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Capelin biology and ecology

Capelin (*Mallotus villosus*) in the Iceland–East Greenland–Jan Mayen ecosystem

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The stock of capelin, *Mallotus villosus* (Müller), that inhabits the area between Iceland, East Greenland, and the island of Jan Mayen spawns in shallow coastal water south and west of Iceland. Juveniles grow up over the continental shelf off north Iceland and off East Greenland west of the Denmark Strait. The main feeding area of adults is the Iceland Sea, the oceanic area from about 68 to 72°N, between the Jan Mayen Ridge and the East Greenland continental shelf. After the feeding season, the adult stock assembles over the outer shelf off north Iceland and migrates to the spawning grounds along the south and west coasts from December to March. The main oceanographic features of Icelandic waters and the Iceland Sea are described and capelin migrations related to the distribution of water masses and the ocean current systems in the area. In the past two decades there have been large variations in capelin migrations and catchability, especially during the feeding season. However, these variations can only be explained in part by the available environmental data. Year-class abundance appears to be determined by survival during the first winter, in tune with the greater environmental variability off north Iceland than south and west of Iceland, where these capelin spawn and the larvae start drifting. Adult growth is positively related to the flow of Atlantic water into the area north of Iceland, indicating improved feeding conditions in the Iceland Sea when the Irminger Current is strong. There can be large interannual variations in number and weight-at-age in the adult stock. The main predators are whales, seabirds, and fish, especially cod. The combined annual removal by predators is estimated to have been 2.1–3.4 million tonnes in the early 1990s. The mean weight-at-age of cod aged 5–8 years dropped by up to 25–30% when capelin abundance was low in the early 1980s and 1990s. The relatively low mean weight of cod in the past 3 years may well be due to changed distribution and migration of capelin, resulting in reduced access of cod to this most important item in their diet.

Keywords: capelin, ecology, environment, migrations, predator, prey.

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Introduction

The biology of capelin, *Mallotus villosus* (Müller), in Icelandic waters and in the oceanic area between Iceland, Greenland, and the island of Jan Mayen, i.e. the Iceland Sea and the Denmark Strait, was described by Vilhjálmsson (1994). They are considered to be a separate stock, with spawning grounds in shallow water (10–150 m) off the south and west coasts of Iceland. Spawning peaks in March and the larvae hatch in about 3 weeks, whereafter they drift with the surface currents in a clockwise direction to the shelf area north and east of Iceland, and to a varying degree across the northern Irminger Sea to the East Greenland plateau.

Most juveniles grow up over, or in the vicinity of, the continental shelf off northwest, north, and northeast Iceland and on the East Greenland plateau, west of Vestfirdir (the northwestern peninsula of Iceland, see Figure 1a). Growth is fastest during the first two years, but slows thereafter. The larger part of each year-class matures and spawns at age 3, the remainder at age 4; there are few spawners aged 2, and 5-year-old spawners are rare. Spawning mortality is high, as in other capelin stocks, so in practical terms, the spawning stock is renewed annually.

Maturing capelin aged 2 and 3 years (spawning at ages 3 and 4 the following year) usually undertake extensive northward feeding migrations into the Iceland

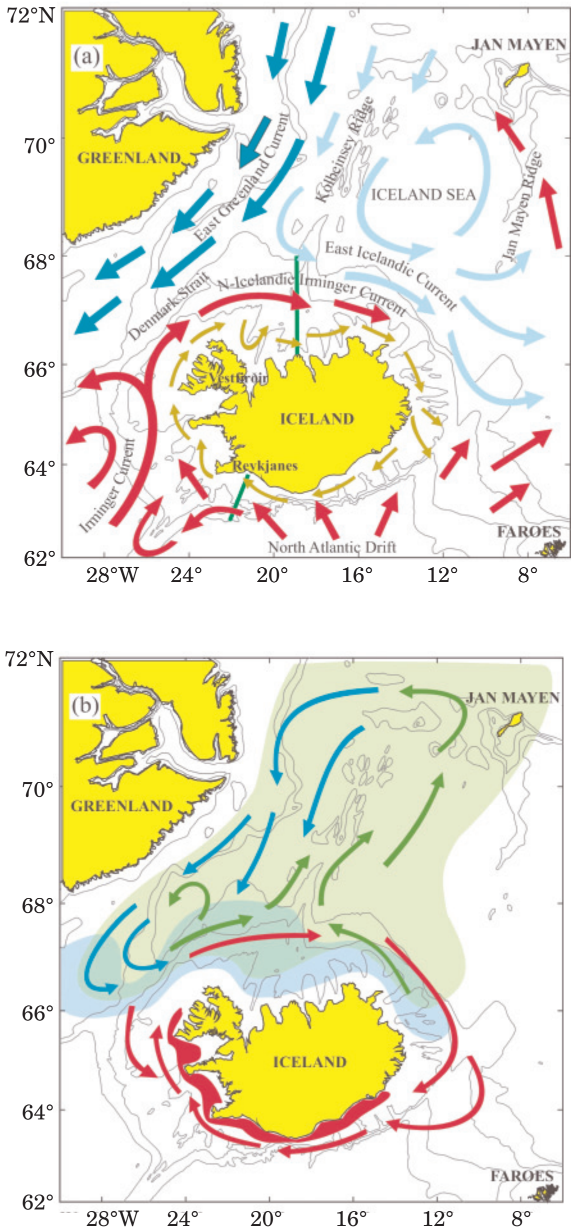

Figure 1. (a) Ocean currents in the Iceland–East Greenland–Jan Mayen area. Red, relatively warm Atlantic water; dark blue, cold, polar water of low salinity; light blue, Arctic water; yellow, Icelandic coastal current. Redrawn after Stefánsson and Ólafsson (1991). Depth contours are 200, 500, and 1000 m. Nomenclature as referred to in text. The two straight, green lines mark the locations of the standard hydrobiological sections off Siglunes (north Iceland) and Selvogsbanki (southwest Iceland). (b) Distribution and migrations of capelin in the Iceland–East Greenland–Jan Mayen area. Red, spawning grounds; green, adult feeding area; blue, distribution and feeding area of juveniles; green arrows, adult feeding migrations; blue arrows, return migrations; red arrows, spawning migrations. Depth contours are 200, 500, and 1000 m. Modified after Vilhjálmsson (1997).

Sea and the Denmark Strait in spring and summer. The return migration takes place in September and October. By November, the adults have usually assembled near the shelf edge off northwest, north, and northeast Iceland, from where the spawning migration starts in December/January, in most years following a clockwise direction along the outer edge of the Icelandic continental shelf. On occasion, however, large spawning migrations may arrive on the spawning grounds off west and southwest Iceland directly from the northwest.

Capelin are pelagic, migratory, planktivorous fish, and changes of their physical and biological environment may have profound effects on their abundance, migrations, distribution, and growth. Because of this, their ecological importance, and the large fishery (Gudmundsdottir and Vilhjálmsson, 2002; Vilhjálmsson and Carscadden, 2002), intensive research on, and monitoring of the state of, the capelin stock in the Iceland–East Greenland–Jan Mayen area has been conducted since the late 1970s.

As in other locations, capelin play a key role in the marine ecosystem in the area. They not only fall prey to several species of marine mammal and seabird, but they are also the main single item in the diet of Icelandic cod (*Gadus morhua*) and of importance as food for several other commercial fish species in Icelandic and Greenland waters.

The purpose of this contribution is to attempt to explain the apparent reactions of capelin to their physical and biological environment, as well as their relationships with other marine stocks found in Icelandic and adjacent waters.

