predatory impacts. It has been shown that under experimental conditions juvenile herring may graze down cohorts of 0-group capelin (Øiestad 1983; Moksnes and Øiestad 1987). This has proven difficult to verify in the natural habitat (Huse and Toresen 1994) while the relatively large numbers of cod presently occupying the Barents Sea have certainly taken a very heavy toll of the adult capelin (Mehl 1989, 1991; Bogstad and Mehl 1996).

Figure 23 shows data describing the catch and stock developments of the Barents Sea capelin for the 1973/74 - 1995/96 seasons. These data, it may be argued, lend support to both a fishery dependent and independent stock decline. Thus, the extremely low spawning stocks of 1975 and 1980 both produced large year classes. However, a closer examination reveals certain caveats in these sets of data. Some of the apparent imbalance between assessed fishable (adult) stock biomass in the early part of the season on the one hand, and the catch plus remaining spawning stock abundance on the other, may *i.a.* be explained by growth and/or by the summer/autumn fishery taking a fairly heavy toll of the juvenile part of the stock. Nevertheless, it seems unreasonable to assume that this accounts for all of the irregularities in this set of data. Thus, the apparently low spawning stocks of 1975 and 1980 may in actual fact have been much larger, either due to direct underestimates of adult stock biomass in the previous autumn or difficulties in determining maturing ratios so early in the biological year.

On the other hand, it is clear that the fishery took an ever increasing toll of the maturing stock in the period 1983-1986 and certainly reduced the spawning stock much below the targeted minimum of 400-500 thousand tonnes in these years. Such extremely low spawning stock abundance as recorded in 1983-1988 would in most circumstances probably have been unable to produce large year classes, but in the first four of these cases the low abundance of capelin, which remained to spawn, was largely brought about by the fishery. To the present author it seems, therefore, reasonable to lay the blame for the capelin stock collapse in the mid-1980s, and in particular the long period of recovery, mainly on the fishery, but to a lesser extent on predation by herring and cod. In all likelihood, the rapid rise of the Barents Sea capelin stock in 1989-1990 was largely brought about by good environmental conditions. In contrast to the stock decline of the 1980s, it seems that human exploitation was not at fault for the stock collapse in 1994. This was, in the present authors view, almost certainly first and foremost due to predatory pressure, be it by herring, cod or both.

It has been theorized that the presence of juvenile herring is a prerequisite for stabilizing the Barents Sea ecosystem in the long run (Hamre 1990). This does not sound convincing, in particular if large year classes of juvenile herring graze down whole cohorts of capelin larvae. During the last 40-50 years, the propagation of the Norwegian spring spawning herring has depended on few large year classes at long intervals (Fig. 24), which normally spend the first 3-4 years of their lives in the southern Barents Sea before migrating out of the area (Anon. 1995). Therefore, if the juvenile herring more or less graze down whole capelin cohorts and then leave the Barents Sea, a more plausible argument seems to be that the advent of a large year class of herring would tend to destabilize the Barents Sea ecosystem. On leaving the area, these herring would thus leave the Barents Sea devoid of pelagic fish food for the cod and other dependent species over a period of at least 2-3 years. However, as pointed out by Jakobsson *et al.* 1996 there is evidence of a much lesser recruitment variance to the Norwegian spring spawning herring stock in the period

