Ecosystem structure in the Iceland Sea and recent changes to the capelin (*Mallotus villosus*) population

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The objective of the Iceland Sea Ecosystem Project was to analyse principal ecosystem patterns, including the life history of capelin. Ten surveys were conducted for this purpose between 2006 and 2008, and hydrographic data from 1970 to 2011 were analysed. Long-term temporal patterns indicate an increase in the temperature of surface and intermediate waters during recent years in the Iceland Sea. The phytoplankton consisted mainly of diatoms in spring, with flagellates and dinoflagellates appearing later in the year. Zooplankton and fish were dominated by a few species. In late summer, the pelagic foodweb ranged between trophic levels 2.4 and 3.6. Trends in nutrients and primary production showed a clear seasonal pattern with a spring bloom in late May, followed by a peak in secondary production in July/August. The spatial structure of the lower ecosystem levels in summer was stable across the 3 years, determined mainly by the structure of the water masses. The pelagic fish fauna consisted primarily of adult pelagic fish and transient numbers of larval species. The spatial pattern of capelin indicated northward displacement of 0-group capelin and westward displacement of older capelin in recent years. The annual biomass was estimated at 3.8 million tonnes of phytoplankton, ~21 million tonnes of zooplankton, and 1.0 million tonnes of fish.

Keywords: capelin, ecosystem, Iceland Sea, Subarctic.

Introduction

The Iceland Sea is usually defined as the waters delimited by Greenland to the west, the Denmark Strait and the continental shelf break north of Iceland to the south, by Jan Mayen and the Jan Mayen Fracture Zone to the north, and the Jan Mayen Ridge to the east (Figure 1). The Iceland Sea, with bottom depths mostly in the range of 500–2000 m, but shallower on the continental shelf of East Greenland and the outer shelf north of Iceland, is relatively shallow compared with the adjacent Nordic Seas, i.e. the Norwegian and Greenland Seas. The Kolbeinsey Ridge crosses the central Iceland Sea in a southwest–northeast direction and is as shallow as 500 m in some areas compared with the surrounding waters of depths of >1000 m. The Ridge divides the Iceland Sea into western and eastern parts; the basins west and east of the ridge are named the Blosseville Basin and the Iceland Plateau, respectively.

The ecosystem of the Iceland Sea has not been subjected to extensive scientific exploration to date. Studies have focused mainly on physical and chemical oceanography, such as a description of the main currents, the formation, properties and distribution of the water masses, and tracer studies and modelling, especially in connection with potential overflow water in the Denmark Strait (Swift and Aagaard, 1981; Buch *et al.*, 1996; Rudels *et al.*, 2002; Blindheim and Østerhus, 2005; Jeansson *et al.*, 2008; Vaage *et al.*, 2011). Biogeochemical properties at latitude 68°N in the southern Iceland Sea were described in Ólafsson (2003). Biological studies of lower trophic levels have been rare, and mainly conducted in the southern part of the Iceland Sea, e.g. long-term studies of zooplankton in relation to environmental parameters (Astthorsson and Gislason, 1995) and studies of primary production, and the species composition and life cycles of zooplankton during 1 year (Gislason and Astthorsson, 1998).
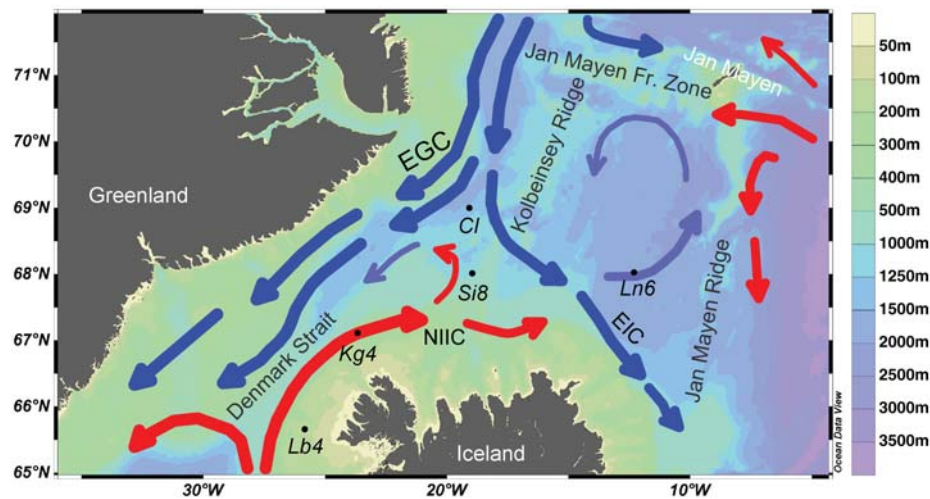
Figure 1. Topography and circulation in the Iceland Sea: East Greenland Current (EGC, blue), North Icelandic Irminger Current (NIIC, red), and East Icelandic Current (EIC, light blue). Adapted after Blindheim and Østerhus (2005) and Hunegnaw *et al.* (2009). Locations of fixed repeated stations are indicated by Lb4 (Látrabjarg station 4), Kg4 (Kögur station 4), Si8 (Siglunes station 8), and Ln6 (Langanes NE station 6), and the location of a station in the central Iceland Sea is indicated by CI.

Studies of the ecology of fish species have mostly been limited to capelin (*Mallotus villosus*), historically the largest fish stock in the area. Extensive acoustic surveys were conducted in the Iceland Sea in the 1980s and 1990s through Icelandic and Norwegian research efforts, with the aim of analysing the life history and catch potential of capelin, as well as linkages to hydrographic conditions (Vilhjálmsson, 1994, 2002).

The main patterns in capelin behaviour and migrations were relatively clear during the 1980s and early 1990s, with environmental factors as important determinants in interannual variability of life-history traits, and fluctuating, though largely predictable, stock trends (Vilhjálmsson, 1994). Since the late 1990s, however, there have been marked changes in the distribution of 0-group, juvenile, and adult capelin in the nursery and feeding areas in the Iceland Sea. Concurrently, autumn stock assessment surveys failed in most years and the fishing fleet failed to encounter fishable capelin shoals, with the result that the summer and autumn fishery came to an end in the early 2000s. Since the mid-2000s, a drastic decline in recruitment and stock size has been observed. Those events have been attributed to an increase in the inflow of Atlantic water north of Iceland (Vilhjálmsson, 2002; Anon., 2011).

The objective of the Iceland Sea Ecosystem Project of 2006–2008 was to contribute to increased understanding of the Iceland Sea ecosystem and adjacent waters, including linkages to the life history and the survival of capelin. Here, we examine climate variability by long-term temperature data, followed by an overview of main structures in the ecosystem, based on data collected within the project. These include hydrographic patterns, phytoplankton and zooplankton species compositions and abundance, trophic structure, and distribution of capelin and other fish, topics analysed further in sister papers in this issue (Gislason and Silva, 2012; Jónsson and Valdimarsson, 2012; Petursdottir *et al.*, 2012).