Oceanographic features of Icelandic waters and adjacent areas

The hydrography of the waters surrounding Iceland and those between Iceland, East Greenland, and the island of Jan Mayen (the Iceland Sea and Denmark Strait; Figure 1a) have been described by many authors (e.g. Stefánsson, 1962, 1985; Malmberg, 1972, 1984; Stefánsson and Ólafson, 1991).The main features of the currents in the Iceland–East Greenland–Jan Mayen area are linked to bottom topography (Figure 1a). Atlantic water of relatively high temperature and salinity predominates off the south and west coasts. Off the Vestfirdir peninsula (northwest Iceland), Atlantic water of the Irminger Current flowing north just west of the Reykjanes Ridge splits into two branches. The larger branch flows west towards Greenland, while the smaller, the North Icelandic Irminger Current, flows eastwards onto the shelf north and, to some extent, east of Iceland. A coastal current, essentially driven by gravity forces resulting from land run-off, runs in a clockwise direction around Iceland.

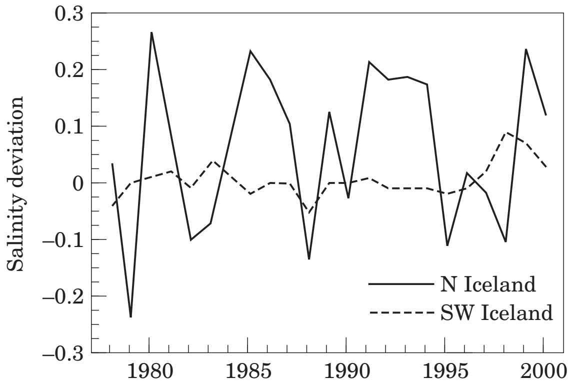

Figure 2. Salinity deviations on the Siglunes (north Iceland) and Selvogsbanki (southwest Iceland) sections in May of the years 1978–2000.

The cold East Greenland Current transports polar water from the Greenland Sea (north of 72°N) southwards along the East Greenland shelf. On meeting the submarine terrace north of Iceland, part of the East Greenland Current branches off and forms the East Icelandic Current. The cold East Icelandic Current is of a less polar character owing to an admixture of warmer Atlantic water from the south as well as from the mixed waters of the Iceland Sea to the north. The East Icelandic Current runs east and then southeast along the outer slope of the shelf off north and northeast Iceland and dissipates into the western Norwegian Sea, north of the Faroes. South and southeast of Jan Mayen, a current flows to the north and northwest, bringing relatively warm, saline water into the Iceland Sea, where a cyclonic eddy is formed in the basin between the Jan Mayen and Kolbeinsey Ridges. For these reasons, conditions in the waters of the Iceland Sea are considerably milder than they would be if the only contributors were the East Greenland and East Icelandic Currents.

Variations in the relative strength of these ocean currents have resulted in large changes in the hydrography of north Icelandic waters, and probably also in the Iceland Sea farther north. On the other hand, the hydrography of the Atlantic water south and west of Iceland is more stable. This is shown in Figure 2, which presents data series from two standard hydrographic sections, off the central north coast and off southwest Iceland respectively (Figure 1a). The Atlantic influence is weakest east of Iceland, and hydrographic variability there is therefore less than north of Iceland, but larger than in the south and west.

The Atlantic water provides an important source of nutrients north of Iceland, both directly through its relatively high nutrient concentration, and indirectly because it renews much more efficiently in the surface layer by eddy diffusion than in the highly stratified Arctic or polar waters. During warm periods with small extension of drift ice, and consequently small or even negligible admixture of polar water to the surface layers, continued inflow of Atlantic water to north of Iceland will maintain favourable mixing conditions. This makes for a longer-lasting period of phytoplankton production and richer stocks of zooplankton during warm periods than during cold ones (Thórdardóttir, 1984; Stefánsson and Ólafson, 1991; Astthorsson and Gislason, 1998).

Capelin–environment relationships

Migrations

Although capelin migration may be variable, there seems to be a common general pattern of movements and distribution of the stock in the study area (Vilhjálmsson, 1994). A schematic representation of this migration pattern is given in Figure 1b.

Comparison of Figure 1a and b shows that the migrations and distribution of capelin are closely linked to the system of ocean currents, and consequently to the distribution of water masses of the Icelandic shelf and in the Iceland Sea. This is especially obvious in the case of the offshore phase of spawning migrations north and east of Iceland in January and early February, as well as their adherence to less-saline, shallow waters of the Icelandic coastal current while migrating west along the south coast and north to the west of Iceland before and during spawning in February/March. The same is true of the distribution of age 1 and 2 juveniles, which mainly occupy the mixed, zooplankton-rich waters of the north Icelandic shelf and the East Greenland plateau, west of Vestfirdir (Figure 1b).

Furthermore, on the basis of Norwegian hydrographic data, scouting and stock assessment surveys, and fisheries data from the late 1970s to the early 1990s, Vilhjálmsson (1994) concluded that the feeding migration of adult capelin to higher latitudes (72°N) during spring and early summer was linked to an east–west temperature gradient, running in a south-southwest–north-northeast direction along or east of the Kolbeinsey Ridge. The return migration usually follows a more westerly route along the eastern border of the East Greenland Current, in mild years even reaching westwards over the outer part of the East Greenland shelf. Despite large changes in stock abundance (see Figure 4a later), this migration pattern continued uninterrupted during the 10-year period 1978–1987, but stopped abruptly in 1988. This was associated with extremely cold conditions in the southern Iceland Sea (less than -1.5°C) apparently blocking any northward migration beyond about 68°N until late summer. The northward feeding migrations were also greatly reduced in the years 1989–1992 and, despite warmer conditions in the northern areas already in 1989, capelin did not resume their previous pattern of feeding migration to higher latitudes until 1993 (Vilhjálmsson, 1994).

Since then, such extensive northward migrations cannot be described as annual occurrences. Figure 3 shows the geographic position of Icelandic catches of capelin (about 80–90% of the total catch) as tonnes per square nautical mile in the fishing seasons 1992/1993–2000/2001. The adult stock biomass at the beginning of the summer season and Icelandic summer/autumn catches of the same fishing seasons are shown in Figure 4a and b respectively. There were no drastic changes in capelin abundance, fleet structure, or fishing technology during the past 10 years, and interest and participation in the fishery remained the same, though catches have been variable. Consequently, catch statistics may be assumed roughly to describe the extent of feeding migrations and availability of capelin to the fishery in summer during those years.

The most reasonable explanation of the different distribution patterns and variable success of the summer/autumn fishery in those years seems to be environmental variability. Considerable research on the hydrography of the Iceland and Greenland Seas was carried out during the latter half of the 20th century (Stefánsson, 1962, 1985; Malmberg, 1972, 1984; Stefánsson and Ólafson, 1991). However, this research was intermittent, was focused mostly on studies of chemical and physical oceanography of Iceland and of ocean waters, and therefore does not throw much light on variations in the migration of capelin north of 68°N.

There is a much greater regularity, both in landings and distribution, of winter catches than there is of the catch taken in summer and autumn of the years 1993–2001, the catching area being more or less continuous from off southeast Iceland to the central west coast (Figure 3). However, in the series presented here, there are two exceptions (1998 and 1999), when practically no catches were made west of the Reykjanes promontory (southwest Iceland; Figure 1a). The scenarios were similar in 1970 and 1978, and seem to be connected to weather-induced changes of the current running west along the south coast, the direction of which may be temporarily reversed (Vilhjálmsson, 1994).

