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Climate variability and the Icelandic marine ecosystem

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Abstract

This paper describes the main features of the Icelandic marine ecosystem and its response to climate variations during the 20th century. The physical oceanographic character and faunal composition in the southern and western parts of the Icelandic marine ecosystem are different from those in the northern and the eastern areas. The former areas are more or less continuously bathed by warm and saline Atlantic water while the latter are more variable and influenced by Atlantic, Arctic and even Polar water masses to different degrees. Mean annual primary production is higher in the Atlantic water than in the more variable waters north and east of Iceland, and higher closer to land than farther offshore. Similarly, zooplankton production is generally higher in the Atlantic water than in the waters north and east of Iceland. The main spawning grounds of most of the exploited fish stocks are in the Atlantic water south of the country while nursery grounds are off the north coast. In the recent years the total catch of fish and invertebrates has been in the range of 1.6–2.4 million ton. Capelin (*Mallotus villosus*) is the most important pelagic stock and cod (*Gadus morhua*) is by far the most important demersal fish stock. Whales are an important component of the Icelandic marine ecosystem, and Icelandic waters are an important habitat for some of the largest seabird populations in the Northeast Atlantic.

In the waters to the north and east of Iceland, available information suggests the existence of a simple bottom-up controlled food chain from phytoplankton through *Calanus*, capelin and to cod. Less is known about the structure of the more complex southern part of the ecosystem. The Icelandic marine ecosystem is highly sensitive to climate variations as demonstrated by abundance and distribution changes of many species during the warm period in the 1930s, the cold period in the late 1960s and warming observed during the recent years. Some of these are highlighted in the paper.

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Keywords: Biomass; Climate variability; Icelandic marine ecosystem; Production

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1. Introduction

This paper presents a description of the main components of the Icelandic marine ecosystem and their response to climatic variation. The physical oceanographic character and faunal composition in the southern and western parts of the Icelandic marine ecosystem differ from those in the northern and the eastern areas. The former areas are bathed by warm and saline Atlantic water while the latter are influenced by Atlantic, Arctic and even Polar water masses, and subject to larger interannual variation (Malmberg and Valdimarsson, 2003; Jonsson and Valdimarsson, 2005a). The distribution of many marine organisms reflects the difference

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between the Atlantic and the Arctic environments (e.g., Gislason and Astthorsson, 2004), but others, such as most of the commercially important fish stocks, exploit both the areas by spawning in the Atlantic water and growing up in the waters off the north and northeast coasts (Astthorsson et al., 1994). Therefore, in spite of the differences in the currents and water masses around Iceland, they create an environment that is generally quite continuous in its nature (Astthorsson and Vilhjalmsson, 2002; Gaard et al., 2005).

The emphasis in this paper is on the ecosystem effects of climate fluctuations in the more variable waters to the north of Iceland. However, due to the distribution of many organisms within both the Atlantic and the Sub-Arctic ecotypes and the lack of detailed regional information, the discussion is in many cases in the wider context of Icelandic waters as a whole. Even in that, basic information is still lacking on some major components of the Icelandic marine ecosystem and their response to climate variability. Some of these gaps in knowledge are discussed in the concluding remarks of the paper and will be addressed in the coming years as an Icelandic component of the planned Ecosystem Studies of Sub-Arctic Seas (ESSAS) Programme (Hunt and Drinkwater, 2005).

2. Oceanographic features

Iceland is located at the junction of the Mid-Atlantic Ridge and the Greenland–Scotland Ridge just south of the Arctic Circle (Fig. 1). The shelf surrounding Iceland mainly follows the 400–500 m depth contour with the total area within the 500 m isobath being about 212,000 km^2. The shelf is narrowest off the south coast while off the west, north and east coasts it is relatively broad, extending for 100–150 km from the coast (Fig. 1).

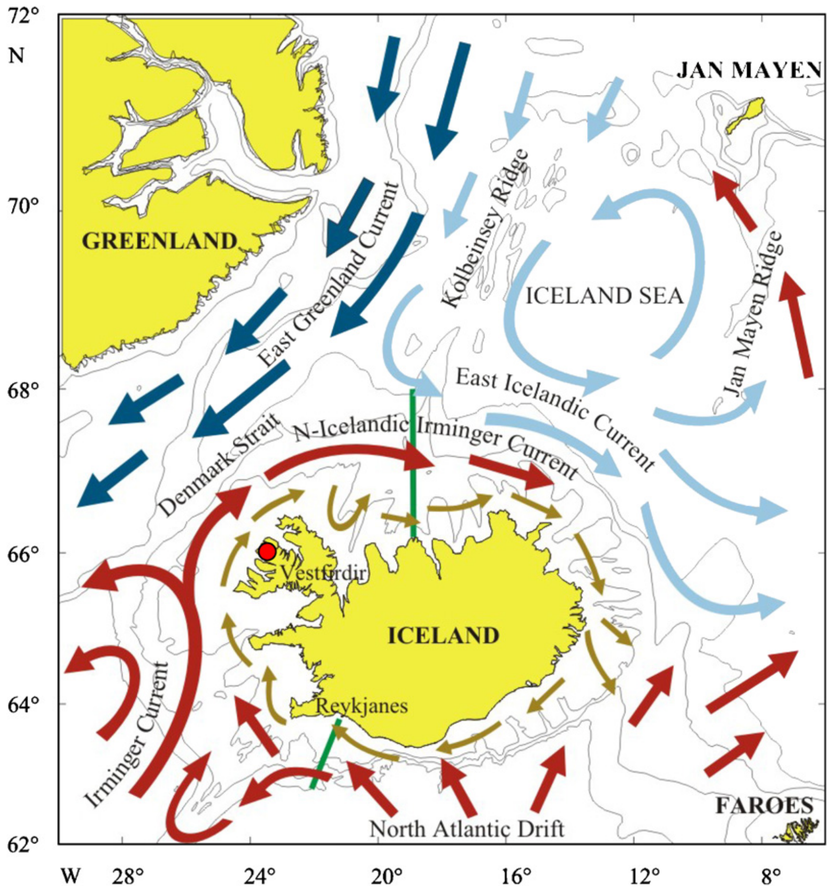

Fig. 1. Surface ocean currents around Iceland. The green lines show hydrographic monitoring transects (Siglunes, north of Iceland; Selvogsbanki, south of Iceland) and the red dot indicates the position of the meteorological station at Thverfjall. Modified from Vilhjalmsson (2002).

The deep Iceland Basin to the south of Iceland, is separated in the west from the Irminger Sea by the Reykjanes Ridge, part of the Mid-Atlantic Ridge, and in the east from the Norwegian Sea by the Iceland–Faroe Ridge. North of Iceland the Kolbeinsey Ridge is a continuation of the Mid-Atlantic Ridge. It stretches to the Jan Mayen Fracture Zone, between Jan Mayen and Greenland, which marks the northern limit of the Iceland Sea and separates it from the Greenland Sea. South from Jan Mayen, the Iceland–Jan Mayen Ridge extends to the Iceland–Faroe Ridge and separates the Iceland Sea from the Norwegian Sea to the east.

The submarine ridges influence the oceanic circulation and water mass distributions around Iceland (Stefansson, 1962; Jonsson and Valdimarsson, 2005a) and consequently the biological production and distribution of the marine populations (Thordardottir, 1994; Astthorsson and Vilhjalmsson, 2002; Gislason and Astthorsson, 2004; Gislason, 2002, 2005). The Greenland–Scotland Ridge is of particular importance since it limits the exchange of water through Denmark Strait and over the Iceland–Faroe Ridge, preventing direct connection of waters below their threshold depths of 620 m and 550 m, respectively. Topography also determines the position of the fronts separating the water masses thereby influencing the associated biological processes and species composition, which tend to differ on either side of the fronts (Poulain et al., 1996; Valdimarsson and Malmberg, 1999; Gislason and Astthorsson, 2004).

Iceland is surrounded by two primary water masses with very different origins and properties (Fig. 1). Originating far south in the North Atlantic, warm and saline Atlantic water is brought towards the southern shores of the country. It then flows westward as the Irminger Current and eventually north along the west coast. Most of this water turns west towards Greenland and subsequently flows southwestward along the slope off Greenland. A smaller branch continues northwards onto the north Icelandic shelf area as the North Icelandic Irminger Current (Valdimarsson and Malmberg, 1999). South of Iceland the temperature of the Atlantic water ranges from 6 to 11 °C depending on the season but the salinity is typically between 35.0 and 35.2.

The other primary water mass is Polar water, which originates in the Arctic Ocean. Relatively fresh ($S<34.5$) and very cold ($T<0\,^{\circ}\mathrm{C}$), it flows out of the Arctic Ocean through Fram Strait between Spitsbergen and Greenland as the East Greenland Current. Below the Polar water the East Greenland Current transports remnants of Atlantic water from the Norwegian Atlantic Current that crosses the Fram Strait and subducts under the Polar water. The East Greenland Current, which also carries sea ice from the Arctic, flows along the shelf and continental slope off East Greenland and mainly exits the Nordic Seas through the Denmark Strait. Mixing and cooling of different proportions of Atlantic and Polar waters form almost all the other water masses in the area. An exception is the low-salinity coastal water mass in summer caused by freshwater run-off that circulates clockwise around Iceland with the general circulation. The cold and low-salinity East Icelandic Current, which flows southeastward along the northeast Icelandic continental slope, carries with it Arctic water that is a mixture of water derived from the inflow of Atlantic water to the Iceland Sea south of Jan Mayen, Polar water from the East Greenland Current and Atlantic water from the North Icelandic Irminger Current (Stefansson, 1962; S. Jonsson, 1992; Swift and Aagaard, 1981). As a result of the deep-water formation north of the Greenland–Scotland Ridge, there are strong bottom currents through Denmark Strait (Jonsson and Valdimarsson, 2004; Macrander et al., 2005) and over the Iceland–Faroe Ridge east of Iceland (Perkins et al., 1998). These currents are important constituents of the thermohaline circulation of the world oceans.