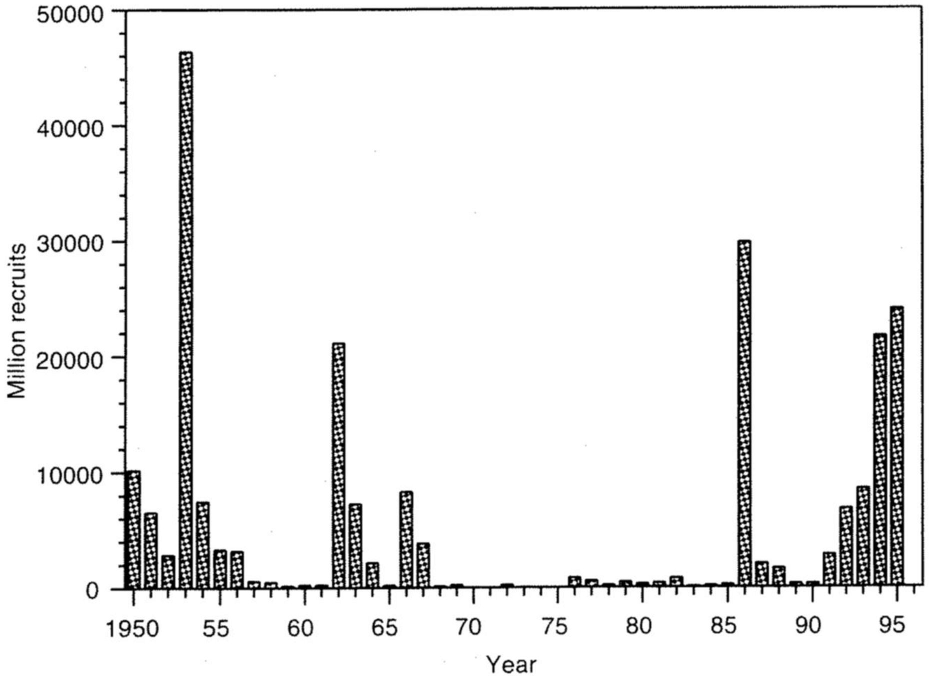

Figure 24. Recruitment of Norwegian spring spawning herring 1950-1995. From Anon. 1996.

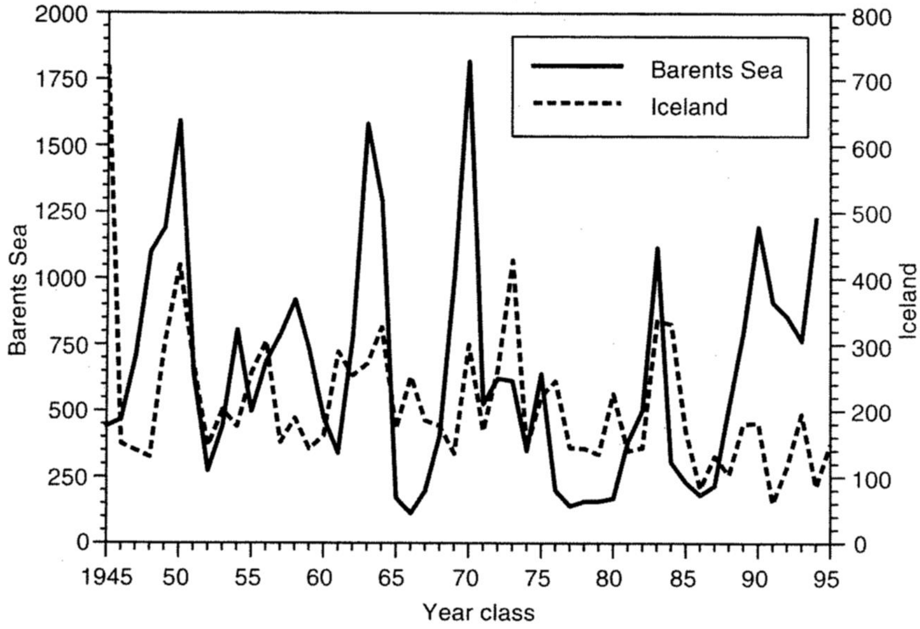

Figure 25. Recruitment of cod at Iceland and in the Barents Sea (number of fish in millions) 1945-1995. From Anon. 1966; 1997.

prior to the 1950s. In those days the presence of juvenile herring in the southwestern Barents Sea may well have had a stabilizing effect on the ecosystem.