Stock and recruitment

The abundance of 0-group capelin has been measured annually since 1970, and that of the older age-classes since 1978. In the period for which data are available for comparison (1979–2001), it appears, albeit with some large deviations, that the measured abundance of 0-group capelin reflects the size of the parent stock. Using a simple linear model, this relationship is significant, but it explains only 23% of 0-group variability (Table 1). However, the data series contains one glaring outlier, the 0-group index of 12 resulting from a spawning-stock biomass (SSB) of 650 000 t in spring 2000 (Figure 5a). Omitting this data point from the analysis, some 38% of the 0-group variability is explained by the parent stock biomass (Figure 5; Table 1). This relationship is in line with the results obtained by Jóhanndóttir and Vilhjálmsson (1999). They also compared the calculated total annual egg deposition and the resulting 0-group indices during the years 1979–1999 and found that, in a linear relationship, total egg deposition explained 45% of the variability of 0-group abundance then.

Comparisons of the 0-group index and total year-class size in numbers at ages 1 and 2, calculated from acoustic estimates, catches, and rates of natural mortality (Gudmundsdottir and Vilhjálmsson, 2002) are not significant (Figure 5b; Table 1). On the other hand, there is a highly significant relationship ($r^2=0.84$, $p<0.0001$) between the numerical abundance of year-classes, measured by acoustics at age 1, and the abundance of adults of the same year-classes at age 2, back-calculated as described by Gudmundsdottir and Vilhjálmsson (2002; see also Figure 6 and Table 1). These comparisons indicate that survival through the first winter of life is of greater importance in finally determining year-class size than larval and 0-group survival rates during the first few months of life.

Capelin are pelagic, planktivorous fish and therefore must be particularly sensitive to the ever-changing hydrobiological conditions of the seas where they feed. However, tests of relationships between hydrography and zooplankton abundance, measured on standard sections southwest and north of Iceland in spring (Figure 1a) and the numbers of capelin at the 0-group stage, as well as at ages 1 and 2, all proved to be not significant when considering the whole period 1978–2001 (Table 1).

Environment and growth

As mentioned earlier, time-series on hydrobiological variables of north Icelandic waters are mostly limited to the region of the Icelandic shelf (south of 68°N), inhabited by most commercial fish stocks that feed on capelin. Because adult capelin usually migrate to feed in summer in the Iceland Sea north of this area (68–72°N), the available environmental data do not directly describe the feeding conditions of those capelin.

Nevertheless, Malmberg and Blindheim (1994) noted certain general similarities between variations in oceanographic conditions north of Iceland in spring on the one hand, and the biomass of adult capelin in the period 1978–1992 on the other. The low sea temperatures and zooplankton production from 1979 to 1981 and again in the early 1990s seemed to be associated with reduced capelin growth and recruitment.

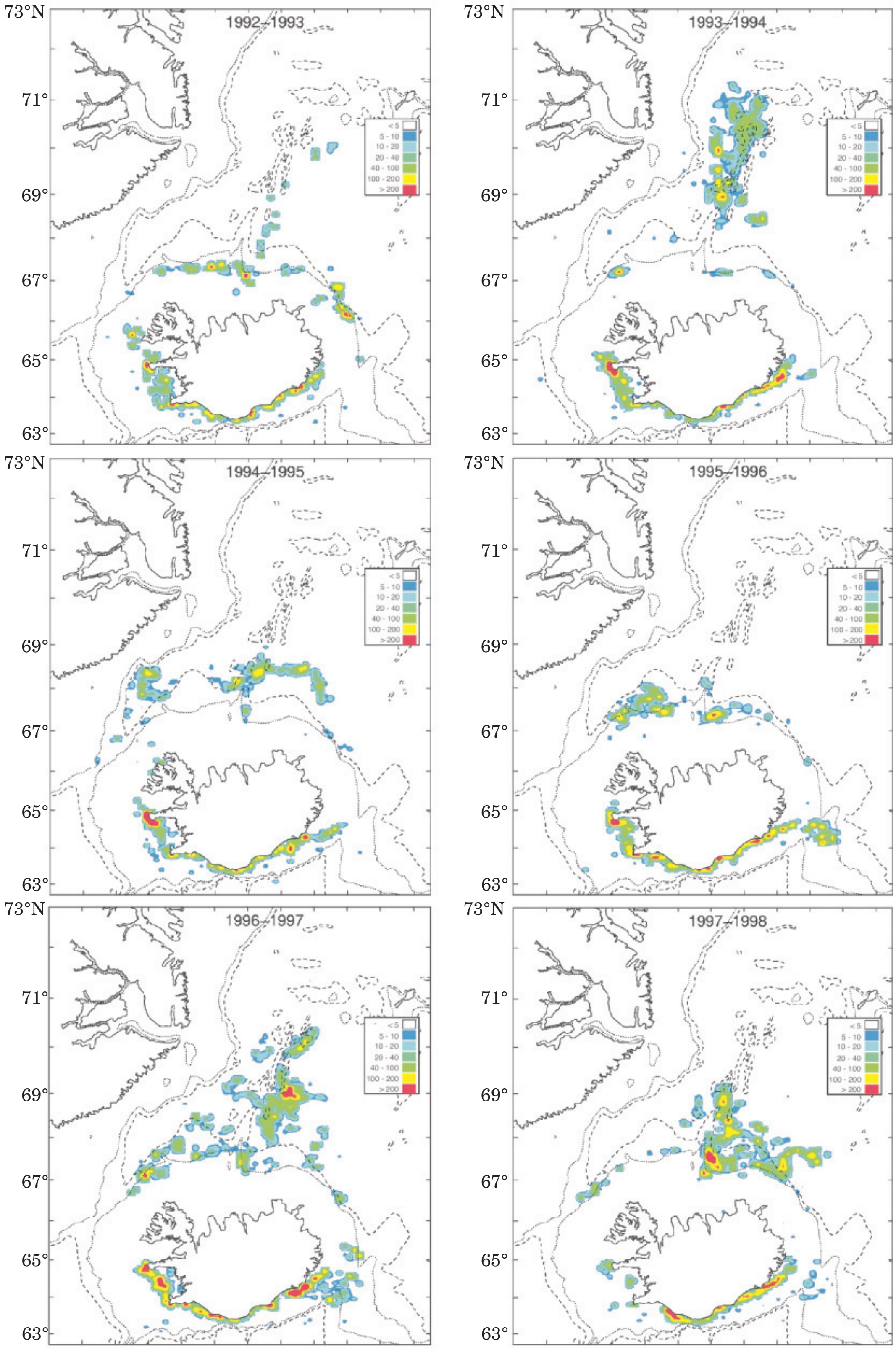

Figure 3. Part 1.