Temperature and salinity conditions are variable, particularly over the shelf north of Iceland, where the Polar Front separates the contrasting Atlantic and Polar water masses (Stefansson, 1962; Malmberg and Valdimarsson, 2003). This is mainly due to large variations in the relative amounts of Atlantic and Polar water over the northern shelf (Jonsson and Valdimarsson, 2005b). Atlantic water is usually evident as a tongue of relatively warm and saline water but the temperature and salinity decrease in the direction of the flow due to mixing with colder, less-saline water from the north and freshwater run-off from land. For over 50 years a hydrographic section across the shelf north of Iceland (Siglunes transect; Fig. 1) has monitored the marine climatic conditions in the area (Fig. 2). After a generally warm period in the northern North Atlantic and in the waters to the north of Iceland from 1920 to 1964, the period from 1965 to 1971 was characterized by low temperature and salinity and often accompanied by sea ice on the northern shelf

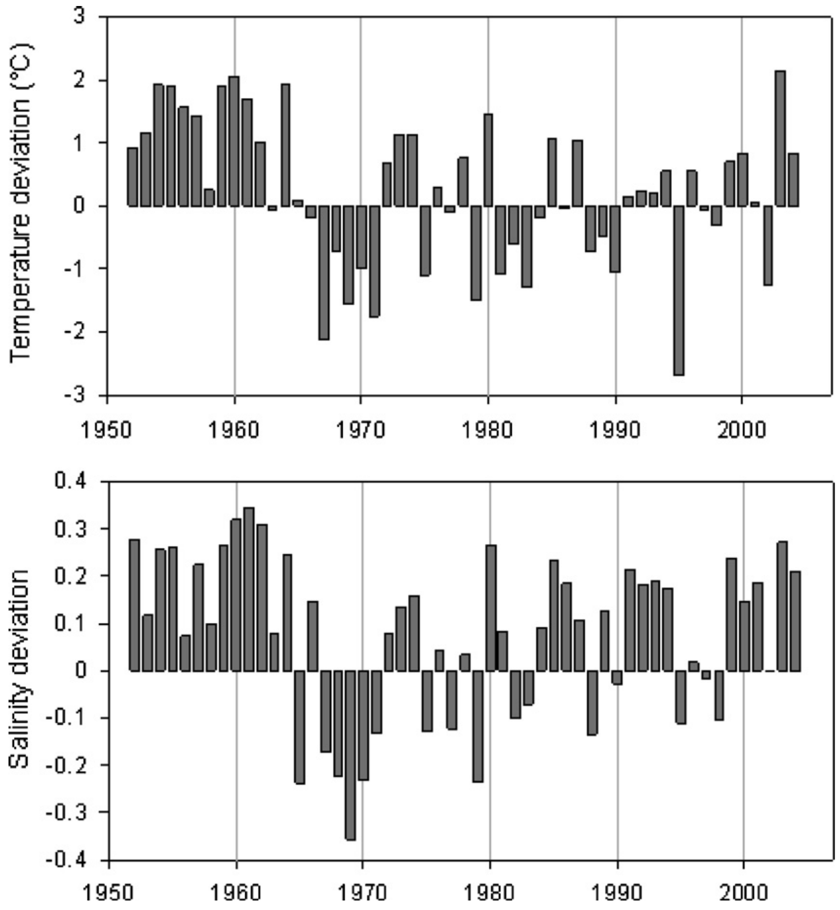

Fig. 2. Temperature and salinity deviations in late spring from the 1961 to 1980 average (3.288 °C and 34.727) on the Siglunes transect (see Fig. 1) to the north of Iceland (the deviation is based on five stations between 4 and 85 km offshore and depths of 0, 20, 50, 75, 100, 150 and 200 m). Based on data in Anon (2005b).

(Malmberg, 1986). Temperature differences in the waters north of Iceland between these two periods were up to 4 °C (Malmberg and Jonsson, 1997). Between 1971 and 1995 "warm" (1972–1974, 1980, 1984–1987 and 1991–1994) and "cold" (1975, 1977, 1979, 1981–1983, 1989, 1990, 1995) periods of 1–4 years alternated. During 1996 temperatures north of Iceland increased again and since then the temperature has been relatively high, indicating an intensified flow of Atlantic water to the area (Malmberg and Valdimarsson, 2003; Jonsson and Valdimarsson, 2005b).

In the warm Atlantic water south of Iceland the marine climate is more stable, although temperature and salinity observations (Selvogsbanki transect; Fig. 1) have demonstrated some interannual variations (Malmberg and Valdimarsson, 2003). For example, salinity was particularly low during the periods 1974–1978, 1985–1988, and again 1992–1995. These periods have been related to "Great Salinity Anomalies" in the northern North Atlantic (Malmberg, 1985; Dickson et al., 1988; Belkin et al., 1998; Belkin, 2004). Also, there has been a gradual increase in salinity and temperature since 1996 (Anon, 2005b; Malmberg and Valdimarsson, 2003). The increased temperature and salinity both north and south of Iceland in the recent years are a part of a larger-scale change observed in the North Atlantic Ocean (Anon, 2004a).

Atmospheric patterns influence the ocean circulation around Iceland. Northerly winds, as measured at Thverfjall in northwest Iceland, tend to reduce the flux of Atlantic water through the Denmark Strait and onto the north Icelandic shelf (Fig. 3), whereas southerly winds increase the flow (Jonsson and Valdimarsson, 2005b). This is in accordance with the strong correlation between the spring

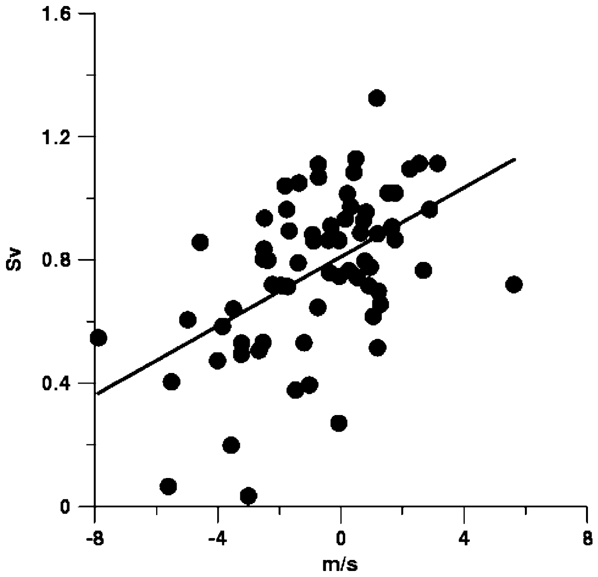

Fig. 3. Relationship ($p < 0.01$) between monthly flux of Atlantic water through Denmark Strait in Sverdrups ($1\,\mathrm{Sv} = 10^6\,\mathrm{m}^3\,\mathrm{s}^{-1}$) and the monthly north-south component of the wind at Thverfjall (see Fig. 1 for location) for the period 1994–2001.

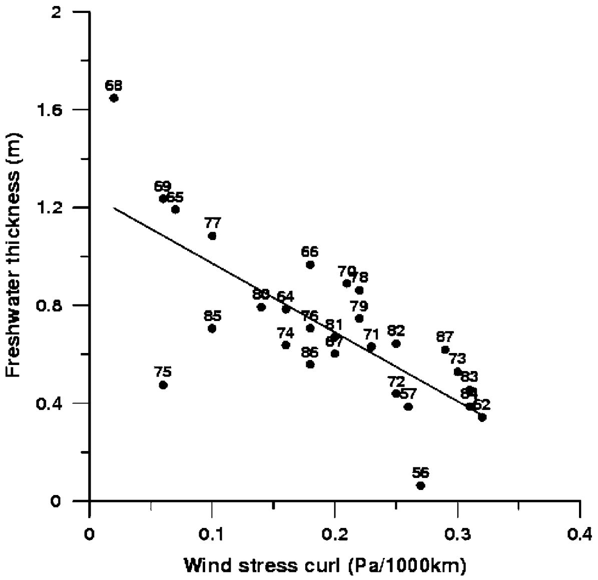

Fig. 4. Relationship between freshwater thickness in spring within the East Icelandic Current and wind-stress curl over the Iceland Sea averaged over 1-year period prior to the salinity measurement. The numbers above the points indicate the year of the salinity measurement. From S. Jonsson (1992).

temperature at Siglunes and the atmospheric pressure gradient across the Denmark Strait found by Blindheim and Malmberg (2005). Olafsson (1999) earlier reported a significant relationship between hydrographic conditions in spring at the Siglunes transect and the frequency of local northerly/southerly wind directions but no correlation with the North Atlantic Oscillation (NAO) index. S. Jonsson (1992) further demonstrated that the amount of freshwater within the East Icelandic Current was related to the local wind-stress curl over the Iceland Sea (Fig. 4). This freshwater content is a measure of the amount of Polar water within the Iceland Sea and affects the convection as well as the biological processes, such as the onset and magnitude of primary production north of Iceland (Thordardottir, 1984).

The above examples indicate that the atmospheric forces driving the observed seasonal and interannual variations in the ocean climate north of Iceland seem to be more local in origin rather than being associated with large-scale atmospheric patterns such as the NAO. This is probably because the NAO index is mainly related to the westerly winds blowing across the Atlantic at mid-latitudes to the south of Iceland.

Most of the sea ice that reaches Iceland originates from the Arctic Ocean and is transported southwards by the East Greenland Current along the east coast of Greenland, although during winter some ice is also formed along the way (Wadhams, 1986). In most years, sea ice on the Icelandic shelf is only a temporary wind-dependent feature (Jakobsson, 2004), usually first seen to the northwest and then transported along the north coast as part of the general clockwise circulation around the country. A normal inflow of Atlantic water over the northern shelf usually melts any ice quite quickly, but if the flow of Atlantic water is blocked and Polar water persists over the shelf, sea ice can drift to the east coast and in extreme cases as far as the south coast. This occurred during the cold period between 1965 and 1971 with drastic effects on the ecosystem (Malmberg, 1986). Sea-ice records at Iceland during the past 120 years generally indicate increased ice coverage during cold periods and reduced ice in warm periods (Figs. 2 and 5).