Material and methods
Material was sampled from ten surveys conducted in the years 2006–2008, mainly in spring and summer (Table 1). Extensive

sampling was carried out during most surveys, covering hydrography (physical and chemical), phytoplankton species composition, primary production and chlorophyll *a* (hereafter Chl *a*), and zooplankton species composition and abundance. Capelin larvae were collected during three surveys in spring and summer 2007. In 2007 and 2008, material was sampled for analyses of trophic structures by fatty acids and stable isotopes (Petursdottir *et al.*, 2012). Three extensive surveys were carried out during summers covering the ecosystem as a whole, i.e. adding fish to the sampling effort. The first of those surveys, in July 2006, covered the Iceland Sea to 71°N 12°E. However, drift ice hindered sampling in the western part of the area. In addition, the East Greenland Shelf was sampled as far as 36°W, as was the northern shelf area of Iceland. The second survey, in August 2007, covered the Iceland Sea to 70°N 12°E and a large part of the Iceland shelf. The third survey, in August 2008, covered the Iceland Sea to 72°N 12°E as well as Jan Mayen waters, along with the western and northern Iceland Shelf and the East Greenland Shelf to 32°W.

Four stations were selected from the hydrographic database of Iceland's Marine Research Institute (MRI) to present the long-term temperature trends in Iceland outer shelf waters that are indicative of hydrographic conditions at the boundaries between Iceland waters and the Iceland Sea. The stations were Látrabjarg 4 and Kögur 4, south and north of the Denmark Strait, respectively, Siglunes 8 in the periphery of the southern Iceland Sea on the western side of the Kolbeinsey Ridge, and Langanes NE 6 over the Iceland Plateau (Figure 1). For an evaluation of long-term changes in the central Iceland Sea, depth profiles of temperature and salinity in the central Iceland Sea, collected at a given station in the years 1951, 1987, 2007, and 2008, were used (Figure 1). During project surveys, a Seabird 9/11+ CTD with rosette was used to collect standard hydrographic data (temperature, salinity, and oxygen) and water bottle samples were taken for salinity and oxygen calibration. CTD data were processed according to the standard procedures.

Table 1. Iceland Sea Ecosystem Project (2006–2008) survey dates, numbers of stations, and programme descriptions

Survey	Date	Stations	Description
B2-2006	7–10 February 2006	15	Hydrography, phytoplankton, zooplankton: sections at 68 and 69°N in the Iceland Sea
B4-2006	18–26 May 2006	34	Hydrography, phytoplankton, zooplankton: four sections in the Iceland Sea
B6-2006	10 July–3 August 2006	191	Ecosystem of the Iceland Sea, Denmark Strait, and Iceland shelf. Northern limit 71°N
A11-2006	21–26 November 2006	2	Zooplankton section at 68°N in the Iceland Sea
B3-2007	12–14 February 2007	11	Hydrography, phytoplankton, zooplankton: sections at 68 and 69°N in the Iceland Sea
B6-2007 (first leg)	12–18 April 2007	39	Capelin larvae: Iceland shelf south and west
B6-2007 (second leg)	19–24 April 2007	30	Hydrography, phytoplankton, zooplankton: three sections in the Iceland Sea
B8-2007	14–27 May 2007	80	Capelin larvae Iceland shelf
B11-2007	8–28 August 2007	216	Ecosystem of the Iceland Sea, Denmark Strait, and Iceland shelf. Northern limit 70°N
B6-2008	1–5 May 2008	22	Hydrography, phytoplankton, zooplankton: sections at 68 and 69°N in the Iceland Sea
A11-2008	6 August–3 September 2008	205	Ecosystem of the Iceland Sea and Iceland shelf. Northern limit 72°N

Nutrient samples (nitrate, silicate, and phosphate) from the surface layers were collected with the water bottles at depths of 0, 10, 20, 30, 50, 100, and 200 m at each CTD station. They were analysed on board with the standard colorimetric methods, except on winter cruises, when they were frozen and analysed in the laboratory back on land. Details of the analytical methods and quality assurance can be found in Ólafsson et al. (2010).

Seawater samples were collected at 0, 5, 10, 20, 30, and 50 m at all hydrographic stations for Chl a measurements. The samples (0.5–2 l) were filtered through GF/F filters 4.7 cm in diameter, then placed in glass tubes, filled with 90% acetone, and kept frozen until measured spectrophotometrically according to Strickland and Parsons (1972).

Primary productivity measurements, based on the uptake of ^{14}C, were performed on samples from 10-m depth at selected stations at the 69°N transect, in a light- and temperature-regulated incubator on board the vessel (Guðmundsson, 1998). Duplicate samples from 10 m were incubated at the seawater temperature of the sampling site under various light conditions, from very low light intensity to super saturation (85–300 μE cm^{-2} s^{-1}), to obtain a P–I curve (photosynthesis–irradiance) satisfactory for maximal primary production. Higher light intensity caused photo inhibition. Secchi readings were undertaken at stations occupied during daylight. The results of the P–I curves, the Secchi readings as a measure of the attenuation of light in the sea, the incoming clear sky sea surface irradiation calculated from the website http://www.sci.fi/~benefon/sol.html for the research area, and the Chl a values with depth, were used to estimate the daily production of carbon to the compensation depth of the euphotic zone (1% light depth; Guðmundsson et al., 2002; Guðmundsson and Valsdóttir, 2004). As the primary production values were calculated from clear sky light intensities, they are assumed to be at their maximum. The weather during the cruises was variable in spring, but more or less calm and under a cloudless sky during summer cruises. This suggests that the primary production may, in some cases, be overestimated, especially in spring.

Phytoplankton mean annual wet-weight biomass was calculated as in Skjoldal et al. (2004). Integrated Chl a values from 0

to 50 m in spring and 0 to 30 m in summer were used, based on the mean Chl a values from 22 to 34 stations north of 68°N in spring, mostly east of the Kolbeinsey Ridge, and 56–59 stations in summer covering the Iceland Sea. A rough estimate of the area north of 68°N is 250 000 km^2, and the period used covers April–September (6 months). Variable distribution of drift ice was not taken into account. Therefore, the biomass estimate is probably too high.

Quantitative samples (100 ml) for phytoplankton identification and enumeration were collected at all hydrographic stations and preserved in neutralized (hexamine) formaldehyde. Counting and identification were conducted using an inverted microscope, according to Hasle (1978), on subsamples (50 ml) from 10 and 30 m deep at selected stations on a 69°N transect. Phytoplankton were identified to species when possible, but otherwise to the lowest possible taxon according to Tomas (1997). Abundance levels are presented in cells per litre.

The zooplankton data were collected with WP2 nets and a Multinet. Both nets had 0.25 m^2 mouth openings and 200 μm mesh size. The WP2 net was towed from 50 m to the surface, and the Multinet was used to obtain depth stratified samples from the whole water column. Analysis of samples for species composition and biomass followed the standard protocols. The zooplankton sampling and analysis are described in more detail by Gislason and Silva (2012).

Trophic levels were calculated according to the relationship (Fisk et al., 2001) $TL_{consumer} = 2 + (\delta^{15}N_{consumer} - \delta^{15}N_{C.hyperboreus})/3.8$, where $TL_{consumer}$ is the trophic level of an organism, $\delta^{15}N_{C.hyperboreus}$ is determined analytically as 5.6 ± 0.1 (mean $\pm$ s.e.), and 3.8 is the isotopic enrichment factor (Hobson and Welch, 1992; Hobson et al., 1995). Calanus hyperboreus represented trophic level 2 because it is primarily herbivorous in May (Søreide et al., 2008).