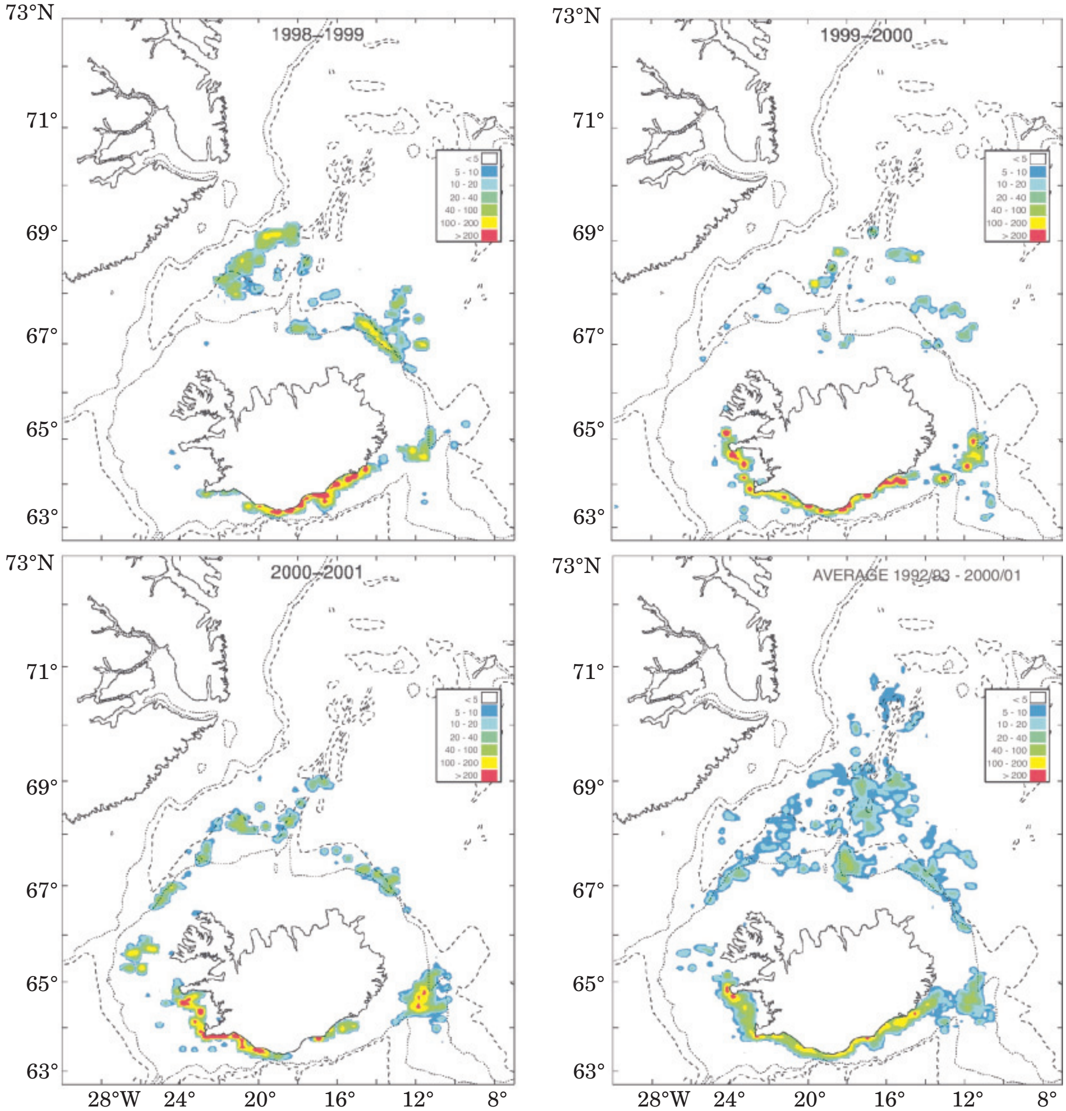

Figure 3. Part 2.

Figure 3. Icelandic catches of capelin in the Iceland–East Greenland–Jan Mayen area in the 1992/1993–2000/2001 fishing seasons. Quantities are expressed in tonnes per square nautical mile. Catches north of 66°30′N are from summer/autumn, and those south of 66°N between January and March.

Astthorsson and Gislason (1998) classified hydrographic conditions north of Iceland during the years 1970–1998 into two categories, cold and warm. Applying principal component analysis to these two categories, they found that zooplankton biomass was significantly greater in warm years than in cold years. Similarly, average weight and weight-at-age of capelin, as well as capelin biomass, were significantly bigger in warm years.

When comparing weight-at-age of adult capelin in winter with hydrographic variability off the central north coast of Iceland in spring of the previous year, a highly significant positive linear relationship emerges. Some 45% of the variability in the weight-at-age of adult capelin aged 3 and 4 years is explained by observed salinity deviations on the Siglunes section (north Iceland; Figure 1). This relationship is shown in Figure 7b. There is also a significant, but somewhat weaker, correlation between capelin weight-at-age in winter and the sea temperature north of Iceland in spring of the year before (Figure 7a). Both these relationships are given in Table 1. The similarity of these

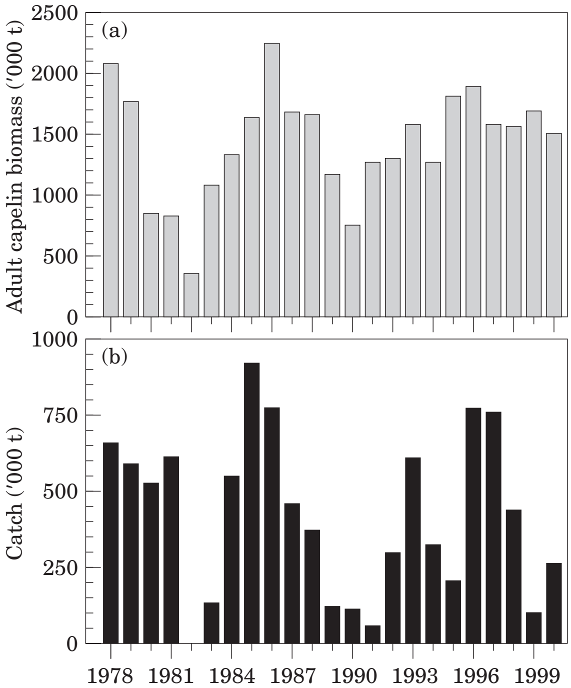

Figure 4. (a) Adult capelin biomass at 1 August of the years 1978–2000, and (b) total international catch in summer/autumn of the same years.

relationships is reasonable, because both salinity and temperature are a measure of the degree of flow of Atlantic water into the north Icelandic area and are therefore autocorrelated.

On the other hand, a significant relationship between zooplankton abundance on the Siglunes section and weight-at-age of capelin is not found for the same series as a whole (Table 1). The most reasonable explanation of this seems to be that variations in the hydrography north of Iceland in spring are indicative of such conditions farther north, but that variations of zooplankton are not. The zooplankton community of the Iceland Sea, where capelin feed in summer, is of an Arctic nature, whereas Atlantic zooplankton populations normally dominate over the Icelandic shelf south of 68°N. Furthermore, point estimates of zooplankton abundance may be misleading, because they only describe abundance at the time of observation and do not necessarily tell what has happened or will happen during the previous and following weeks.

On the basis of the available hydrographic and biological data, it seems likely that the large hydrobiological variability of north Icelandic waters to some extent reflects conditions in the Iceland Sea, the main feeding area of adult capelin. Great environmental variability in the Iceland Sea is further manifested in catch data from the summer fishing season, showing variations, both of geographic position and catch rates, as described earlier. Furthermore, the maximum interannual difference between the lowest and highest average weights of adult capelin aged 3 and 4 years in winter may be as high as 30% for the younger age-class and 25% for the older one (Figure 8).

On returning from their summer foraging in the Iceland Sea in autumn, adult capelin have increased their weight by a factor of 2–4 (depending on age and feeding conditions), and their fat content has risen from about 4 to 15–20% of their body weight (Vilhjálmsson, 1994). A large stock of capelin therefore transfers huge amounts of energy from the more northern and colder Iceland Sea and Denmark Strait to the ecosystem of Icelandic waters proper, where it becomes available to cod and other predators. From late autumn until spawning in March the following year, the stored fat is practically used up, in part for somatic growth, but mainly for gonadal development and fuelling the long migration from the wintering areas north of Iceland to the spawning grounds off the south and west coasts.