3. Phytoplankton

Diatoms of the genera *Thalassiosira* spp. and *Chaetoceros* spp. typically dominate the phytoplankton spring bloom over the Icelandic shelf (Thordardottir and Gudmundsson, 1998). During some years, however, the prymnesiophyte *Phaeocystis pouchetti* may be abundant in the waters to

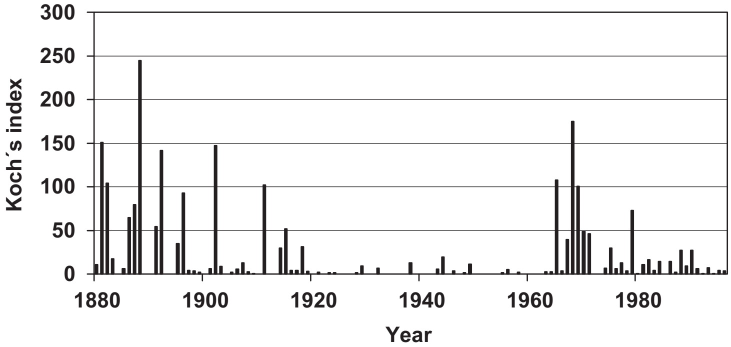

Fig. 5. Koch's (1945) sea-ice index near Iceland 1880–1996. The index is the product of the number of weeks with ice per year and the number of coastal areas near which it was observed. Based on data from Thor Jakobsson, Icelandic Meteorological Office.

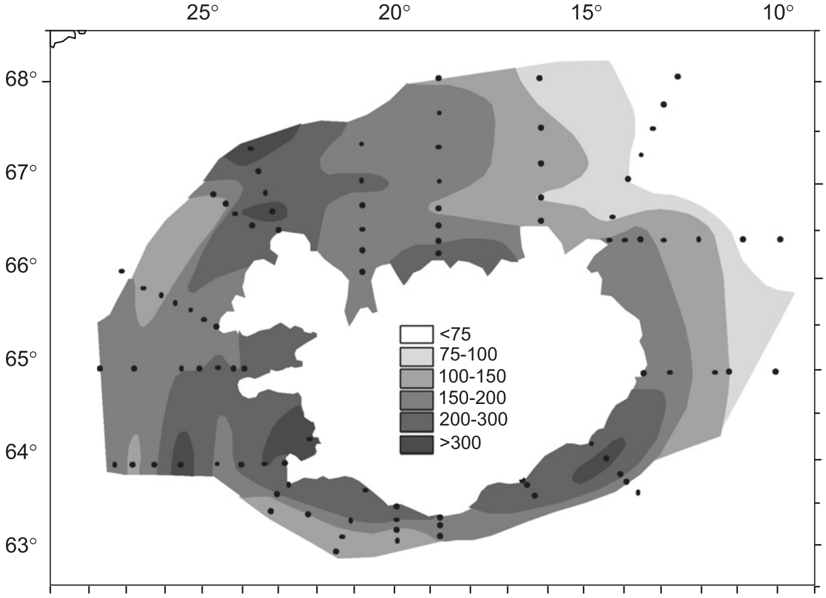

Fig. 6. Average annual primary production ($gC\,m^{-2}\,yr^{-1}$) in Icelandic water based on data from 1958 to 1982. Redrawn from Thordardottir (1994).

the north of Iceland in spring. Dinoflagellates of the genera *Ceratium* spp. and *Protoperidinium* spp. increase in abundance after the spring bloom while diatoms continue to be relatively abundant. In the autumn there is usually a second bloom of diatoms although dinoflagellates may still be abundant (Thordardottir and Gudmundsson, 1998).

On the basis of long-term (1958–1982) production measurements, Thordardottir (1994) estimated the average annual primary productivity in Icelandic waters (Fig. 6). Over the southern and western shelves the primary production tends to decrease seawards while over the northern shelf the productivity decreases from west to east, i.e., in the direction of diminishing admixture of Atlantic water. Relatively high primary production is found in the frontal areas southeast and northwest of Iceland. The annual primary production is generally higher in the warm Atlantic water off the south and west coasts (200–300 $gC\,m^{-2}\,yr^{-1}$) than in the colder Sub-Arctic/Arctic water off the north and east coasts (100–200 $gC\,m^{-}\,yr^{-1}$) (Fig. 6).

Variable hydrographic conditions, particularly over the northern shelf, result in marked interannual changes in the spring development of the phytoplankton (Thordardottir, 1976, 1977, 1984, 1986). Primary production estimates at stations with salinity >34.5 and <34.5 demonstrate that the

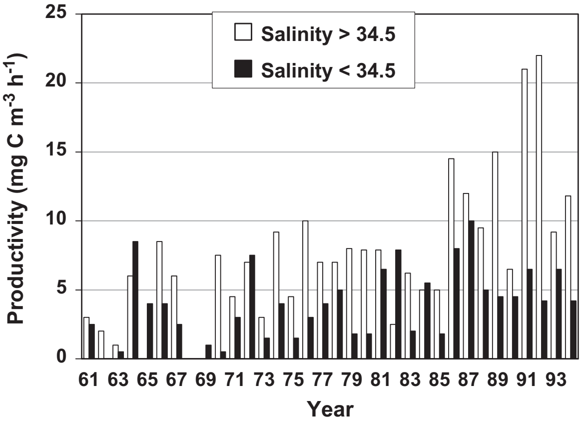

Fig. 7. Comparison of mean productivity (mgC m^{-3} h^{-1}) in the shelf region northeast of Iceland during spring 1961–1993 at stations with salinity >34.5 and stations with salinity <34.5. Adapted from Gudmundsson (1998).

spring production is, on the average, about 2.5 times higher at the high-salinity stations (Fig. 7). During the years of limited Atlantic inflow, nutrient transport to the northern shelf is less, the water column stabilizes sooner after the initial spring bloom due to less dense low-salinity water, nutrients become exhausted and the bloom ends abruptly, leading to low production during the summer (Thordardottir, 1977, 1984; Stefansson and Olafsson, 1991; Gudmundsson, 1998; Astthorsson and Vilhjalmsson, 2002). These variations in primary productivity seem to cascade to higher trophic levels as demonstrated for zooplankton and capelin by Astthorsson and Gislason (1998a).

4. Zooplankton

In terms of numbers of individuals, copepods dominate the mesozooplankton of Icelandic waters with *Calanus finmarchicus* being the most abundant species, often comprising between 60% and 80% of net caught zooplankton in the uppermost 50 m (Astthorsson et al., 1983; Gislason and Astthorsson, 1995, 1998, 2000; Astthorsson and Gislason, 1992, 1999; Gislason, 2002). Other copepod species occurring regularly over the shelf around Iceland are *Pseudocalanus* spp., *Acartia longiremis* and *Oithona* spp., while some species are more confined to the Atlantic water (e.g., *Temora longicornis*, *Centropages hamatus*) or to the Polar water (e.g. *Metridia longa*, *Calanus hyperboreus*, *Calanus glacialis*) (Jespersen, 1940; Hallgrimsson, 1954; Gislason and Astthorsson, 1995, 1998, 2004; Astthorsson and Gislason, 2003). The euphausiids *Thysanoessa raschi* and *Thysanoessa inermis* are common around Iceland, with *T. raschi* being mostly confined to the fjord areas while *T. inermis* is the dominant euphausiid in the waters over the shelves (Einarsson, 1945; Astthorsson, 1990; Gislason and Astthorsson 1995; Astthorsson and Gislason, 1997). In addition, the euphausiids, *Meganyctiphanes norvegica* and *Thysanoessa longicaudata*, are mainly found near the shelf edge in oceanic water to the south and west of Iceland (Einarsson, 1945).

Since the early 1960s, monitoring of zooplankton biomass in the upper 50 m in Icelandic waters has been carried out on standard transects during May–June (Astthorsson et al., 1983; Astthorsson and Gislason, 1995, 1998a; Beare et al., 2000). *C. finmarchicus* is the dominant species of the plankton community, and therefore the biomass mainly reflects the biomass of this species. The spring zooplankton biomass generally ranges from ca. 1–10 g dry wt m^{-2}, with an average of 2–4 g dry wt m^{-2} (Fig. 8). Higher biomass is usually observed in shelf waters off the south and west coasts, in the oceanic waters north and northeast of Iceland where Arctic influence is greatest and large Arctic species dominate (*C. hyperboreus*), and in offshore waters of the Irminger and Norwegian Seas.

Zooplankton biomass time series in the waters to the north of Iceland show maxima occurring approximately every 7–10 years (Fig. 9). Also striking is the collapse in zooplankton biomass during the cold period in the North Atlantic and to the north of Iceland in the 1960s and it was not until the warm period in the 1990s that biomass levels recovered (Astthorsson and Gislason, 1995; Beare et al., 2000). Astthorsson et al. (1983) further reported that during the cold period between 1965 and 1971 the composition of the spring zooplankton north of Iceland changed in such a way that *C. finmarchicus* was to a degree replaced by *C. hyperboreus*, *Metridia longa* and euphausiid nauplii.