Capelin larvae were collected in April 2007 at 41 stations off the south and west coasts of Iceland and in May at 86 stations all around Iceland, using a 1-m^2 opening Tucker trawl (333 μm mesh) towed obliquely from the surface to 50 m then back to the surface at a speed of 2 nautical miles h^{-1}. In August, pelagic 0-group capelin were sampled off the west, north, and east
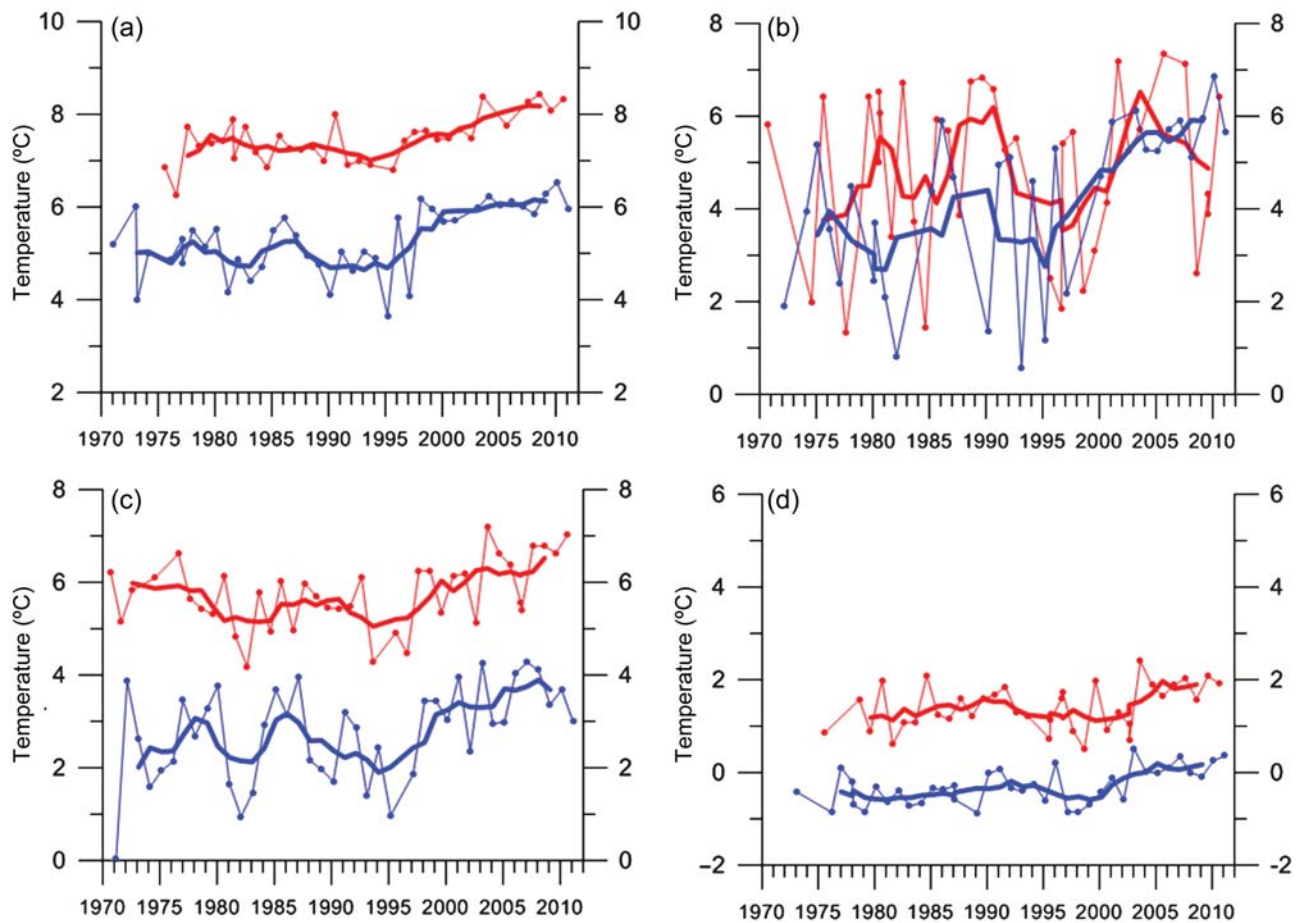
Figure 2. Time-series of temperature in summer (August, red) and winter (February, blue), at fixed repeated stations (a) Lb4, (b) Kg 4, (c) Si8, and (d) Ln6, displayed as annual (thin lines) and 3-year running means (bold lines) over the depths 0–150 m.

coasts of Iceland and in the Iceland Sea. Samples were collected offshore at 44 stations with a Harstad pelagic 0-group trawl (16 × 16 m opening, 5 × 5 mm mesh size in the codend). The trawl was aimed at acoustic targets detected between 20 and 50 m deep, for 0-group capelin, but also operated in deeper water (50–300 m) for older capelin and other fish species.

Otolith microstructure analysis was used to determine the age in days of capelin larvae. Deposition of daily rings has been verified in capelin larvae, after an initial lag phase of several days (Gjøsæter and Monstad, 1985; Ivarjord *et al.*, 2008). Preserved samples were drawn randomly for age analysis, and sagittal otoliths were removed from 120 fish in April, 390 in May, and 100 in August. The otoliths were mounted on microscopic slides and polished until the increments were visible. Counts of growth increments were repeated 3–5 times until a consistent age was obtained. If a count deviated by >10% from any other count, the otolith was discarded (~6% overall). Hatch-date frequency distributions were derived from back-calculated age-class distributions, based on the number of increments from hatch check until time of capture. Hatch dates among regions were compared with a Kolmogorov–Smirnov test.

Acoustic instruments (Simrad split-beam 38 kHz EK 60 echosounder, and BEI 500 post-processor for echo-integration) were operated during the surveys conducted in July and August for a quantitative assessment of pelagic fish species. Before the surveys, the acoustic instruments were calibrated on board using the standard sphere calibration (section 2.3.1 of Foote *et al.*, 1987). The acoustic data were analysed separately for distribution and densities of age-0 capelin, and for distribution and biomass estimation of age 1+ capelin, herring (*Clupea harengus*), and blue whiting (*Micromesistius poutassou*). Pelagic trawls were used to verify species-specific acoustic patterns and to collect otoliths for age analyses of capelin. The trawl data were also used to identify and quantify other fish species. These acoustic and trawl data are assumed to give an approximate, general picture of the presence of pelagic fish species in the area.