Predator–prey relations

Capelin are in the lower range of the marine foodweb and are generally preyed upon by larger fish, marine mammals, and seabirds.

As described earlier, most juvenile capelin aged 0, 1, and 2 years reside over the shelf off northern Iceland and on the East Greenland shelf west of the Denmark Strait (Figure 1b) These parts of the stock are therefore accessible to predatory fish, marine mammals, and seabirds throughout the year. On the other hand, the summer feeding migrations of maturing capelin aged 2 and 3 years (spawning at ages 3 and 4 in March of the following year) into the colder waters of the Iceland Sea and Denmark Strait (Figure 1b), place the larger part of the adult stock out of reach of most predatory fish, except Greenland halibut (*Reinhardtius hippoglossoides*) for about 5–6 months. However, the same capelin are available to whales and seabirds then. By October/November, when the adult capelin have returned to the vicinity of the shelf break off northwest, north, and northeast Iceland, they also become readily available to the local fish predators, and remain so until at the end of the spawning period in late March/early April of the following year.

The main fish predator of Icelandic capelin is Atlantic cod, but capelin are also staple in the diet of Greenland halibut, eaten in quantity by saithe (*Pollachius virens*), and even haddock (*Melanogrammus aeglefinus*) in the spawning season, to name but three other major commercial stocks.

Cod of all ages eat capelin, small (<40 cm) ones mainly juveniles, 40–60 cm ones an increasing proportion of adult capelin, and large cod (>60 cm) almost exclusively adults (Pálsson, 1997). It is estimated that

Table 1. Summary statistics for the data comparisons listed in text.

Relationship	Slope (p)	Intercept (p)	d.f.	r^2 (p)
Stock and recruitment				
SSB/0-group × 10	0.72 (0.028)	13.6 (0.304)	21	0.23 (0.021)
SSB/0-group × 10	0.91 (0.002)	6.9 (0.554)	20*	0.38 (0.002)
0-group/N_1	0.57 (0.306)	117.7 (0.0002)	21	0.05 (0.307)
0-group/N_{2tot}	0.35 (0.354)	76.8 (0.0002)	21	0.04 (0.354)
$N_{1acoustics}/N_{2mat.}$	0.56 (<0.0001)	20.7 (0.0009)	17	0.84 (<0.0001)
Capelin biomass and mean weight of cod, 1978/1979–1997/1998				
FSB/Av.Wt/Age 4†	0.12 (0.160)	1458 (<0.001)	18	0.13 (0.059)
FSB/Av.Wt/Age 5†	0.36 (<0.001)	1904 (<0.001)	18	0.59 (<0.001)
FSB/Av.Wt/Age 6†	0.68 (<0.001)	2569 (<0.001)	18	0.88 (<0.001)
FSB/Av.Wt/Age 7†	0.82 (<0.001)	3705 (<0.001)	18	0.69 (<0.001)
FSB/Av.Wt/Age 8†	0.71 (0.004)	5290 (<0.001)	18	0.36 (0.004)
FSB/Av.Wt/Age 9†	0.39 (0.068)	7128 (<0.001)	18	0.14 (0.059)
Capelin biomass and mean weight of cod, 1978/1979–2000/2001				
FSB/Av.Wt/Age 4†	0.11 (0.160)	1465 (<0.001)	21	0.09 (0.160)
FSB/Av.Wt/Age 5†	0.33 (<0.001)	1919 (<0.001)	21	0.46 (<0.001)
FSB/Av.Wt/Age 6†	0.62 (<0.001)	2590 (<0.001)	21	0.68 (<0.001)
FSB/Av.Wt/Age 7†	0.78 (<0.001)	3723 (<0.001)	21	0.63 (<0.001)
FSB/Av.Wt/Age 8†	0.69 (0.004)	5312 (<0.001)	21	0.33 (0.004)
FSB/Av.Wt/Age 9†	0.42 (0.068)	7123 (<0.001)	21	0.15 (<0.068)
Environmental parameters and mean weight of capelin				
TempSi/Wt/Age 3	1.07 (<0.001)	19.6 (<0.001)	30	0.36 (<0.001)
TempSi/Wt/Age 4	1.19 (<0.001)	25.3 (<0.001)	30	0.29 (<0.001)
SalSi/Wt/Age 3	8.77 (<0.001)	19.2 (<0.001)	30	0.44 (<0.001)
SalSi/Wt/Age 4	8.42 (<0.001)	24.9 (<0.001)	30	0.44 (<0.001)
ZooSi/Wt/Age3	0.04 (0.828)	19.1 (<0.001)	30	0.001 (0.828)
Hydrography and zooplankton biomass				
SalSi/ZooSi	0.021 (0.136)	− 0.035 (0.486)	30	0.07 (0.136)
TempSi/ZooSi	0.112 (0.226)	− 0.479 (0.145)	30	0.05 (0.226)

*Year 2000 (outlier – Figure 5a) deleted.
†These ages refer to predatory cod.

capelin constitute on average almost 50% by weight of the total food consumption by cod. However, the contribution of capelin to the diet of cod by weight varies from 80 to 90% during the capelin spawning season in March to less than 25% in summer (Pálsson, 1997).

Total consumption of Icelandic capelin by cod during the years 1982–1995 has been modelled in the range 345 000–845 000 t annually, with an average of about 620 000 t (Björnsson *et al*., 1997). However, very recent studies indicate that removal of capelin by cod may be even larger, and amount to about 1.5 times the fishable cod biomass (H. Björnsson, unpublished data). As shown in Figure 9, the fishable part of the cod stock (aged 4+) ranged between about 550 000 and 1 050 000 t in the period 1982–1995, with an average of 810 000 t. Using the multiplication factor of 1.5, the average annual removal of capelin by cod is estimated at about 1.2 million tonnes, somewhat higher than the modelled consumption of 620 000 t for the same period (Table 2). The abundance of cod has since declined considerably, and in the past 10 years the fishable biomass has varied between about 530 000 and 730 000 t, with an average of 620 000 t (Figure 9; Anon., 2001; ICES, 2001). Again using the multiplication factor of 1.5, this translates into an average annual consumption of capelin by cod during the past decade of some 930 000 t.

Saithe and Greenland halibut stocks are much smaller than that of cod, and their removal of capelin is therefore less. It has been estimated that the annual consumption of capelin by saithe could be of the order of 100 000 t (Jónsson, 1997). Sólmundsson (1997) estimated that capelin constituted about 25% of the diet of Greenland halibut, but he did not attempt to quantify capelin consumption by that predator. Assuming the average fishable biomass of Greenland halibut to be about 220 000 t between 1992 and 1995 (ICES, 2000b), Greenland halibut could probably have consumed at least the same weight of capelin annually in those years. Einarsson (1997) states that very large quantities of capelin are eaten by adult haddock in shallow water south and, in particular, west of Iceland during the capelin spawning season in March. Haddock feeding during that short period is so intense that, although only