In spite of the intense research activity concerning the Barents Sea ecosystem during the present as well as the past decade, there are many questions which we can only answer in part or not at all. For example, it seems that assessments of stock abundance of juvenile and adult capelin in September alone have provided insufficient evidence to enable us to determine the fate of various year classes, *i.e.* how they were actually affected by the herring, the cod and the fishery. Winter surveys of the spawning component, if such surveys were possible and had been carried out, would no doubt have yielded more valuable information of this kind.

But whatever the cause of the present instability of the Barents Sea ecosystem, the situation should remind us that once the balance of an ecosystem has been greatly disturbed, whether by human activities or natural causes, it may take decades to attain again the previous equilibrium or a new one.

In comparison to the Barents Sea ecosystem, that of Icelandic waters and adjacent areas appears to be almost tame with regard to changes of capelin abundance. Probably, the main reason is the far greater variability of recruitment to the northeast arctic cod as compared to that of the Icelandic cod (Fig. 25). Furthermore, in recent years the Barents Sea cod stock has been composed of strong or better than average year classes from 1983 and 1988 onwards, while the Icelandic stock of cod has become depleted to a historic low through overfishing and very poor recruitment since 1984. Thus, although the near collapse of the Icelandic capelin stock in the early 1980s and in 1989-1990 resulted in similar negative deviations of weight-at-age among Icelandic cod as observed for Barents Sea cod, the reduction was less severe (Anon. 1996b; 1997).

The fishery does not seem to have been the major culprit of the observed changes in capelin abundance in the Iceland-Greenland-Jan Mayen area (Fig. 26). However, it may easily be argued that this was mostly due to luck, since the remaining spawning stocks, responsible for the recovery after the stock collapse in the 1980s, were very low in comparative terms (Vilhjálmsson 1994). On the other hand, the summer and autumn capelin fishery may well have accentuated the observed variance of weight at age among the Icelandic cod described earlier.

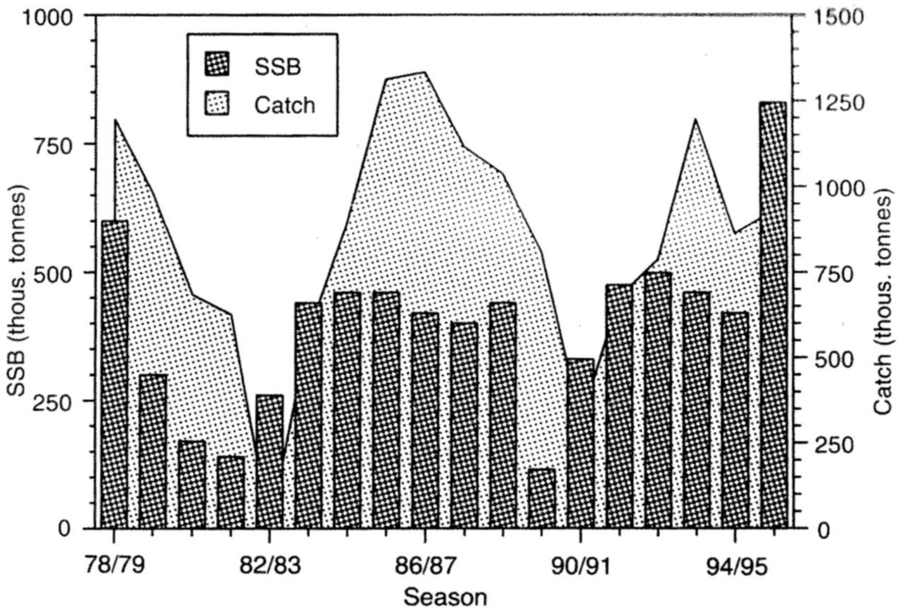

Figure 26. The catch of Icelandic capelin and the remaining spawning stock biomass (SSB) in the 1978/79-1995/96 seasons. From Anon. 1996.