Zooplankton biomass variability to the north of Iceland is positively related to temperature (Fig. 10), which again reflects the inflow of Atlantic water into the area. On the average, zooplankton biomass in the "warm" years is about 2 times higher than in the "cold" years (Astthorsson and Gislason, 1994, 1998a). Astthorsson and Gislason (1998a) and Astthorsson and Vilhjalmsson (2002) noted that the greater inflow of Atlantic water leading to increased primary production, results in good

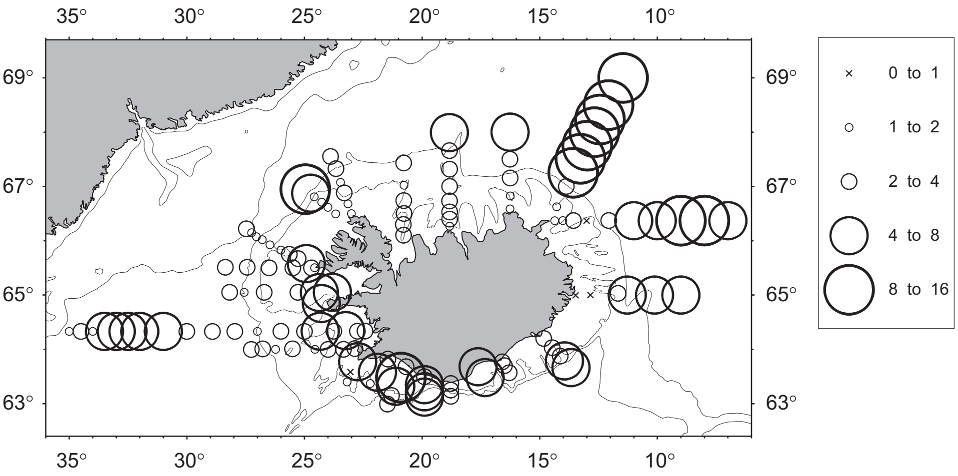

Fig. 8. Average biomass of zooplankton (mg dry wt m^{-2}) around Iceland in May–June 1960–2004. Contours are at 200 and 500 m. From Gislason (2002) plus additional data.

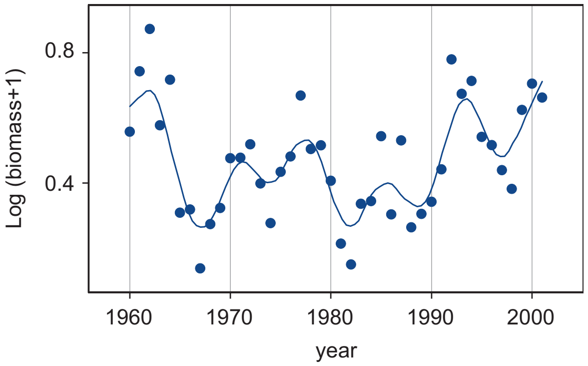

Fig. 9. Variation in spring zooplankton biomass (log mg dry wt m^{-2}) in the waters to the north of Iceland during 1960–2001. The data point for each year is based on observations from 26 stations on average. The curved line shows a 7-year running mean.

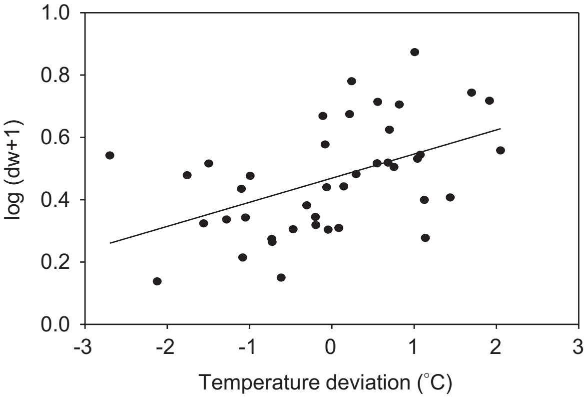

Fig. 10. Relationship between spring zooplankton biomass north of Iceland and temperature deviations on the Siglunes transect. The zooplankton data cover the period 1960–2001 and are based on 26 observations per year on average.

feeding conditions for zooplankton. Further, the stronger inflow of Atlantic water may advect more zooplankton from south and west, and also the warm temperatures will promote increased growth and faster development times of zooplankton.

5. Exploited fish and invertebrate populations

5.1. Annual catch

The annual catch of fish from Icelandic waters has increased from around 200,000 ton at the beginning of the 20th century to about 2 million ton at present (Fig. 11) and currently about 30 species of fish and invertebrates are exploited (Astthorsson and Vilhjalmsson, 2002; Anon, 2005a). During the last five decades the annual catch of demersal fish has fluctuated between 450,000 and 850,000 ton. Cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*), redfish (mainly *Sebastes marinus*) and Greenland halibut (*Reinhardtius hippoglossoides*) are the economically most important demersal fish species in Icelandic waters and of these, cod has been by far the most important. Around 1950, pelagic fisheries for herring (*Clupea harengus*) started to increase. This fishery, which was mainly based on the Atlanto-Scandian (also referred to as Norwegian spring spawning) herring, reached a peak of about 600,000 ton just before a collapse in the late 1960s,

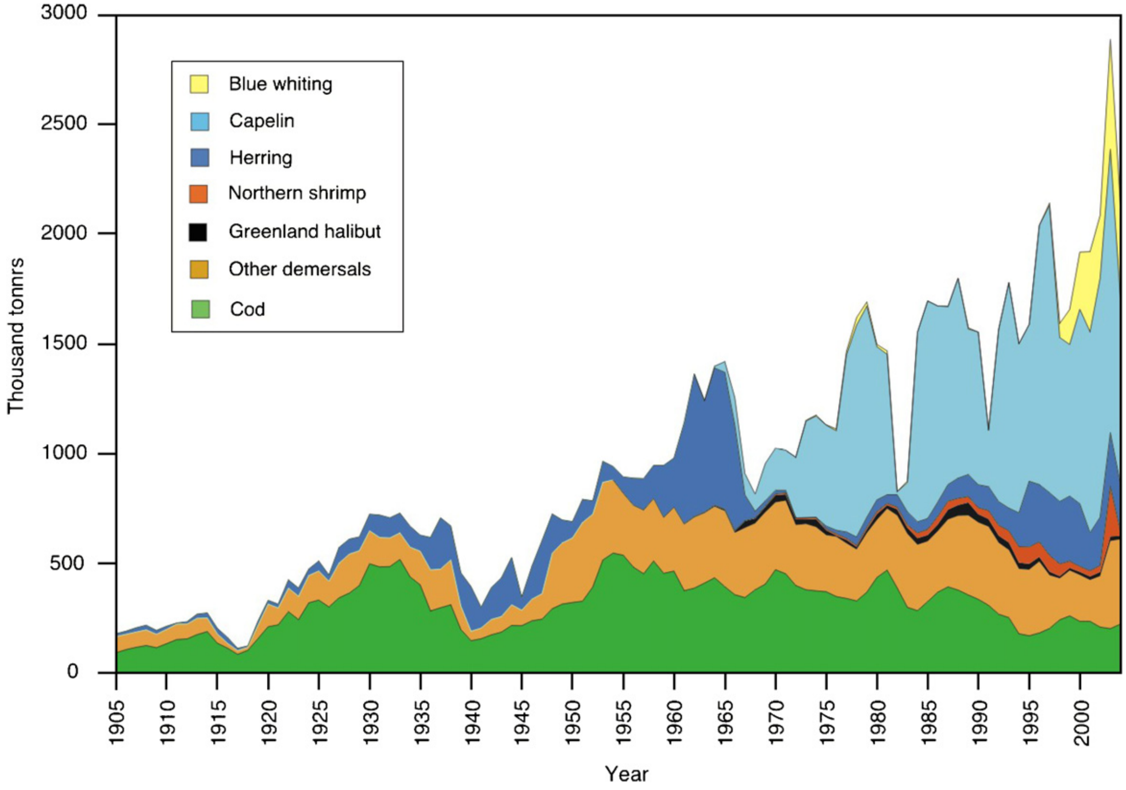

Fig. 11. The catch of fish and invertebrates in Icelandic waters during 1905–2004.

which was due to the combined effect of overfishing and environmental change (Jakobsson, 1980; Dragesund et al., 1980). After the herring stocks collapsed, the capelin fishery expanded and in the recent years has yielded about 1 million ton annually. A capelin collapse in the early 1980s led to a fishing ban for almost 2 years and also an abrupt reduction in the catches was enforced for one season about 10 years later. Except for these two occasions, the annual yield of the capelin fishery has remained fairly constant (Fig. 11). In the recent years the abundance of blue whiting (*Micromesistius poutassou*) has increased markedly in the waters around Iceland and in 2004, the fishery within the Icelandic 200 mile exclusive economic zone (EEZ) amounted to about 300,000 ton. These intensified migrations of the blue whiting to the waters around Iceland are thought to be partly connected to the climatic warming that has taken place.

Only five species of invertebrates, northern shrimp (*Pandalus borealis*), Norway lobster (*Nephrops norvegicus*), Iceland scallop (*Pecten islandicus*), ocean quahog (*Arctica islandica*), and common welk (*Buccinum undatum*) are currently exploited commercially in Icelandic waters and of these the shrimp fishery is the most important. Initially, an inshore fishery amounting to a few thousand tonnes per year, during the late 1980s an offshore fishery developed on the outer part of the northern shelf. Since then, the total shrimp catch has increased from about 10,000 to 70,000 ton. Recently, however, the offshore shrimp fishery has declined. This has been attributed to higher predatory pressure by cod (Anon, 2005a), but could possibly be caused by reduced recruitment due to recent warming, as the main distribution of northern shrimp is typically in the colder water on the shelf north of Iceland.

5.2. Capelin

Capelin is unique, being the only stock of high-Arctic origin exploited in large quantities in Icelandic waters (Vilhjalmsson, 1994, 2002). It is the largest pelagic stock in Icelandic waters and also the most important food source for cod. Capelin is also consumed in large quantities by most other demersal fish species, whales and seabirds. Capelin spawning takes place off the south and southwest coasts of Iceland in February–March but the nursery and feeding grounds are on the shelves off the northwest, north and northeast coasts. Feeding migrations of adults to the deep Sub-Arctic and Arctic waters of the Iceland Sea occur during June–September (Vilhjalmsson, 1994; Astthorsson and Gislason, 1998b). Upon returning to the northern shelf, and until spawning off the southwest coast, capelin is preyed upon by cod in large quantities (Palsson, 1983; Magnusson and Palsson, 1991). These extensive capelin migrations transfer large quantities of the zooplankton production in the Iceland Sea into the Icelandic shelf ecosystem (Vilhjalmsson, 1997a, 2002).