Results
Climate variability
Temporal patterns in temperature on selected, repeated hydrographic stations on the shelf and over the shelf break west and north of Iceland show the same trend with increases since the late 1990s (Figure 2). Salinity tends towards higher levels in the same period (not shown). Station Kögur (Figure 2b) shows clear changes in variability, from large fluctuations in the earlier years, indicating the presence of a frontal zone, to more stable winter temperatures with Atlantic character in the 2000s. Stations Siglunes 8 (Figure 2c) and Langanes NA 6 (Figure 2d), both on latitude 68°N, show slightly increasing temperatures since the turn of the century.
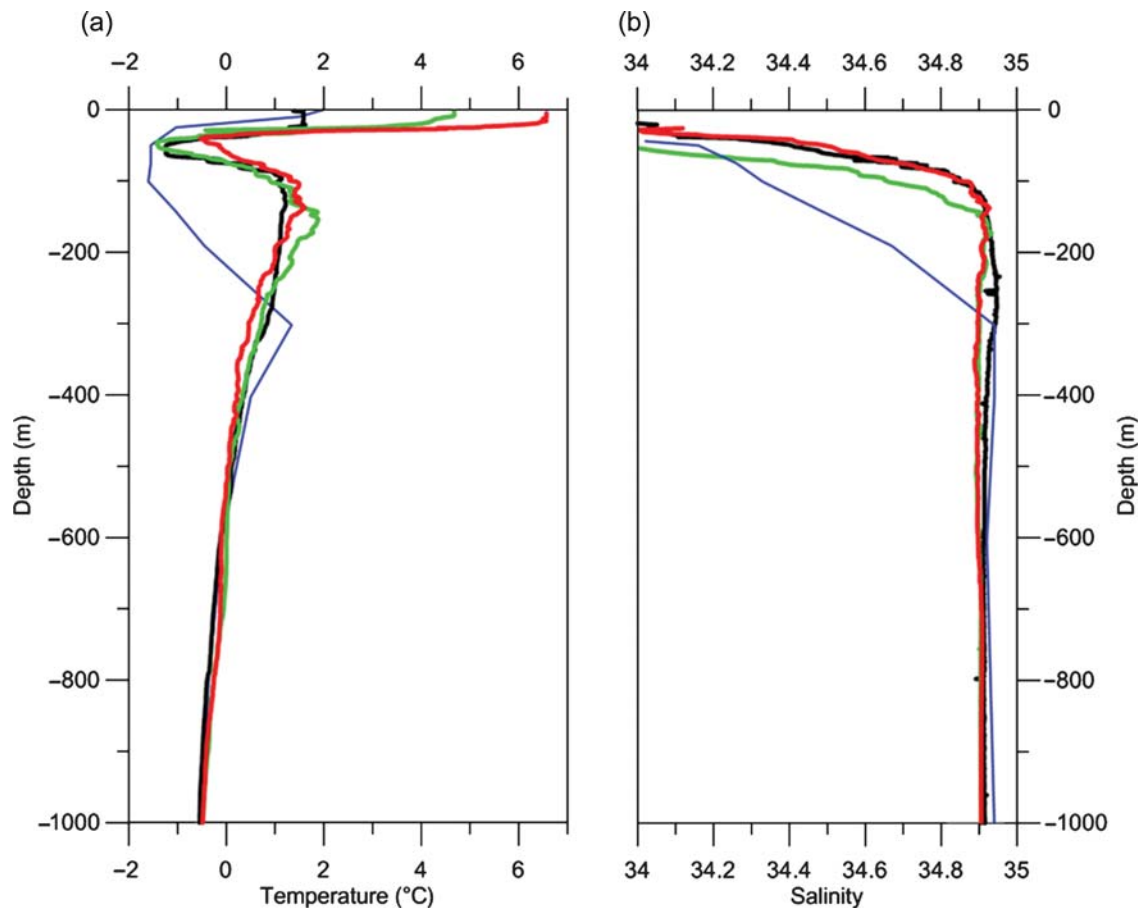
Figure 3. Profiles of (a) temperature and (b) salinity in the central Iceland Sea (station CI) on (blue) 17 August 1951, (brown) 22 September 1987, (green) 19 August 2007, and (red) 15 August 2008, from interpolated water-sampler data for 1951 and CTD data for the other years.

Increased influence of Atlantic water in most recent years is also indicated in the central Iceland Sea based on data from a station on the western side of the Kolbeinsey Ridge in the years 1951, 1987, 2007, and 2008. The surface layers were warmer in the final 2 years and the Return Atlantic Water (RAW) was almost 0.7°C warmer in 2007 than in 1987 (Figure 3). This is in line with maximum temperatures in the West Spitsbergen Current in 2006 (Walczowski and Piechura, 2011).

Biological structure

This is described in terms of frequency of occurrence of a given species in samples. For phytoplankton, however, species composition has not been analysed as closely as for zooplankton or fish; instead, a grouping of dinoflagellates, flagellates, and diatoms was used (Figure 4a). Diatoms had already started their spring bloom in April and were peaked in late May. Silicate concentrations decreased sharply at the same time. In July, diatoms were scarce and silicate concentrations were very low within the stratified layer (<30 m). Flagellates were many throughout the growth season and seem to be an important component of the phytoplankton community. Dinoflagellates were found in similar numbers throughout summer and were most likely mainly mixotrophic/heterotrophic species.

In all, 101 zooplankton species and taxonomic groups were identified in 247 WP2 and Multinet samples (Figure 4b). Several

species were rare, and 24 species and groups were found in one sample only. *Calanus finmarchicus* was the only species present in all samples. The ten most abundant species and groups in terms of numbers were as follows, in decreasing order of abundance: *C. finmarchicus*, chaetognaths, *Oithona* spp., *Pseudocalanus* spp., *Oncaea* spp., *C. hyperboreus*, *Metridia longa*, foraminiferans, *Microcalanus* spp., and *C. glacialis*.

In all, 32 fish species were identified in 138 pelagic trawl tows conducted in July 2006 (39 tows) and August of 2007 and 2008 (44 and 55 tows, respectively). Capelin were recorded in 52.9% of the tows, 0-group cod (*Gadus morhua*) in 42.8% and 0-group haddock (*Melanogrammus aeglefinus*) in 25.4%. Blue whiting, 0-group whiting (*Merlangius merlangus*), and polar cod (*Boreogadus saida*) were recorded in 10.1, 8.7, and 8.0% of the tows, respectively, and herring in 5.8%. The remaining species were in 0.7–5.1% of the tows, i.e. in 1–7 tows (Figure 4c).