Apart from the higher recruitment variability of the northeast arctic cod as compared to the Icelandic cod, the main difference between the Barents Sea ecosystem and that of Icelandic waters with respect to the harvesting of capelin, lies presently in the state of the cod stocks inhabiting these waters as described above. The apparent balance of the Icelandic ecosystem is in this respect unnatural and created by irresponsible human interference. It follows naturally that the food requirements of the Icelandic cod have been greatly reduced, thus leaving a surplus yield of capelin which otherwise would not be available to the fishery. Another example of the effect of reduced predation by the Icelandic cod is the large increase in the abundance of offshore red shrimp (*Pandalus borealis*) north of Iceland, which is reflected in the increased catch of that species (Anon. 1997; Fig. 27). This is not the kind of situation anyone prefers, with the obvious exception of the capelin and shrimp harvesting sectors, but it has been created and is exploited accordingly with respect to capelin and red shrimp.

The present exploitation of the Icelandic capelin in periods of high abundance includes a summer and autumn season, lasting from July to December and a winter fishery in January-March. Preliminary catch quotas, based on juvenile capelin abundance in the previous year, are set prior to the opening of the season, but final decisions on the total allowable catch (TAC) are based on in-season assessments of abundance obtained in late autumn and/or early in the following year. As a rule, the summer/autumn fishery can be directed to avoid large catches of juveniles through area closures, but the catch taken in summer and early autumn will, nevertheless, in part consist of fish that are growing at a fairly fast rate. The key to a ra-

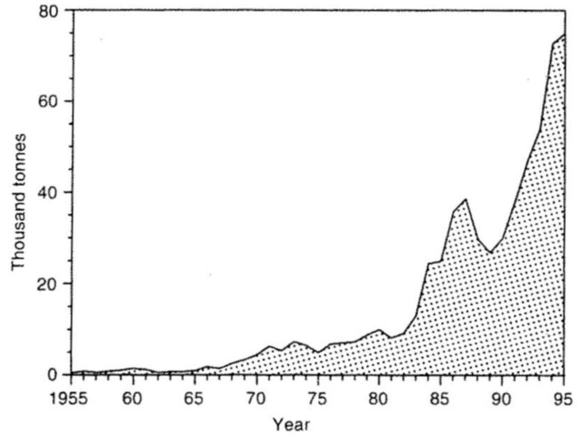

Figure 27. The catch of red shrimp (*Pandalus borealis*) in Icelandic waters 1955-1995. From Anon. 1996b.

tional exploitation of this stock lies in the fact that under normal circumstances it is possible to assess the abundance of the fishable stock nearly at any time after the adult capelin have arrived in the north Icelandic area in October/November until shortly before spawning begins in February/March. This has made it possible to check previous estimates and adjust TACs on a real time basis.

Hopefully, the Icelandic cod will some day regain its natural abundance and, when that happens, the exploitation of the Icelandic capelin will have to be revised. It is, for example, unlikely that a summer fishery which may remove a large part of the mature capelin, so obviously important in the diet of the Icelandic cod, can be allowed before the cod have had their share. The fishing for capelin would then have to be restricted to the late autumn and winter months and conducted under adequate supervision with regard to capelin abundance. In the meantime, steps are being taken for obtaining a fuller understanding of the role of the capelin in the Icelandic ecosystem, not only with regard to the cod but also with respect to predators such as minke and humpback whales, whose numbers have multiplied in the last couple of decades (Sigurjónsson and Víkingsson 1992, 1995).

Since the 1970s, the capelin in the Newfoundland-Labrador region have not been looked upon as a feasible objective for a large scale fishery. In the mid-1970s, foreign vessels, mainly from Norway, Russia and Iceland, fished this stock or stocks, but they collapsed after a few years. At about this time, Canada extended its jurisdiction to 200 nautical miles and a system was devised for managing marine resources within the new Canadian jurisdiction.