The key role of capelin in the Icelandic marine ecosystem is clearly demonstrated by the changes that have occurred in the weight at age of cod in response to fluctuations in the capelin biomass (Fig. 12). During the near collapse of the capelin in the early 1980s and 1990s, the weight of cod, in particular among age groups 4–8, decreased by about 25–30% (Vilhjalmsson, 1997a). The condition of the cod in both periods only improved when the capelin abundance increased. This indicates that, in Icelandic waters, cod cannot fully substitute for the loss of the capelin by converting to other food sources. Most recently, cod condition has been poorer than expected given the high capelin biomass (Fig. 12). This has been attributed to a more northerly distribution and later arrival of adult capelin to the north Icelandic shelf because of recent warming north of Iceland. Also, the spawning migrations northeast and east of Iceland have to a large extent taken place in deep waters off the shelf break. During this phase, the capelin have therefore been far less accessible to cod than they used to be until the late 20th century. Furthermore, in the last 5 years, capelin larval drift routes have changed and the 0-group drifted north and then west onto the Greenland plateau to the west of the Denmark Strait instead of onto the north Icelandic shelf. During this period, practically no capelin have grown up in Icelandic waters and thus juvenile capelin have not been available to juvenile cod (Anon, 2005a; Palsson, 1983; Vilhjalmsson, personal communication). Sæmundsson (1934) reported that, during warming in the late 1920s and early 1930s, the Icelandic capelin became scarce on the main spawning grounds off the south coast of Iceland while it spawned in great quantities off the north coast.

5.3. Cod

Cod, the most important exploited demersal fish stock in Icelandic waters, during the past 100 years of exploitation has undergone marked changes in distribution and abundance. These changes are considered to be caused by variability in recruitment, which is partly a response to environmental conditions (e.g., Jakobsson, 1992; Astthorsson et al., 1994; Schopka, 1994; Astthorsson and Vilhjalmsson, 2002; Jonsson and Valdimarsson, 2005b). More recently, however, the fishery and its effect on factors such as the age and size composition of the stock seems to be becoming a more important factor in deciding the development of the stock (Marteinsdottir and Thorarinsson, 1998; Anon, 2005a).

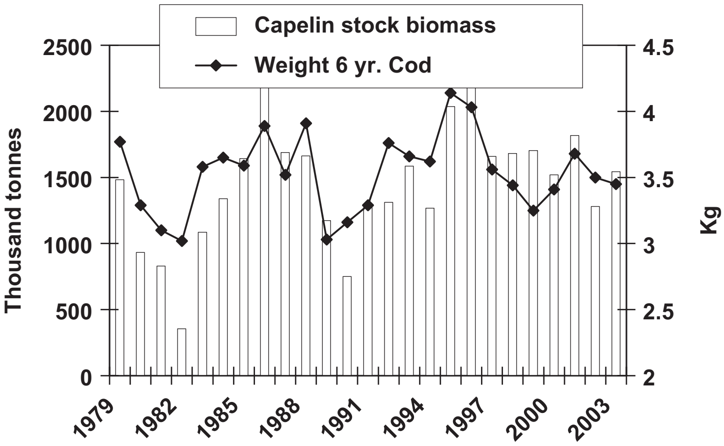

Fig. 12. Changes in capelin biomass and mean weight of Icelandic cod at the age of 6 years. From Astthorsson and Vilhjalmsson (2002) plus additional data.

The Icelandic cod stock spawns in April–May, mainly in the Atlantic water to the south and west of Iceland. The eggs and larvae then drift with clockwise currents to the nursery and feeding grounds off the north coast. During some years a fraction of the larvae may also drift to Greenland waters, where they spend their juvenile years before returning to Icelandic waters as mature individuals to spawn (Astthorsson et al., 1994; Marteinsdottir and Astthorsson, 2005).

Year-class strength (measured as numbers of 3-year olds) of the Icelandic cod stock, including the component of the year class of immigrants from Greenland, is presented in Fig. 13. All of the largest year classes are due to immigrants from Greenland while pure Icelandic year classes never seem to exceed 300–350 million individuals. Further, a marked change occurred around 1985 with subsequent years frequently producing lower than 200 million recruits. Five extremely poor year classes (1986, 1991, 1994, 1996 and 2001) were observed, at levels previously never encountered (below 100 million individuals).

The warming of the northern North Atlantic in the early 1920s extended the distribution area of cod along the east and west coasts of Greenland (e.g. Vilhjalmsson, 1997b). Combined with the drift of larval cod from Iceland to Greenland and the subsequent return of these fish as mature individuals, this warming is considered to be the main reason for the outburst of superabundant year classes at Iceland in the early 1920s (Schopka, 1994). Prior to 1985 immigration of cod from Greenland took place at fairly regular intervals while during the last two decades it has not been observed (Fig. 13). Dickson and Brander (1993) attributed increased larval exchange between Iceland and Greenland in the "warm" years to a strengthening of the Irminger/West Greenland Current system. Schopka (1994) further considered a poorer state of the cod stock at Iceland to be a possible reason for less frequent drift of larvae from the Icelandic ecosystem and towards Greenland in the recent years. In spite of favourable environmental conditions in Icelandic waters in the recent years, and markedly so since 1996 (Fig. 2), the

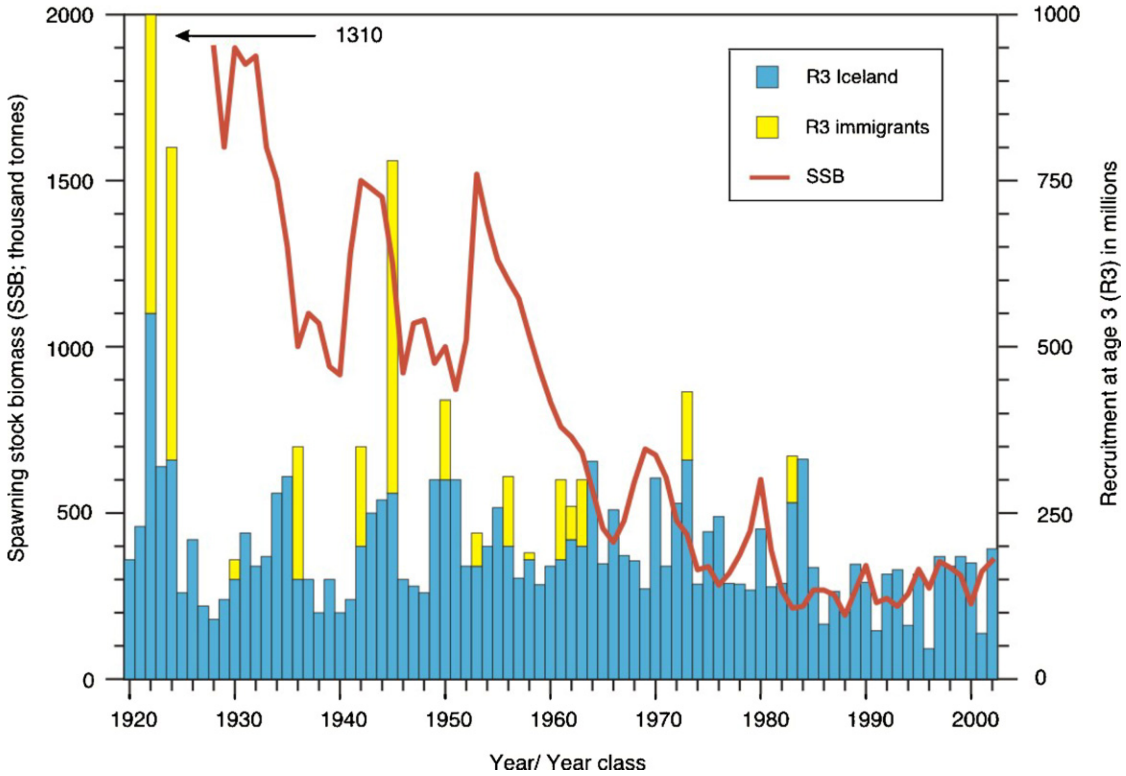

Fig. 13. Recruitment (at age 3) and spawning stock biomass (SSB) of the Icelandic cod stock 1920–2002. The recruits are shown separately for the Iceland (blue bar) and the Greenland (yellow bar) components of the stock. Based on Astthorsson and Vilhjalmsson (2002) plus additional data.

recruitment of the cod stock has been below the long-term average. A stronger inflow of Atlantic water onto the northern shelf has, however, resulted in a more eastward distribution of the young year classes (Anon, 2005a). The importance of the high fecundity, large females in the spawning stock for successful recruitment of the Icelandic cod stock has been noted (Marteinsdottir and Thorarinsson, 1998) but currently they are only a tiny fraction of their levels during the early part of the last century (Anon, 2005a). The poor recruitment during recent favourable environmental conditions is most probably due to the combined low stock size, young age composition and high fishing pressure. While that situation lasts, it seems unlikely that, in spite of a warming climate, an extensive drift of larvae to Greenland and return migration of mature fish to Iceland will take place. It should be noted, however, that coinciding with increased temperatures at West Greenland in the recent years some initial signs of the recovery of the cod stock there have also been observed (Anon, 2005c; Wieland and Storr-Paulsen, 2005).