As stated earlier, *C. hyperboreus* in May represents trophic level 2, with the lowest $\delta^{15}N$ value measured (5.6‰, mean value). *M. longa* had the lowest $\delta^{15}N$ mean value in the August samples (7.2‰), whereas adult capelin and blue whiting had the highest value, 11.7 and 11.6‰, respectively. The mean trophic level of the four zooplankton groups differed only marginally, ranging from 2.6 to 2.9. Individual species within the zooplankton groups ranged between 2.4 (the copepod *M. longa*) and 3.1 (the copepod *Paraeuchaeta glacialis*; further detail in Pétursdottir
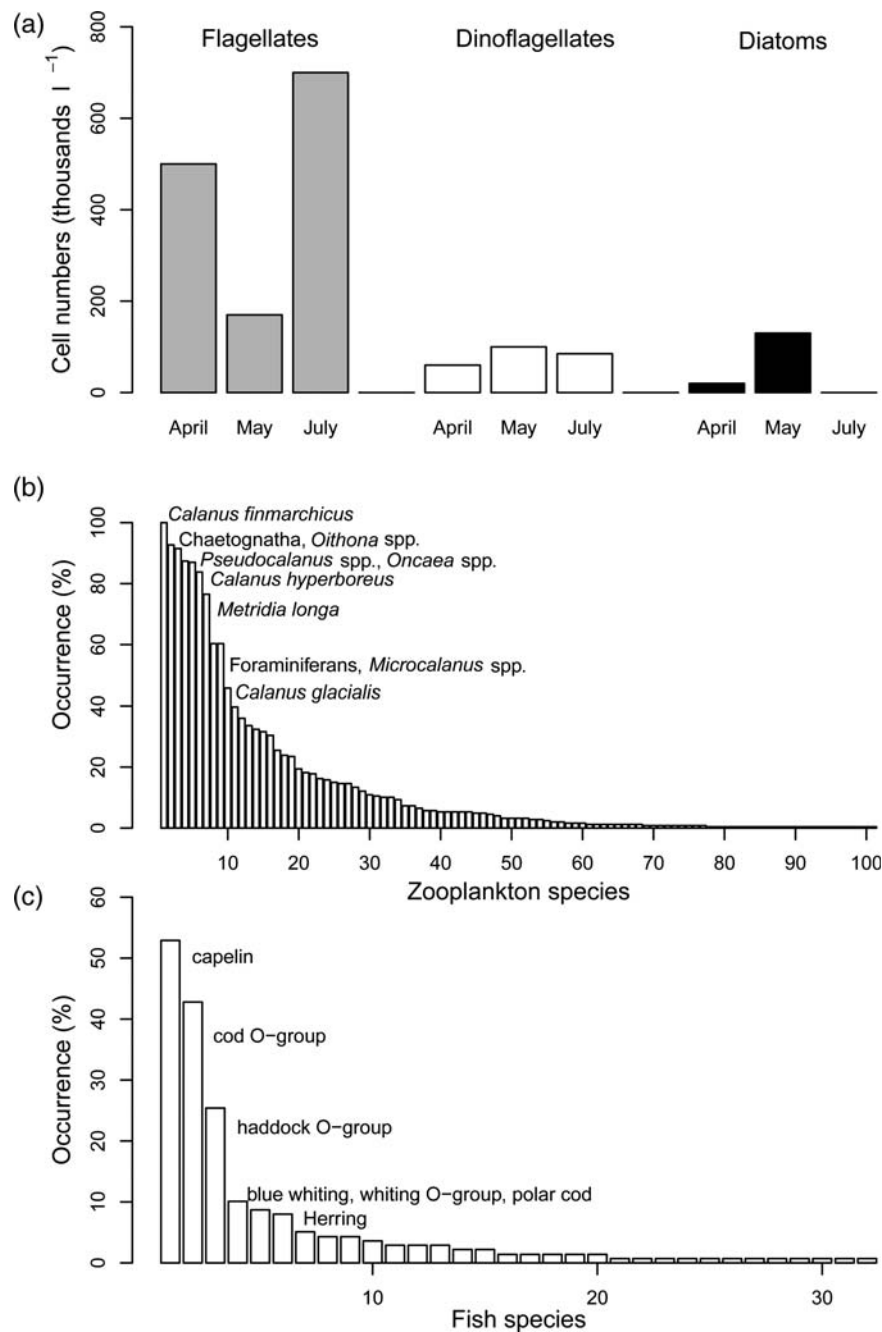
Figure 4. Biodiversity in the Iceland Sea, 2006–2008. (a) Cell numbers of phytoplankton groups in April, May, and July, (b) relative occurrence of 101 mesozooplankton species and groups in 247 WP2 and Multinet samples, and (c) relative occurrence of 32 fish species in 138 pelagic trawl tows.

et al., 2012). The trophic level increased for the remaining groups to a maximum of 3.6 for adult capelin and blue whiting (Figure 5).
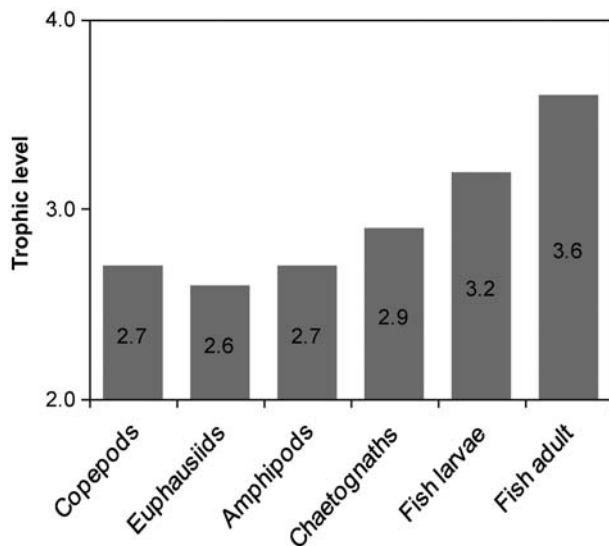
Seasonality

The analysis of seasonality is based on data collected along the 69°N transect during the years 2006–2008 (Figure 6). Nitrate concentrations that fuelled the spring bloom were around 10 μmol l^{-1} at the end of the winter mixing, and fell quickly at the onset of the bloom; the lowest concentrations of nitrate were 1.8 μmol l^{-1} in late summer (July/August). Primary production (PP) was

highest during the spring bloom in late May (>1 g C m^{-2} d^{-1}), but much lower in April/May during the pre-bloom. In July, the PP value had decreased to half and in August to 30% of the spring-bloom value. The seasonal variability in mesozooplankton total numbers was characterized by low winter values ($\sim$30 000 ind. m^{-2}), higher values in spring (May, $\sim$70 000–90 000 ind. m^{-2}), and one main peak during summer in July and August ($\sim$350 000–370 000 ind. m^{-2}). After August, the numbers decreased again, and in November, numbers were again relatively low ($\sim$60 000 ind. m^{-2}).
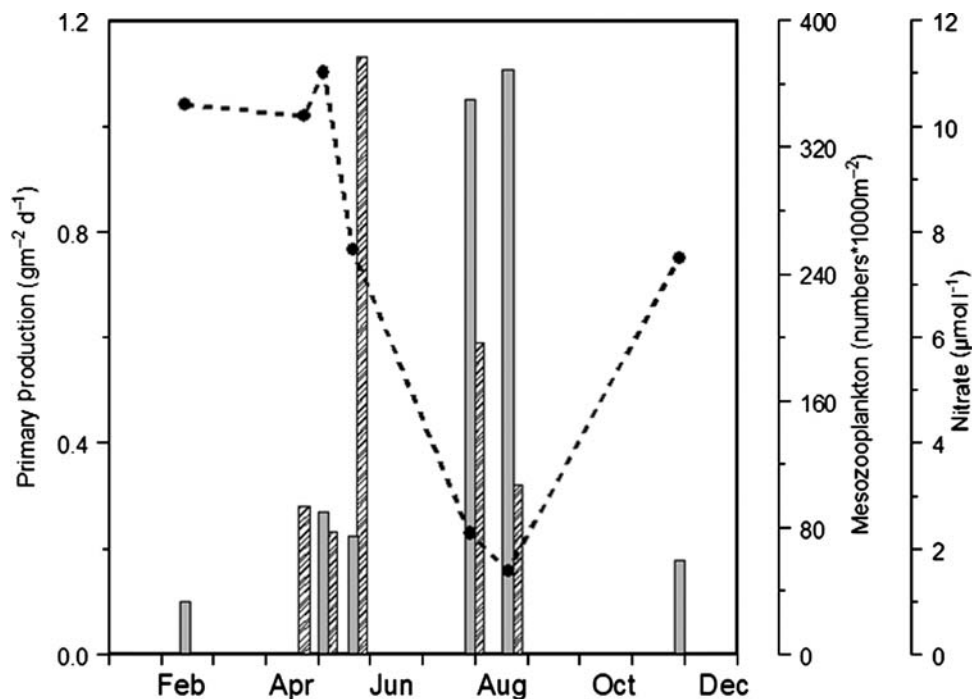
Spatial structure