In the Newfoundland-Labrador area the main concern at the time was to rebuild the northern cod stock which then was overfished and in low abundance. A conservative fishing strategy was implemented for the cod. In view of the importance of capelin in the diet of the cod it was decided to harvest capelin only for human consumption, taking no more than 10% of estimated capelin abundance in any single year.

Unfortunately, the Canadian experiment failed. A complete change in the offshore fleet fishing for cod and other groundfish species, including the technology of fish finding and catching, was effected in a few years. These innovations and the skill in applying them resulted in an enhancement of the efficiency of the offshore fishery of cod, which was not recognized soon enough. In addition, recruitment has been much below expectations in the last 15-20 years. The abundance of the northern cod was, therefore, consistently overestimated in the 1980s. The stock collapsed and a complete fishing ban is now in force as regards the northern cod and has been since 1992 (Harris *et al.* 1990; Bishop *et al.* 1993; Anon. 1996b).

This stock collapse had in all probability little to do with changes in capelin abundance, but was brought about by the overfishing of cod coinciding with an inhospitable environment as compared to the preceding decades. At times, the hydrobiological conditions on the shelf areas off Labrador as well as eastern and southeastern Newfoundland are probably marginal for the self propagation of cod. It is likely that under such conditions stock abundance has to be at a fairly high level to bridge the gap between favourable periods.

Lately, most other fish stocks, preying on capelin in the Newfoundland-Labrador area, have also been depleted. Although the large increase in the abundance of marine mammals, in particular the seal populations off the coast of Labrador, must to some extent counteract the relief in fish predation, there is little doubt that the total amount of capelin removed by predators from the Newfoundland-Labrador ecosystem has been much reduced in the last decade.

Nevertheless, the capelin abundance recorded in acoustic surveys in the past few years has been very low compared to that of the 1980s. The reasons for this are by no means clear, although there are indications of changed migration pattern and distribution, which may be linked to impairment of the marine climate, experienced in these waters in the 1990s (*e.g.* Miller 1992; Anon. 1995b). Due to restraints of ship time, acoustic surveys of capelin abundance were run along a standardized random grid with practically no room for adjustments. Such surveys may therefore miss major capelin concentrations in times of deviations from the "normal" reference situation used when planning them. The necessary knowledge of capelin abundance and distribution in the Newfoundland-Labrador area is probably insufficient for justifying a large scale capelin fishery in these waters although the potential may be there, at least at times. The cautious approach to a capelin fishery taken by the Canadians may, therefore, be considered prudent under the circumstances. Furthermore, it seems unlikely that there can be room for any large scale fishery of the Newfoundland-Labrador capelin when the stocks of its main fish predators, in particular the northern cod, have regained their former abundance.

A general consensus seems to have been reached in most quarters that one should approach the exploitation of marine ecosystems in a holistic way and with caution. Although much knowledge has been gained in past decades about the role played by capelin in the exploited ecosystems which they are part of, our knowledge is far from complete. Longer time series, covering various parts of the year, are needed with respect to the interactions between capelin and their various predators as well as capelin/plankton relationships and both direct and indirect effects of variations of the marine environment in general. Information on the role and effect of top predators, such as marine mammals and birds, is woefully inadequate due to the ban on exploitation, not to mention scientific sampling, reduced or even abandoned altogether through pressure by the ill-informed and almost hysterical public opinion.

Nevertheless, teams of scientists are busy modelling such interactions and the possible effects of human interference. At present, modelling seems to hold the highest promise of gaining insight in and understanding of marine ecosystems. However, we will have to be careful and should occasionally ponder an old quote from the writings of the late Oscar Wilde: "*We may forgive a man for making a useful thing – as long as he does not admire it.*" In other words, the returns of a model will never be any better than the data fed to it. Furthermore, as long as we keep our boxes of tricks transparent and understand what is happening within them all is well and we will learn. If, however, we fall into the trap of admiring a beautifully performing model without understanding what is going on, we will hit the wall – sooner or later!

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