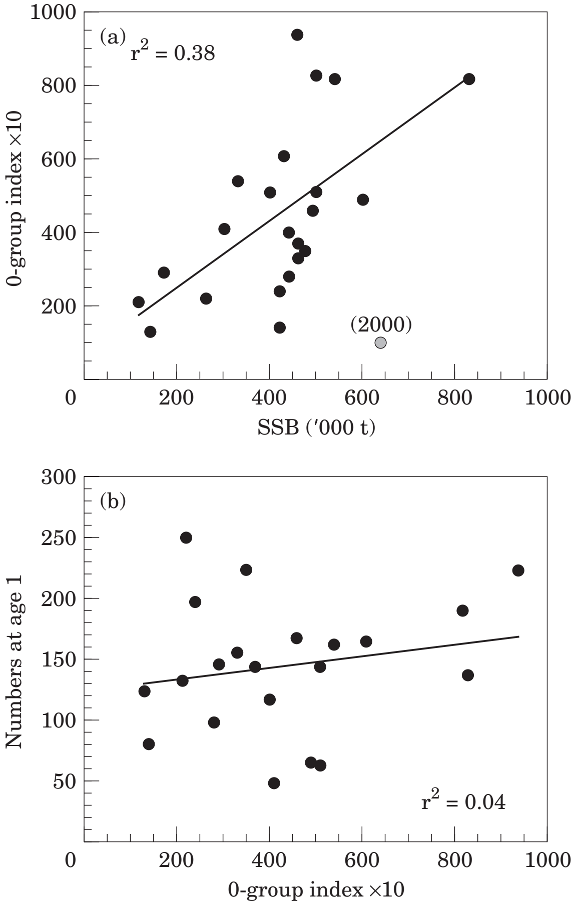

Figure 5. Relationship between (a) spawning-stock biomass and (b) year-class size at age 1 (10^9) and the resulting 0-group index. See also Table 1.

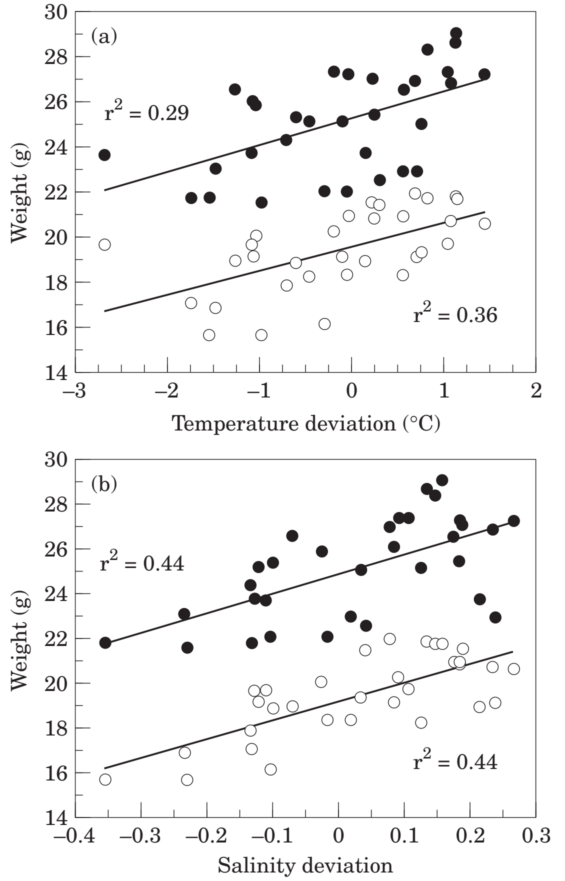

Figure 7. Relationships between (a) temperature and (b) salinity deviations in spring on the Siglunes section (north Iceland; Figure 1) and average weights of adult (age 3 and 4) capelin in winter of the following year during the years 1970/1971–2000/2001. See also Table 1.

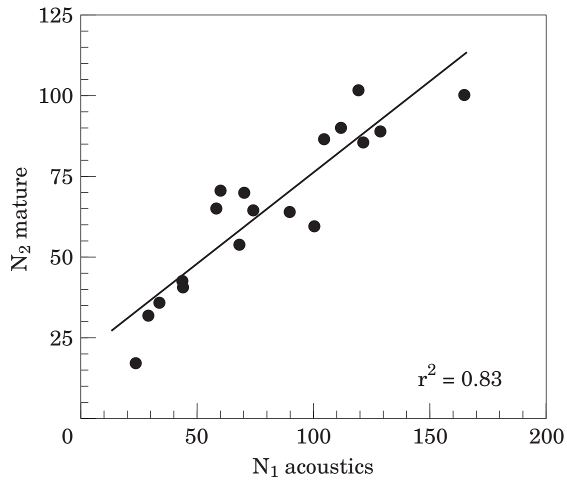

Figure 6. Relationship between measured numbers (10^9) of the year-classes of 1979–1998 at ages 1 and 2. See also Table 1.

small amounts of capelin are taken in other areas and months, capelin constitute approximately 50% of the estimated total food ingested by Icelandic haddock over the whole year. Gorge-feeding by haddock on capelin in their spawning season, and the low contribution by capelin to the diet of haddock at other times of the year, also suggests that haddock take advantage of the poor physical condition of capelin after spawning. Einarsson (1997) did not attempt to further quantify capelin consumption by haddock, but such intense feeding could probably equal the haddock spawning stock biomass, i.e. about 80 000 t annually during the years 1992–1995. Estimates of annual capelin removal by these three fish predators are given in Table 2.

When weight-at-age of cod in winter is plotted against abundance of adult capelin in summer of the year before, a clear and significant positive relationship between capelin and cod aged 5–8 years emerges (Figure 10; Table 1). Therefore, when the capelin stock

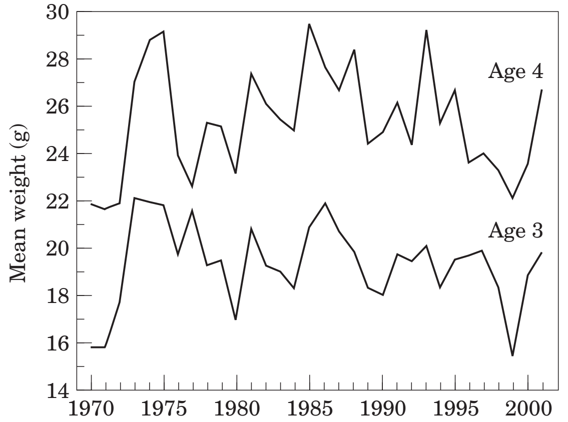

Figure 8. Variations in mean weight of adult capelin at ages 3 and 4 in winter of the years 1970–2001.

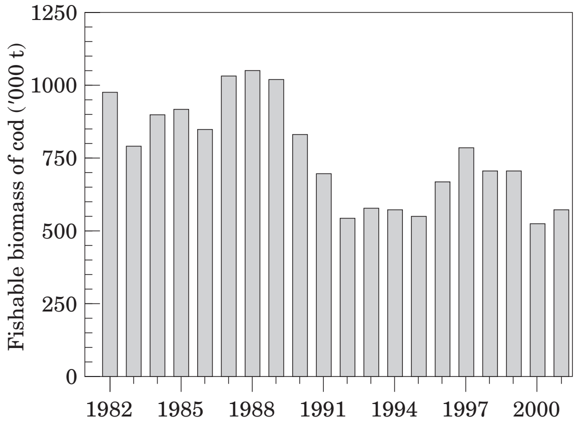

Figure 9. Changes in fishable stock biomass (age 4+) of Icelandic cod, 1982–2001.

collapsed in the early 1980s, the average weight of cod of those ages decreased by about 25%. The capelin stock decline in the early 1990s resulted in a similar drop in mean weight of cod. However, the effect on the cod stock was smaller and of shorter duration, in line with the measured changes in capelin abundance during the two periods. Therefore, it appears that Icelandic cod of medium age and size are unable to find substitute food during periods of capelin shortage.