Near-surface (50 m) summer temperatures in July 2006 demonstrate the spatial distribution of three main water masses in the Iceland Sea, i.e. (i) the cold, fresh polar waters of the East Greenland Current to the west, (ii) the warmer, more-saline Atlantic waters, entering through the Denmark Strait as the North Icelandic Irminger Current in the south, and south of Jan Mayen in the east, and (iii) the mixed Arctic surface waters on, and east of, the Kolbeinsey Ridge (Figure 7a). Temperature and salinity of the surface layers were similar during the three summer cruises except that, in August 2008, the surface layers were warmer in the southern and eastern areas than in August 2007 and July 2006. In the eastern part of the Iceland Sea, nitrate concentrations, integrated from the surface down to 30 m (Figure 7b), and phosphate (not shown) were not fully utilized in the surface layers in July 2006, but were depleted in the western part. Silicate, however, was depleted down to ∼50 m in the eastern part (not shown). Similar results were found in 2007, but in 2008 all nutrients were fully depleted in the mixed surface layer. Integrated Chl a biomass within the surface layer (0–30 m) was very low west of the Kolbeinsey Ridge (19°W; Figure 7c). Some biomass was recorded east of the Ridge, but the highest biomass was in the shelf areas near Jan Mayen, Iceland, and East Greenland. Lower Chl a values were recorded in August 2007 and 2008 in the eastern and central areas. The biomass of mesozooplankton in the surface layers (0–50 m) was variable, but generally highest in the western parts of the Iceland Sea in the cold waters close to Greenland, except for one shelf station off the northeast coast of Iceland (Figure 7d).

In April 2007, capelin larvae were recorded along the south and the west coasts of Iceland. In May, the distribution was continuous along the north coast, with smaller patches in the south. In August, on the other hand, the pelagic trawl caught surviving larvae (0-group) in a small area in the southern Iceland Sea and at a single station off the northeast coast, whereas acoustic densities were recorded in a larger area, in particular to the west and north (Figure 8a). The summer distribution of juvenile and adult capelin (age 1+) in the years 2006–2008 can be grouped into three main spatial patterns. First, in July 2006, concentrations of mainly age 2+ capelin were recorded on the East Greenland

Figure 5. The mean trophic level of three zooplankton groups, chaetognaths, fish larvae, and adult fish in August 2007 and 2008. The numbers inside the bars indicate the mean of the respective group.

Figure 6. Seasonality of nitrate concentration (black dotted line), primary production (hatched bars), and mesozooplankton (solid grey bars) on a section at 69°N based on composites of the years 2006–2008.
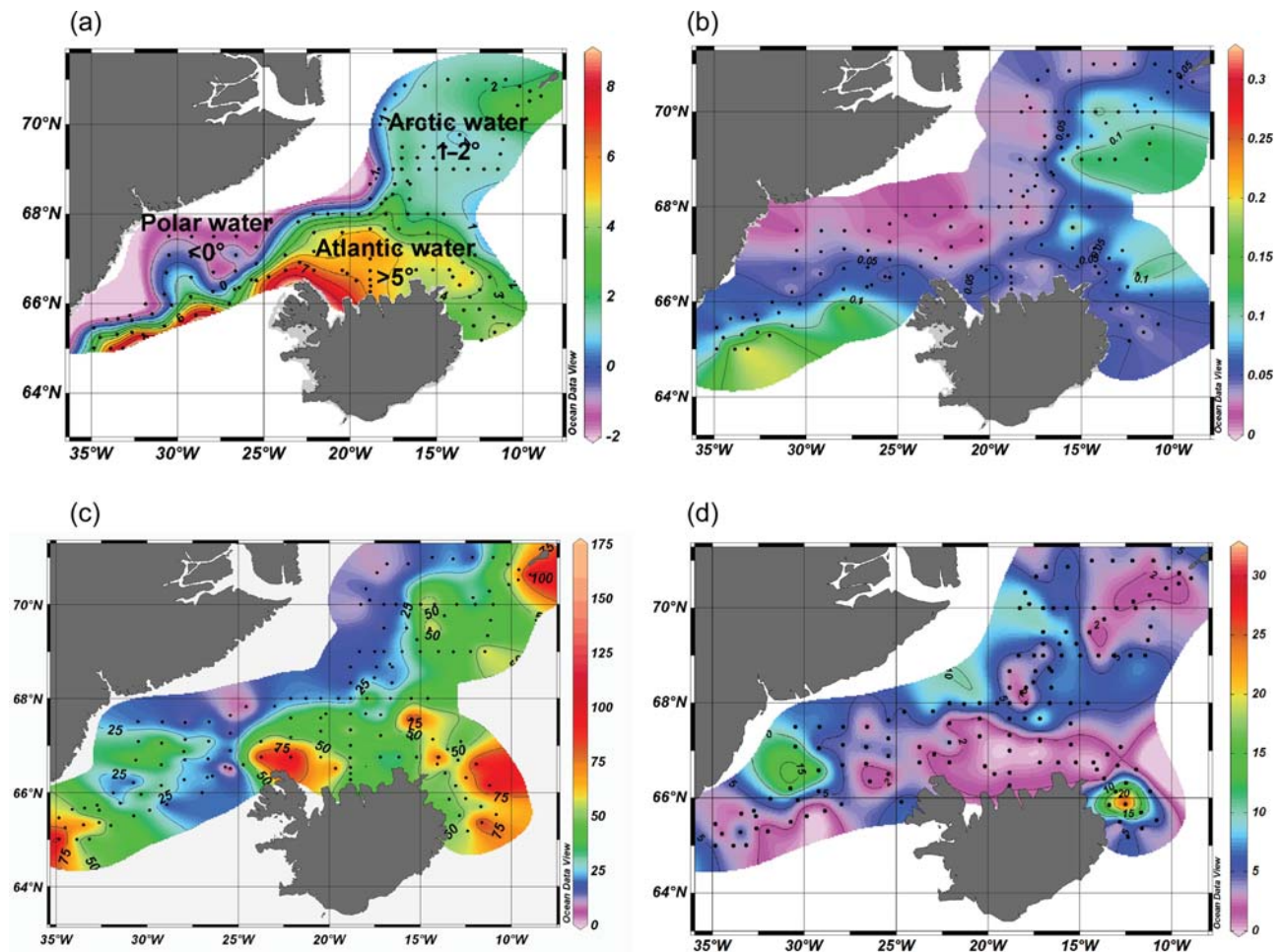
Figure 7. Spatial distributions of lower ecosystem levels in July 2006. (a) Sea temperature (°C at 50 m), (b) nitrate (mol m^{-3} at 0–30 m), (c) Chl *a* (mg m^{-2} at 0–30 m), and (d) mesozooplankton (g m^{-2} at 0–50 m).

shelf south of the Denmark Strait. Second, in all 3 years, scattered patches, mainly of capelin aged 1 year, were recorded along the northern edge of the Iceland shelf. Finally, in August 2007 and 2008, concentrations of capelin aged 2 and 1 were recorded along the edge of the East Greenland shelf in the western central Iceland Sea (Figure 8b). Herring (mostly Norwegian spring-spawning herring) were mainly found in the central Iceland Sea in August 2007 and in smaller quantities in August 2008 east of Iceland. Blue whiting were recorded primarily along the southern shelf edge off East Greenland and off the east coast of Iceland in July 2006, as well as in the central and eastern Iceland Sea in August 2007 (Figure 8c). 0-Group cod and haddock were mainly recorded in 2007 along the shelf edge north of Iceland and in the southern Iceland Sea above the Kolbeinsey Ridge (Figure 8d).