5.4. *Other fish stocks*

At a dynamic boundary area, such as that to the north of Iceland where the Atlantic and Polar water masses converge, relatively small changes in the distribution and properties of water masses can have marked effects on the distribution and abundance of marine animals living there. Thus, Sæmundsson (1934) and Fridriksson (1948) reported on large distribution and abundance changes for about 20 marine fish species associated with the warming that occurred in the waters around Iceland in the 1920s and 1930s. Vilhjalmsson (1997b) also reviewed the changes in the distribution and abundance of fish stocks in Icelandic and nearby waters during the 20th century and concluded that the variations in the climate in the area may have long lasting and far ranging effects on the marine ecosystem.

Marked changes in the fish distributions and abundances also have been observed during the recent warming. These are particularly evident from the Icelandic groundfish survey, which covers about 600 fixed stations on the shelf around Iceland and has been conducted annually since 1985 (Palsson et al., 1989). According to Valdimarsson et al. (2005), southern gadoids such as haddock, saithe and whiting (*Merlangius merlangus*) and the monkfish (*Lophius piscatorius*) are amongst the species that have shown the largest distribution extension and increase in abundance. Recruitment investigations on haddock have further demonstrated that, except for the 2001 year class, all year classes between 1998 and 2003 have been strong. In fact, the 2003 year class is estimated to be the strongest in 45 years. This increased recruitment and more northward and northeastward distribution of haddock (Fig. 14) is believed to be related to the positive temperature anomaly in the recent years (Anon, 2005a). Prior to 1985, monkfish was mainly confined to the deeper waters off the south coasts (G. Jonsson, 1992) but in the recent years it has increased in abundance and become distributed along the whole of the west coast and onto the northern shelf (Fig. 15). Recent shifts in the distribution of the Icelandic summer spawning herring around Iceland have also been associated with the warming (Gudmundsdottir and Sigurdsson, 2004) and the same probably applies to the increase of blue whiting in Icelandic waters.

6. Marine mammals

About 18 species of cetaceans (whales, dolphins and porpoises) and seven species of pinnipeds (seals and walrus) inhabit the coastal and offshore waters around Iceland and more than half of these species have been exploited during the past centuries (Sigurjonsson and Hauksson, 1994).

On the basis of the extensive surveys conducted in 1987, 1989 and 1995 by the Marine Research Institute in cooperation with adjacent nations in the North Atlantic, Sigurjonsson and Vikingsson (1997) summarized the information on the abundance and distribution of cetaceans. Of the 18 species of cetaceans found in Icelandic waters, 12 are toothed cetaceans and six are baleen whales. Many of these species are found all around Iceland but generally are most common off the west and east coasts. Most of the species are migratory to some degree and occur in greatest abundances around Iceland during the summer (Sigurjonsson and Vikingsson, 1997). Minke whale (*Balaenoptera acutorostrata*) is the most numerous stock of baleen whales (ca. 60,000 animals), while the stocks of fin (*Balaenoptera physalus*) and sei whales (*Balaenoptera borealis*) are also quite large (ca. 10,000 each) (Fig. 16). The populations of humpback (*Megaptera novaeangliae*) and blue whale (*Balaenoptera musculus*) have increased in the recent years, because they have been protected from hunting since 1955 and 1959, respectively (Sigurjonsson and Gunnlaugsson, 1990). Of the toothed whales, the long finned pilot whale (*Globicephala melas*) is the most abundant (ca. 58,000), followed by northern bottlenose (*Hyperoodon ampullatus*) and white sided dolphin (*Lagenorhynchus acutus*) (both at ca. 40,000).

The total annual food consumption of the 12 most common species of cetaceans in Iceland and adjacent waters is estimated to be about 6 million ton (Sigurjonsson and Vikingsson, 1997) or about 3 times the total annual landing by the Icelandic fishing fleet in the recent years. About 2 million ton of this consumption is estimated to be finfish, mostly capelin. Humpback (*M. novaeangliae*) and minke whales consume the largest amount of capelin, respectively, 800,000 and 610,000 ton (Vilhjalmsson, 2002, personal communication). Due to the large food consumption required by cetaceans and their distribution, which often overlaps with the fishing grounds around Iceland, further studies into their feeding ecology and role in the Icelandic marine ecosystem are of great importance.

Studies on the biological parameters in fin whales based on material sampled between 1967 and 1989 demonstrated large fluctuations in the age at sexual maturity (Lockyer and Sigurjonsson, 1991; Konradsson et al., 1991). Age at sexual maturity was found to decline steadily from 11 years in the year classes from the late 1940s, to 8 years in those from the late 1960s. Then a reversal was observed, and the year classes from the late 1970s became mature at an increased age of about 10 years. For the period above Sigurjonsson (1992) demonstrated negative correlations between mean age at maturity of fin whales in Icelandic waters and the abundance of euphausiids in continuous plankton recorder (CPR) samples from the deep waters southwest of Iceland. This was considered to reflect that a higher abundance of euphausiids would mean better feeding conditions for the fin whales and thus faster growth rates and maturity at an earlier age. Energetic studies on fin whales also indicate a correlation between body condition (blubber thickness, girth, chemical composition) and fecundity of females supporting a close correlation between food availability and fecundity (e.g. Vikingsson, 1990). Effects of climate on zooplankton populations can, through trophic interactions, influence the production of cetacean stocks.

Recent records of strandings on Icelandic shores of striped dolphin (*Stenella coeruleoalba*) are of

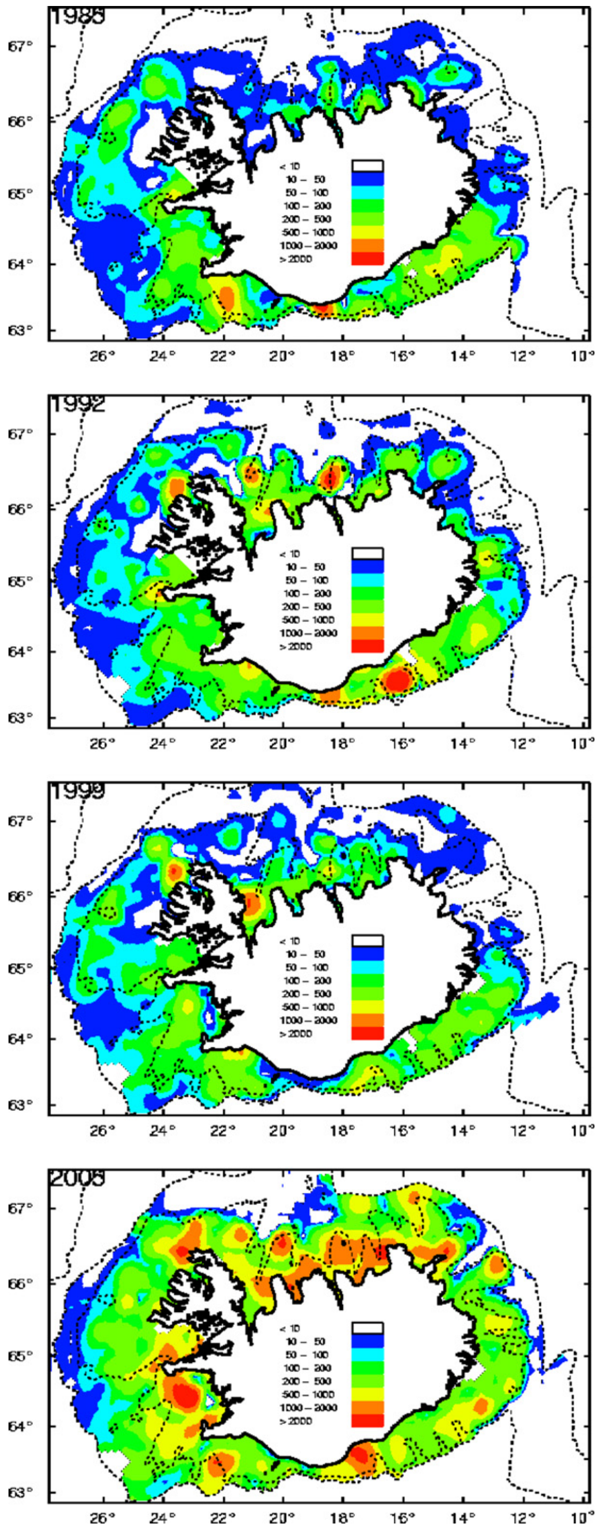

Fig. 14. Distribution and abundance (number per tow) of haddock in the Icelandic groundfish survey during 1985, 1992, 1999 and 2005 (based on ca. 600 stations covering the shelf area around Iceland).

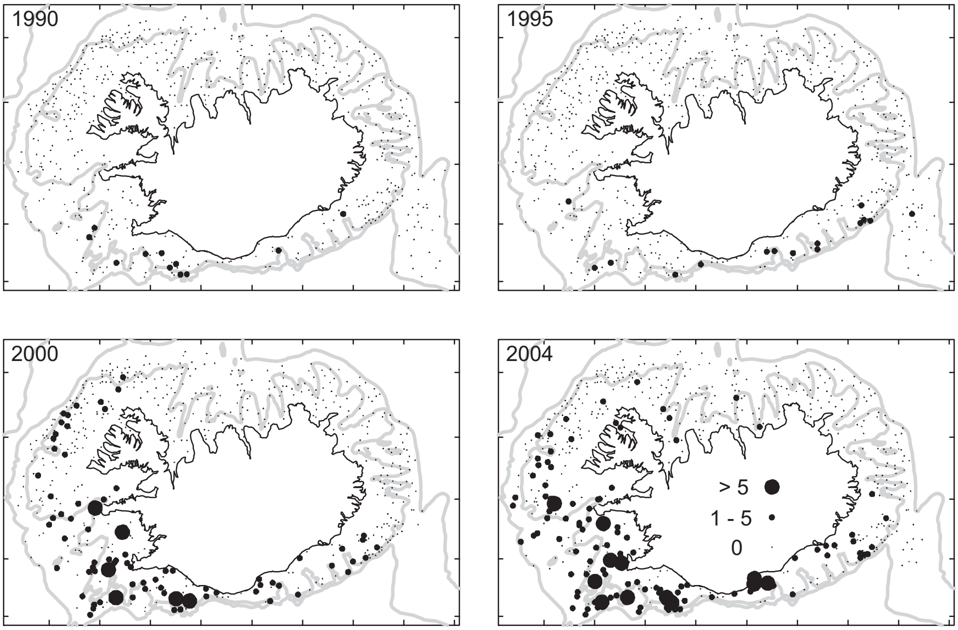

Fig. 15. Distribution and abundance (number per tow) of monkfish in the Icelandic groundfish survey during 1990, 1995, 2000 and 2004 (based on ca. 600 stations covering the shelf area around Iceland).