Younger cod, which eat mostly juvenile capelin, do not exhibit such clear responses to variations in abundance of that part of the capelin stock. This is probably because the fat, and therefore the energy content, of juvenile capelin is many times lower than that of adult capelin (Vilhjálmsson, 1994), as well as because less fatty krill and other crustaceans (mainly red shrimp, *Pandalus borealis*) are preyed on extensively by juvenile cod. The same is true for older, larger cod, which can and do take advantage of larger fish prey (Pálsson, 1997). Relationships between capelin abundance and growth of other fish predators have not yet been demonstrated off Iceland.

Apart from man and fish, the most important capelin predators are marine mammals and seabirds. By far the largest players are without doubt minke (*Balaenoptera acutorostrata*) and humpback (*Megaptera novaeangliae*) whales, but considerable quantities may also be taken by fin whales (*Balaenoptera physalus*) and even dolphins (e.g. *Phocoena phocoena*). For the first three whale species, estimates based on data for the period 1987–1995 indicated an annual combined removal of some 800 000 t of capelin (Table 2; Sigurjónsson and Víkingsson, 1997; Sigurjónsson *et al.*, 2000). However, the total calculated consumption by fin whales (some 63 000 t) is derived from stomach samples of animals taken west and southwest of Iceland. These locations are outside the main distribution areas of capelin, and the proportion of capelin in the diet of these fin whales amounted to only 2.4%, while the bulk consisted of krill. It is known that, in other northern areas, fin whales often take fish, especially capelin, as an important secondary prey (Sigurjónsson, 1995), or even as their main prey item (Mitchell, 1975). Because the summer migrations of fin whales continue north to the Iceland Sea, and thus into the distribution area of adult capelin, Stefánsson *et al.* (1997) reasoned that capelin in the Iceland–East Greenland–Jan Mayen area could represent up to 30% of the total diet of fin whales, instead of the 2.5% indicated by the local data on stomach contents of these whale species. According to an estimate by the same authors, this would amount to an annual capelin removal by fin whales of the order of some 780 000 t (Table 2). Furthermore, numerous aerial and seaborne counts of large whales give a strong indication that the population of humpback whales in Icelandic waters has increased at a steady rate of 11.2% annually since 1956. This would raise the annual humpback removal of capelin to some 800 000 t, as compared with previous estimates of 120 000 t (Gunnlaugsson and Vikingsson, 2001; Gunnaugsson, pers. comm.).

It is my opinion that the new, higher estimate of capelin consumption by humpback whales is much more realistic than the old one. Humpback hunting ceased more than 50 years ago, and there is no doubt that their numbers have increased greatly since the summer/autumn fishery for capelin in the Iceland Sea and Denmark Strait commenced in the late 1970s. Witness to this is the fact that, in the past decade and a half, humpback whales have increasingly been caught in capelin seines in both their summer feeding areas and in the deeper water winter fishing areas north and east of Iceland. In recent years, entrapments of 1–2 whales have become commonplace, and on one or two occasions the incredible figure of five was reported. Naturally, such

Table 2. The main predators of capelin in the Iceland–East Greenland–Jan Mayen area.

Predator species	Annual consumption of capelin ('000 t)	Annual consumption of capelin ('000 t)	Source
Cod, *Gadus morhua*	620		Björnsson *et al.*, 1997
Cod		900‡	H. Björnsson, MRI, unpublished
Saithe, *Pollachius virens*	100	100	Jónsson, 1997
Haddock, *Melanogrammus aeglefinus*	80	80†	Einarsson, 1997
Greenland halibut, *Reinhardtius hippoglossoides*	220†	220†	Sólmundsson, 1997
Minke whale, *Balaenoptera acutorostrata*	610	610	Sigurjónsson and Víkingsson, 1998; Sigurjónsson *et al.*, 2000
Humpback whale, *Megaptera novaeangliae*	120	120	Stefánsson *et al.*, 1997; Sigurjónsson and Víkingsson, 1998
Humpback whale		800‡	Gunlaugsson and Vikingsson, 2001
Fin whale, *Balaenoptera physalus*	60		Sigurjónsson and Víkingsson, 1998
Fin whale		780	Stefánsson *et al.* (1997)
Guillemot, *Uria aalge*	70*	140*	Lilliendal and Sólmundsson, 1997
Brünnlich's guillemot, *Uria lomvia*	40*	80*	Lilliendal and Sólmundsson, 1997
Razorbill, *Alca torda*	15*	30*	Lilliendal and Sólmundsson, 1997
Puffin, *Fratercula arctica*	25*	50*	Lilliendal and Sólmundsson, 1997
Kittiwake, *Rissa dactyla*	15*	30*	Lilliendal and Sólmundsson, 1997
Northern fulmar, *Fulmarus glacialis*	10*	20*	Lilliendal and Sólmundsson, 1997
Total	1985	3840	
Fishery (average annual catch of past 10 years)	1050	1050	ICES, 2001
Total	3035	4890	

*Summer consumption only.
†Author's translation of source information into likely annual consumption.
‡New estimates of present annual consumption.

entrapments are considered by the fishers to be a nuisance, but the whales generally, and given time, escape either over the float line or, in the worst cases for damage, through the netting. It is of note that there are no reports of humpback whales being killed in the process of entrapment and escape, with or without the current author present. The new estimate of capelin consumption by humpback whales would raise the annual removal by large cetaceans to about 2.2 million tonnes.

Capelin removal by dolphins has not been quantified, but it appears to be mostly limited to the capelin spawning season (Sigurjónsson and Vikinsson, 1997). Seal stocks in the study area are small (Bogason, 1997; Hauksson, 1997), and their impact on this capelin stock is negligible.

The annual removal of capelin by six species of seabirds during summer (May–July) is estimated at about 175 000 t (Lilliendal and Sólmundsson, 1997). While there are no estimates of capelin consumption by birds at other times of the year, a conservative estimate of the total annual removal could be about 350 000 t.

Based on the evidence available at present, the combined removal of capelin by marine mammals and birds could be of the order of 1–2 million tonnes. On average, the combined annual removal of capelin by all its natural predators mentioned above might range between roughly 2 and 3.8 million tonnes (Table 2). In addition, the fishery has removed an average of about 900 000 t annually during the period 1977–2001, though for the past 10 years that average has been slightly higher, at 1 055 000 t (ICES, 2001; Table 2).

Discussion

Capelin in the Iceland–East Greenland–Jan Mayen area appear to be highly sensitive to environmental variations in the waters they occupy. As described earlier, the main nursery areas are the mixed waters of the north Icelandic shelf, and the spawning migrations closely follow the boundary between the cold East Icelandic Current and the warmer waters of the shelf north and east of Iceland. After entering coastal waters southeast of Iceland, spawners migrate with the less-saline, cooler coastal current to spawn farther west along the south coast and west of Iceland.