Capelin larvae collected in April and May 2007 hatched significantly later off the northwest coast than off the southwest coast (Figure 9a–d). The larvae along the northeast coast hatched even later (not shown). The early hatching ogive in April off the northwest coast (Figure 9b) was not found again in May (Figure 9d). The frequency distributions of hatch dates show that most of the surviving capelin larvae caught in the Iceland Sea in August 2007 had hatched in May (Figure 9e), with fewer hatching in April and June.

Mean annual biomass

Phytoplankton wet-weight biomass (from Chl *a*) was estimated to be 3.8 × 10^6 t in the years 2006–2008. The annual mean biomass of the mesozooplankton was estimated at 10 g dry weight m^{-2} based on samples collected through the whole water column and during all seasons. Given that the area of the Iceland Sea is ∼250 000 km^2, the average mesozooplankton biomass in the whole Iceland Sea would be ∼2.5 million tonnes dry weight. Assuming the dry-weight content of mesozooplankton to be 20% of wet weight, this translates into 12.5 million tonnes wet weight.

The mean annual biomass of fish, i.e. capelin, herring, and blue whiting, was calculated from acoustic measurements, and it amounted to 988 000 t. The largest quantities were contributed by herring (566 000 t) and blue whiting (284 000 t), and just 138 000 t by capelin.

Discussion

Trends in climate variability indicate a warming in the waters next to the Iceland Sea, as reported for the Northeast Atlantic and the Nordic Seas as far north as the Spitsbergen Current off West Spitsbergen (Hátún *et al.*, 2005; Holliday *et al.*, 2008; Hakkinen
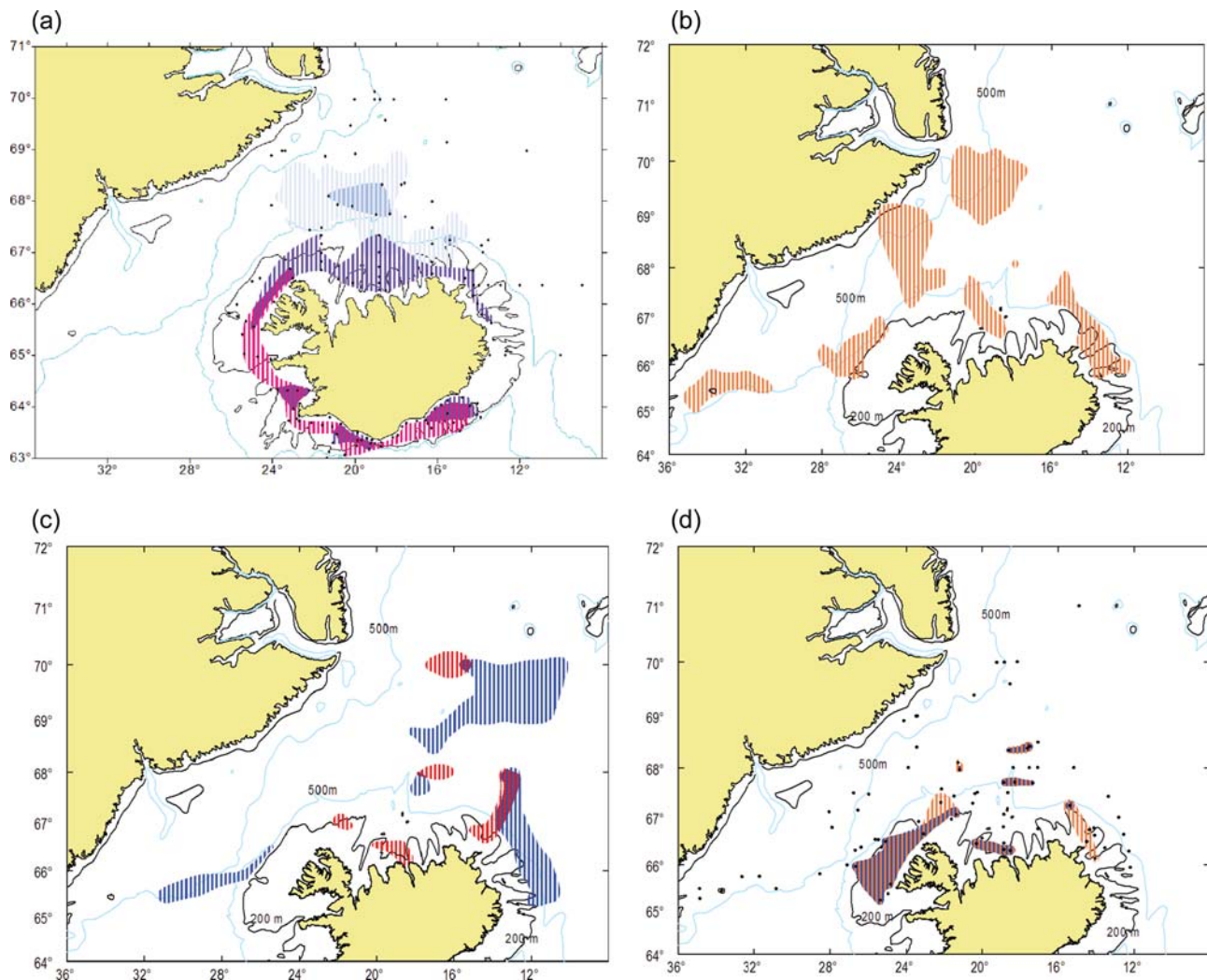
Figure 8. Spatial distributions of the main fish species, (a) capelin larvae in 2007 in April (pink), May (violet), and August (blue, trawl samples; light blue, acoustic density), (b) juvenile and adult capelin (age 1+) in July/August 2006–2008 (acoustic index), (c) adult herring (red) and blue whiting (blue) in July/August 2006–2008 (acoustic index), and (d) 0-group cod (brown) and haddock (blue) in July/August 2006–2008 (trawl samples).

and Rhines, 2009; Walczowski and Piechura, 2011). In recent decades, warmer, more-saline waters have been recorded in the area around Iceland too (Malmberg and Valdimarsson, 2003; Valdimarsson and Jónsson, 2007). Higher, more-stable winter temperatures at Kögur 4 in recent years indicate a northward movement of the Arctic front between the warmer Atlantic waters off northern Iceland and the cold waters of the East Icelandic Current. As indicated by profiles from previous and current years (Figure 3), temperature variability is extensive in the Iceland Sea, and the interplay between the distribution of sea ice and melt water makes it difficult to compare the older and more recent data to determine whether climatic changes have really been observed. However, it can be postulated that the observed increase in temperature and salinity in the West Spitsbergen Current, and the changes observed in the RAW east of Greenland in the north (Hughes et al., 2011), have resulted in warmer RAW entering the Iceland Sea. In general, the Iceland Sea seems to have been warmed from both the south and the north in recent years.