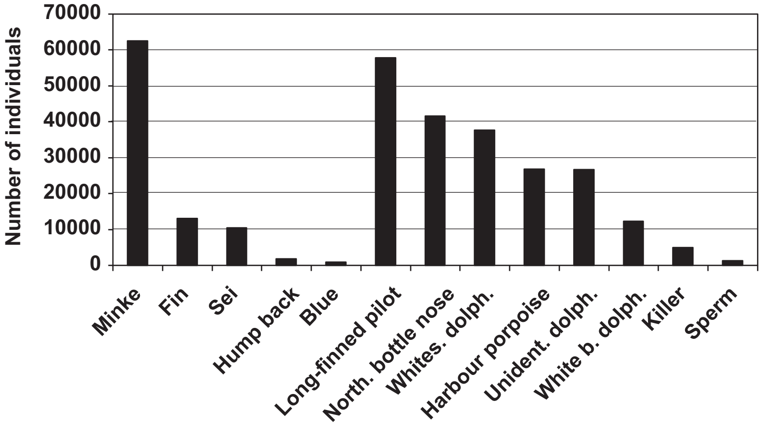

Fig. 16. Abundance of the 13 most common whale species in Icelandic waters. Based on Sigurjonsson and Vikingsson (1997) and G. Vikingsson (personal communication).

particular interest in the context of distribution of cetaceans in relation to climate. The first stranding record of this species was in 1984 (Bloch et al., 1996) but during 1998–2005 another five strandings were recorded (Vikingsson, 2004, personal communication; Hjartarson and Olafsdottir, 2005). These five strandings were well separated in time and space showing that they could not have resulted from a single incidental migration event. The main distribution area of striped dolphin is in the Atlantic Ocean far to the south of Iceland and in the Mediterranean where it is the most abundant dolphin species (Bloch et al., 1996; Vikingsson, 2004). The increased frequency of strandings of this southern species in Iceland and elsewhere in the North Atlantic may be result from changing environmental conditions (Bloch et al., 1996; Vikingsson, 2004, Hjartarson and Olafsdottir, 2005). In Japanese waters, the distribution of striped dolphin is mainly confined to temperatures above 18 °C and the northern distribution boundary has been observed to shift seasonally northwards in relation to temperature (Perrin et al., 1994).

Two species of seals, common seal (*Phoca vitulina*) and grey seal (*Halicoerus grypus*) breed in Icelandic waters, while five northern vagrant species of pinnipeds are found in the area (Sigurjonsson and Hauksson, 1994; Hauksson, 1993, 2004). The common seal is observed in the coastal areas all around the country, while the grey seal is mainly found off the west, northwest and southeast coasts.

The seal populations at Iceland have been harvested through the centuries, both for food and fur. Hunting of both the species combined is currently limited to about 1000 individuals annually, well below the level of ca. 6000 animals of several decades ago. Regular surveys of the common seal and grey seal populations have been undertaken in Icelandic coastal waters since 1980 and 1982, respectively (Anon, 2005a). Stock estimates for both species have declined considerably since initial surveys, common seals from about 30,000 individuals to about 10,000 and grey seals from about 9000 to 6000. The steady decrease in the population size of both the species is mainly considered to be due to overexploitation (Anon, 2005a).

The total food consumption of common seals and grey seals is estimated to be 28,000 and 30,000 ton, respectively (Bogason, 1997; Hauksson, 1997). The most important prey of both the species were cod and sand lance (*Ammodytes spp.*), which comprised, respectively, 42% and 14% of the total food intake for the common seal and 24% and 22% for the grey seal.

7. Seabirds

Iceland and Icelandic waters are important areas for some of the largest seabird populations in the Northeast Atlantic with the largest seabird cliffs on the Westfjord Peninsula on the northwest coast (Petersen, 1994). The distribution of the seabirds around Iceland is mainly related to the marine feeding conditions as breeding locations do not seem to be limiting (Gardarsson, 1995). The proportion of seabirds is about 30% of the approximately 70 species of all birds breeding in the country. However, the importance of seabirds in the Icelandic bird fauna is much greater based on abundance and biomass.

In total, the breeding populations of the 23 seabird species have been estimated to be about 7.7 million pairs (Anon, 2002). Assuming that immature birds are about 30% of the breeding populations (Cairns et al., 1990; Furness, 1978) total population size is about 20 million individuals. The biomass of the breeding populations of the seabirds in Icelandic waters was estimated to be 11,000 ton (Anon, 2002) and when the immature component is added (Cairns et al., 1990; Furness, 1978; K. Lilliendahl, personal communication) this value increases to a total of about 14,000 ton. A more recent estimate of abundance and biomass of seabirds in the Iceland and East Greenland area combined suggests that the values presented here for Iceland alone may be somewhat conservative (Anon, 2004b).

The Atlantic puffin (*Fratercula arctica*) is the largest seabird population with about 2.8 million breeding pairs or about 40% of the total number of seabirds at Iceland. This is followed by northern fulmar (*Fulmarus glacialis*), with 1.5 million breeding pairs, and the common guillimot (*Uria algae*), with about 990,000 breeding pairs (Fig. 17). Lilliendahl and Solmundsson (1997) estimated that the summer food consumption of the six most numerous seabird species of Icelandic waters was about 442,000 ton. Sandeel and capelin were by far the most important food items constituting 184,000 and 171,000 ton, respectively. The six largest seabird populations consume about 8% of the total capelin biomass in Icelandic waters during summer.

There is no information available on the recent trends in the sizes of the major seabird populations due to the lack of monitoring. However, the more northern distribution of capelin during the recent warming has been suggested to have contributed to the massive mid-winter decline of alcids (*Uria* spp.) along the west, northwest and north coasts of Iceland in the winter of 2001–2002 (Nielsen and Einarsson, 2004). Climate-related changes in prey distribution are believed to have caused mortality in other seabird populations as well (Durant et al., 2004).

During the 20th century marked changes have been observed in the size of the breeding population of the high Arctic little auk (*Alle alle*) to the north of Iceland. It is the rarest of all Icelandic seabird species and at the turn of the 20th century the breeding population on the island of Grimsey (66°30′N, 18°00′W) to the north of Iceland was considered to be only 150–200 pairs while breeding also was known to take place at several other localities on the north Icelandic mainland (Petersen, 1998). During the recent decades, Grimsey has been the only known breeding site and its breeding

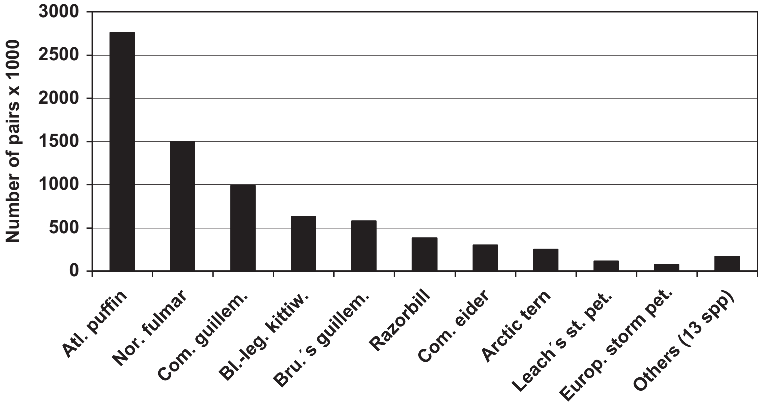

Fig. 17. Breeding pairs of seabirds at Iceland. Based on Petersen (1994) and Anon (2002).

population gradually declined to only a few pairs during the 1990s, a single pair between 1993 and 1996 and no breeding in 1997 and 1998. The main reason for the decline in the little auk population north of Iceland during the 20th century has been considered to be the gradual climatic warming (Bardarson, 1986) but whether that effect is direct through physiological processes or indirectly through food availability is not known.

8. Total biomass and production

In an attempt to provide a more holistic view of the Icelandic marine ecosystem and in order to facilitate a comparison to other Sub-Arctic ecosystems, we present a summary of available information on biomass and production of the main components or groups in the ecosystem. The sources of information for the biomass estimates and production calculations are summarized in Table 1. As biomass estimates for all of the fish stocks, except mesopelagic fish, we have used averages for the period 1995–2004 presented in Anon (2004c), whereas for other groups they are single estimates from the respective references listed in Table 1. For *C. finmarchicus* the production was calculated from egg production rates (Gislason, 2005), whereas for other zooplankton species the production/biomass ratios are used to calculate production (Sakshaug et al., 1994). For fish, whales and seabirds the production was calculated on the basis of a size related production/biomass relationship presented by Banse and Mosher (1980) combined with the relevant biomass information similar to Skjoldal et al. (2004) for the Norwegian Sea. The production estimates in terms of carbon are based on wet weights assuming that, for zooplankton, dry weight is 20% of wet weight and C content is 50% of dry weight (Skjoldal et al., 2004), and for fish and higher animals dry weight is 33% of wet weight and C content is 40% of dry weight (Sakshaug et al., 1994).