Owing to the scarceness of environmental data for the main capelin feeding area in the Iceland Sea, it is not possible to quantify the effects of the environment on capelin biology. This makes it impossible to identify other potential, e.g. density-dependent, effects. For example, in the 1990s, growth rates were related to fishable stock abundance by number, indicating

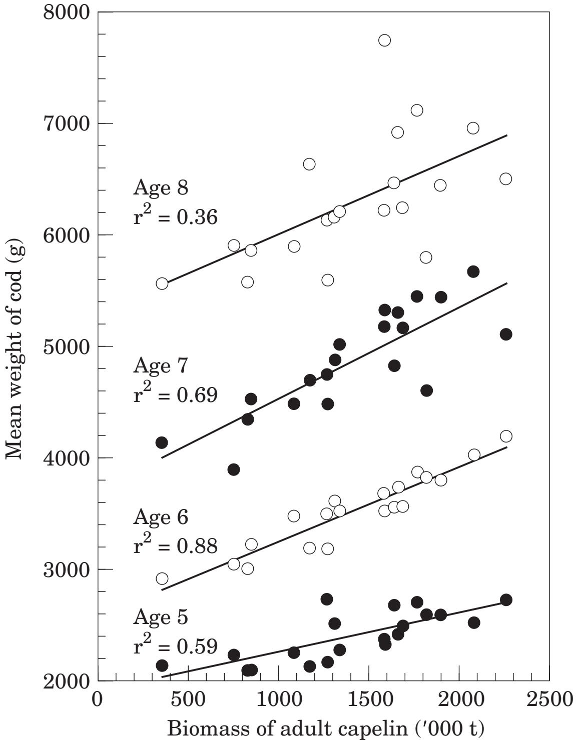

Figure 10. Relationship between the biomass of adult capelin and the mean weight of cod aged 5–8 years in winter of the following year during the years 1978/1979–1997/1998. See also Table 1.

competition (e.g. ICES, 1999, 2000a, 2001). However, this relationship does not hold for the whole data series 1979–2001, suggesting that density-independent effects (i.e. environment) may at times override density-dependent effects (competition).

Landings and the distribution of catches (Figures 4, 5b) reveal large changes during the years 1992–2000, in terms of migrations and availability of capelin to the fishery in summer and autumn. Therefore, feeding migrations north to 70–72°N are indicated by the catch distribution only in 1992, 1993, and 1996, whereas this seems to have been an annual occurrence in the late 1970s and until 1988, when a northward migration was prevented by a tongue of very cold water reaching east to 12°W just off the shelf break north of Iceland (Vilhjálmsson, 1994). According to the catch distribution, it also seems that, during the feeding seasons of 1996 and 1997, the stock was distributed eastwards (east of the Kolbeinsey Ridge), whereas a westward distribution is apparent for 1994, 1995, 1998, and 2000. As already stated, the success of the summer/autumn fishery was highly variable during the period 1992–2000 despite the consistently high abundance of capelin (Figure 4). This variability is, therefore, most likely environmentally induced.

As pointed out earlier, there is a strong relationship between the growth of cod of medium size and age, and the biomass of adult capelin. Owing to a rapid and unforeseen decline of recruitment to the fishable capelin stock in the late 1970s, it is clear that the large summer/autumn fishery in 1980 and 1981 removed a major share of the adult capelin before they arrived on their winter grounds off northern Iceland (Figure 4). The fishery for capelin must therefore be held largely responsible for the drop in weight-at-age of cod in those years. However, the summer fishery failed during the stock decline in the early 1990s and therefore cannot be held responsible for that stock decline and its effects.

During the past three years the capelin/cod relationship has been upset. This is especially apparent in the case of 5- and 6-year-old cod, for which there is a reduction of r^2 by 0.13 and 0.2 respectively, when the cod/capelin data pairs 1998/1999–2000/2001 are included (Table 1) These age-classes seem to be the ones most dependent on capelin for their food. Because the capelin stock was healthy during those years (Figure 9), this relationship is thought to have been upset by changed capelin distribution and migrations. With one exception, adult capelin abundance was successfully assessed on and near the outer slope of the shelf off north and northeast Iceland in autumn of the years 1991–1997. The only exception was autumn 1994, when effective surveying of capelin was impossible because of storms and drift ice (Vilhjálmsson and Carscadden, 2002). On the other hand, the November/December surveys in 1998, 1999, and 2000 all failed to locate but minor parts of the adult capelin stock measured in January/February of 1999, 2000, and 2001 (ICES, 1999, 2000a, 2001). All surveys covered the "usual" distribution area of adult capelin in late autumn, which overlaps to a large extent that of cod. Therefore, it has to be concluded that there were few adult capelin over the outer shelf north of Iceland in autumn of those years, resulting in a large reduction in availability of capelin to cod during October–January of the seasons 1998/1999–2000/2001, compared with previous periods. The most likely reason seems to be increased inflow of Atlantic water to the north of Iceland, which began in late 1997 and has persisted since (Anon., 2000).

On average, the combined removal of capelin by the predators listed in Table 2 could have been between about 2 and 3.8 million tonnes annually during the 1980s and the first half of the 1990s. This is a massive removal and would appear to be at variance with acoustic assessments of capelin stock size and the setting of responsible TACs. However, the discrepancy need not be as large as it looks. Capelin consumption by minke whales mostly takes place over and in the vicinity of the continental shelf off northern Iceland in summer. Therefore, the capelin consumed by this major predator probably consists in the main of immature fish aged 0, 1, and 2 years.

Because acoustic assessments of both immature and adult fishable capelin are carried out between November and February, minke, fin, and in part humpback, whales have already taken their share. The same is true for at least half the seabird consumption and most of the capelin taken by juvenile cod (ages 0–3).

On the other hand, capelin consumption by adult cod and other fish predators occurs, in the main, during the winter months of October–March. Nevertheless, the mortality rate of capelin, calculated from stomach contents and feeding rates of these predators during that period, is considerably larger than the mortality rates derived from successive acoustic estimates and catches (Vilhjálmsson, 1994). While this difference needs to be resolved, it is of serious consequence only in cases when capelin abundance is low or has been reduced to a large degree by the summer fishery, as happened in 1980 and 1981.

The available estimates of capelin removal by most, if not all, their natural predators are probably quite imprecise, especially in the case of whales, for which practically no stomach content samples have been available for decades owing to the moratorium on whaling. Nevertheless, one can accept the overall picture that capelin is one of the most important single prey species in the Iceland–East Greenland–Jan Mayen ecosystem. At present, all its main fish predators are at relatively low levels of stock abundance, and stock sizes of whales are presumably increasing because of the whaling moratorium. When the state of the stocks of fish predators improves, the now large capelin fishery will have to be scaled down if the aim is to maintain an ecological balance with the fish predators. An obvious first action would be to curtail or eliminate the summer fishing season (July–September), which catches capelin in their northern feeding areas before cod and other fish predators have gained access to this highly important item in their diet.

Concluding remarks

Both direct and indirect evidence points to a strong environment/capelin relationship which is manifested in the large variability, not only of capelin migrations and growth in the summer feeding period, but also in their behaviour and consequently the success of the summer/autumn fishery. Unfortunately, the data at present available for the main adult feeding areas (north of 68°N) are too few to explain the mechanisms of reactions between adult capelin and their environment, and can at best be used as proxies. This is an unacceptable lack of knowledge, not only from a purely scientific point of view, but also because information on migrations and growth are fundamental to modelling species interactions for management purposes. Systematic observations of environmental factors, likely to affect capelin migrations, distribution, growth, and availability to the fishery in these northern areas, should therefore be planned, to extend initially over a period of, say, 5 years, and to start as soon as possible.

The necessity of establishing such a programme is all the more urgent because environmental variability of the Iceland Sea in the capelin feeding season in summer and autumn almost certainly determines the distribution of adult fish between October and early December, when acoustic surveys of fishable stock are conducted. Experience has shown that there may be large variations in the geographic location of the adult stock in autumn (Vilhjálmsson, 1994; Vilhjálmsson and Carscadden, 2002). Having no previous knowledge of the approximate position of the stock, autumn surveys are more likely to fail, perhaps leading to serious management problems in cases when stock abundance is less than predicted.

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