The estimated biomass values expressed as wet weight were calculated for an area of 758,000 km^2, corresponding to the Icelandic 200-mile EEZ (Fig. 18). The total biomass of all the major components in the Icelandic marine ecosystem is about 56 million ton wet weight. Phytoplankton is the largest component amounting to about 29 million ton or 51% of the total biomass. Zooplankton is the second largest group amounting to about 17 million ton or 30% of the total. Of the zooplankton, *C. finmarchicus* is the largest single species/group amounting to about 7 million ton. No information is available on microzooplankton in Icelandic waters and similarly amphipods, gelatinous medusae and squid are not included in the zooplankton/nekton biomass. All of these groups have been found to be very significant components of nearby Nordic Seas ecosystems (Dalpadado et al., 1998; Bjørke and Gjøsæter, 2004) and therefore the zooplankton component presented here is likely underestimated. Pelagic fish biomass amounts to about 8.8 million ton or about half of the zooplankton biomass estimates. This number includes an estimate of mesopelagic fish of 950,000 ton based on average oceanic biomass values in Gjøsæter and Kawaguchi (1980), but can only be regarded as an approximation for Icelandic waters as no direct measurements of the biomass of mesopelagic fish have been undertaken in the area. The combined biomass of the largest demersal

Table 1
Sources of information for biomass estimates and calculation of production for the main components of the Icelandic marine ecosystem

Group	Biomass	Weight at maturity	Production
Phytoplankton	K. Gudmundsson, (personal communication)		Thordardottir (1994)
Calanus finmarchicus	Gislason (2002)		Gislason (2005)
C. hyperboreus	Own data		Own estimate
Euphausiids	Own data		Own estimate and Sakshaug et al. (1994)
Other plankton	Own data		Own estimate and Mauchline (1998)
Capelin	Anon (2004c)	Anon (2004c)	Banse and Mosher (1980)
Herring	Anon (2004c)	Skjoldal et al. (2004)	Banse and Mosher (1980)
Blue whiting	Anon (2004c)	Skjoldal et al. (2004)	Banse and Mosher (1980)
Oceanic redfish	Anon (2004c) and Th. Sigurdsson (personal communication)	Anon (2004c)	Banse and Mosher (1980)
Mesopelagic fish	Gjøsæter and Kawaguchi (1980)	Skjoldal et al. (2004)	Banse and Mosher (1980)
Cod	Anon (2004c)	Anon (2004c)	Banse and Mosher (1980)
Haddock, saithe	Anon (2004c)	Anon (2004c)	Banse and Mosher (1980)
Other fish	Anon (2004c)	Anon (2004c)	Banse and Mosher (1980)
Large baleen whales	Sigurjonsson and Vikingsson (1997)	Sigurjonsson and Vikingsson (1997)	Banse and Mosher (1980)
Minke whale	Sigurjonsson and Vikingsson (1997)	Sigurjonsson and Vikingsson (1997)	Banse and Mosher (1980)
Sperm whale	Sigurjonsson and Vikingsson (1997)	Sigurjonsson and Vikingsson (1997)	Banse and Mosher (1980)
Other toothed whales	Sigurjonsson and Vikingsson (1997)	Sigurjonsson and Vikingsson (1997)	Banse and Mosher (1980)
Seabirds	Anon (2002)	Anon (2002)	Sakshaug et al. (1994)

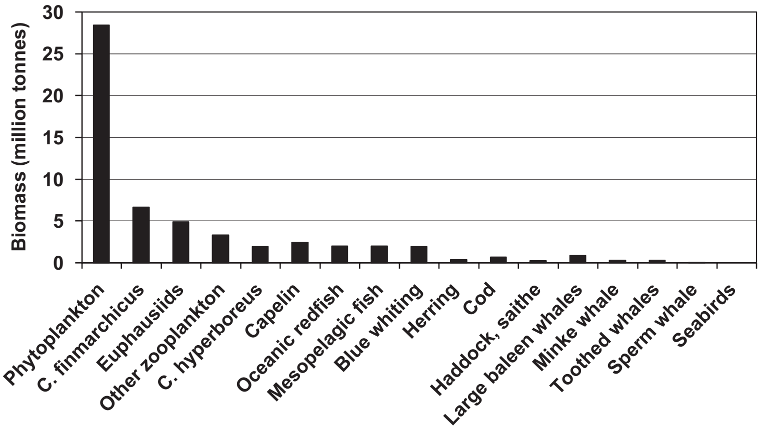

Fig. 18. Estimated wet biomass of the main components within the Icelandic EEC based on sources in Table 1.

species, i.e., cod, haddock and saithe, is about 1 million ton (about 2% of the total biomass) or similar to that of the baleen whales. The biomass of the large baleen whales is about 900,000 ton while that of minke whales and toothed whales is each estimated to be about 300,000 ton. The total biomass of seabirds is about 14,000 ton and that of seals only about 2000 ton (Fig. 18). Several demersal species (e.g., Greenland halibut and several other flatfishes), redfish (*S. marinus*) and invertebrates with an annual catch of about 100,000 ton in the recent years (Anon, 2004c) have not been included in Fig. 18 as information on their stock sizes is very limited.

Fig. 19 shows the calculated annual production in terms of carbon per m^2 for selected trophic levels in the Icelandic marine ecosystem. The total annual primary production within the Icelandic EEZ was estimated by Thordardottir (1994) to be 1220 million ton or 160 gC m^{-2} yr^{-1}. The annual production

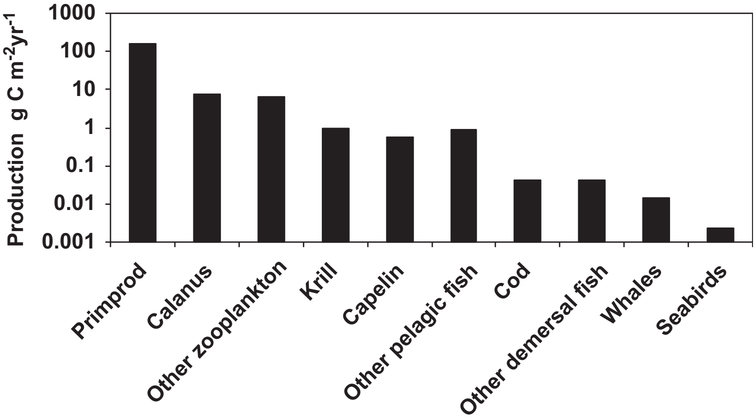

Fig. 19. Estimated production (gC m^{-2} y^{-1}) for selected components of the Icelandic marine ecosystem based on sources in Table 1.

of *Calanus* (mainly *C. finmarchcus*) is estimated to be about 7 gC m^{-2} yr^{-1} and the production of other zooplankton is of a similar magnitude (~6 gC m^{-2} yr^{-1}). The combined production of pelagic fish (in decreasing order: capelin, mesopelagic fish, blue whiting, oceanic redfish (*Sebastes mentella*) and herring) is estimated to be about 1.5 gC m^{-2} yr^{-1} and of these the production of capelin is by far the largest (~0.5 gC m^{-2} yr^{-1}). The production of cod is estimated to be about 0.04 gC m^{-2} yr^{-1}, which is almost the same as that of all other demersal species. The production of other top predators, namely whales and seabirds, is small in comparison to that at lower trophic levels but, as pointed out above, their food consumption is not.

As described earlier, capelin exploits the Atlantic water south of Iceland for spawning but its main distribution and feeding area is in the Sub-Arctic waters to the north of Iceland. The actual area where the main production takes place therefore may be smaller than the one used to calculate their production (The Icelandic EEZ) and thus the production per unit area is likely to be higher than that presented in Fig. 19. The same also applies to different degrees to most of the other groups considered in Fig. 19, but at present we feel that the spatial and temporal resolution of the data do not allow analysis confined to, for example, the Sub-Arctic component of the ecosystem only. The present estimates of production in Icelandic waters must be considered rather uncertain. It is, however, interesting to note that the production estimates are in most cases similar to those reported by Sakshaug et al. (1994) for the Barents Sea. This may indicate that the main processes determining the production in the two ecosystems are also somewhat similar and possibly regulated in a similar manner.

9. Concluding remarks

In this paper we have attempted to summarize the main features of the Icelandic marine ecosystem and how some important components have been affected by climate variability during the 20th century. A marked warm period occurred between 1920 and 1940, a cold period was observed in the late 1960s and during the past decade marked signs of warming have again been observed. During all of these periods the environmental changes affected the abundance and distribution of many commercial fish stocks and also other components of the Icelandic marine ecosystem. Considering this, and also model forecasts for future climatic scenarios (ACIA, 2004), it is very important for a fisheries nation such as Iceland to gain an understanding of its marine environment and particularly so for the waters to the north where the impact of climate variation is likely to be greatest.

Astthorsson and Vilhjalmsson (2002) presented a conceptual model for the Sub-Arctic waters to the north of Iceland where the food chain from phytoplankton-zooplankton–capelin and to cod was considered to be bottom-up controlled and highly sensitive to climate variability. We have further noted above the key role that capelin play in the Icelandic marine ecosystem and their role in transferring zooplankton production from the Iceland Sea to the more southern part of the Icelandic ecosystem. The growth of the capelin stock is believed to depend mainly on the environmental conditions in the Iceland Sea (Malmberg and Blindheim, 1994; Vilhjalmsson, 1994; Astthorsson and Gislason, 1998a) and the nearby waters, but there are also certain indications that a small spawning stock will lead to a poor recruitment (Vilhjalmsson, 2002). Furthermore, predation by whales, fish and the fisheries exploitation are considered important factors in determining the development of the spawning stock. Since 1998, the distribution and the main fishing area of capelin in the Iceland Sea have changed and this has lead to difficulties in assessing the size of the stock. Studies to gain a further understanding of the Sub-Arctic ecosystem north of Iceland (The Iceland Sea Ecosystem Programme) are under way as an Icelandic component of ESSAS. They are centred around defining and quantifying the environmental and biological factors that determine the distribution and production of capelin in order to better forecast the capelin stock abundance and distribution in a varying environment.

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