Species diversity and the trophic structure of the foodweb indicated a simple, biological structure in the Iceland Sea during our study. The phytoplankton growth season started in April. Although the phytoplankton biomass was small at that time, it extended from the surface to a depth of >100 m in the unstratified water column. Small diatoms were abundant in the pre-bloom period, but larger species, such as *Chaetoceros* spp. and *Thalassiosira* spp., appeared later. A similar pattern has been observed in the Norwegian Sea (Dale et al., 1999; Rey, 2004) and in the North Atlantic (Sieracki et al., 1993; Taylor et al., 1993). Small flagellates (<10 μm) made up an important part of the phytoplankton biomass over the growth season, which is also comparable with observations in the Norwegian Sea (Rey, 2004), in the Irminger Sea (Guðfinnsson et al., 2008) and in the Barents Sea (Sakshaug et al., 2009). Dinoflagellates play an important role in the Iceland Sea and consist of autotrophic, heterotrophic, and mixotrophic phytoplankton, as has been found in the Norwegian Sea (Rey, 2004). The mesozooplankton was characterized by a few abundant species and many rare ones. For instance,
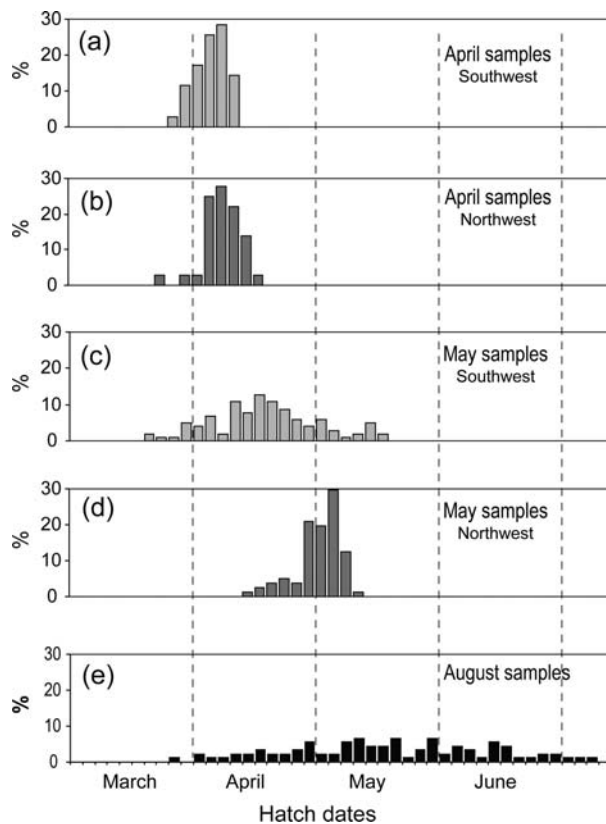
Figure 9. Hatch-date frequency distributions of capelin larvae (a) off the southwest coast of Iceland in April, (b) off the northwest coast in April, (c) off the southwest coast in May, (d) off the northwest coast in May, and (e) in the southern Iceland Sea in August.

only one species (*C. finmarchicus*) was present in all 247 samples and 6 species in more than 200 samples. This is in accord with many Arctic and subarctic systems where the main biological production is represented by relatively few species (e.g. Kosobokova and Hirche, 2000). In terms of species occurrence, the fish fauna contained few species and was dominated by capelin, with 0-group cod and haddock. In terms of biomass, herring was the largest, followed by blue whiting. However, a large portion of the blue whiting biomass was recorded outside the Iceland Sea proper. The herring were recorded in a few, relatively small, patches, occupying a very limited area of the Iceland Sea, and partly within Iceland's shelf waters. Adult capelin were recorded in a few, small patches. It is of note that capelin (all age groups) were only recorded in ~50% of the tows taken in summers of 2006–2008, and displaying a smaller biomass and more-restricted distribution range of the species in the Iceland Sea than in previous years.

Based on this study, there are 3–4 trophic levels in the pelagic ecosystem of the Iceland Sea. In late summer, the copepod *M. longa* and the euphausiid *M. norvegica* occupied the lowest trophic level of 2.4, followed by other zooplankton species, and adult capelin and blue whiting occupied the highest level (3.6). The number of trophic levels and the trophic level values of individual species were generally similar to those in the high latitude, pelagic ecosystem near Svalbard, in the European Arctic (Søreide *et al.*, 2006; Tamelander *et al.*, 2006).

There was a clear seasonal pattern in production, although the data represent composites of 3 years. PP seems to display a pattern

and production values similar to those observed at the outer limits of the shelf north of Iceland (Thordardottir, 1977, 1984) and in the Norwegian and Greenland Seas (Rey *et al.*, 2000; Rey, 2004), with a spring bloom in May (>1 g C m^{-2} d^{-1}), a post-bloom in June/July (<0.6 g C m^{-2} d^{-1}), and a further decline towards autumn (<0.3 g C m^{-2} d^{-1}). In the pre-bloom period, nutrient concentrations are high, but as the spring bloom develops, the silicate concentration is used up quickly, i.e. within ~2 weeks. PP in the post-bloom is based primarily on dinoflagellates and small flagellates, because diatoms are outcompeted as a consequence of silicate concentrations being exhausted. Late summer production is therefore most probably based on regenerated nutrients, as has been found for the Norwegian Sea (Skjoldal *et al.*, 2004). Zooplankton numbers peaked in July/August, at a similar time as phytoplankton biomass declined, thus indicating that zooplankton grazing contributed to the decline in phytoplankton biomass.

Extensive coverage in our summer surveys revealed a stable spatial structure in the ecosystem. The summer hydrography of the Iceland Sea in all 3 years was dominated by Polar and Atlantic water masses, with a mixture of the two in the central area. Nutrient distributions in late summer in the surface layers (0–30 m) reflected the distributions of the main water masses. Nitrate concentrations were very low in Polar Water but ~3–4 μmol l^{-1} in the Arctic Water of the central Iceland Sea. Silicate, however, was more abundant in Polar Water and completely utilized down to 50 m in the central Iceland Sea, with concentrations <0.5 μmol l^{-1}. Phytoplankton biomass, measured as Chl *a*, was low in late summer. The mixed layer depth was 20–30 m because the water was heavily stratified. Dinoflagellates and small flagellates dominated the phytoplankton, but diatoms were only found at the bottom of the mixed layer. A similar situation has been observed in the Norwegian Sea (Rey, 2004). The mesozooplankton was distributed more to the west in 2006 than in 2007 and 2008. This may be related to the fact that sea ice was present mainly in the western parts of the study area in 2006. Melting sea ice may have created conditions favourable for phytoplankton growth (Sakshaug, 1997), especially in spring, which in turn may lead to more zooplankton growth and biomass near the ice edge and in areas from where the ice had recently retreated.

PP levels and mesozooplankton densities in the surface layers were clearly at a higher level in July 2006 than in August 2007 and 2008 (data not shown). The reason for this may partly be related to the difference in the time of sampling, because the annual decline in phytoplankton is typically in late summer. In 2006, the zooplankton were mainly distributed on the western side of the Kolbeinsey Ridge, which may have given the phytoplankton on the eastern side an opportunity to continue to grow as nutrients were still available.

Most of the capelin larvae found off the south and west coasts in April 2007 were newly hatched, whereas newly hatched larvae were almost exclusively found off the north coast in May (Figure 8a). The spawning seems to have started at approximately the same time in all spawning locations, because the benthic eggs need ~3–4 weeks longer to hatch at the lower bottom temperatures off the north and east coasts (Frank and Leggett, 1981). Age readings indicate that the size difference in capelin larvae between areas is explained mainly by differences in age and not by differences in growth rates. Hatch-date distributions of capelin larvae and estimates of average larval drift of 3 nautical miles d^{-1} (Stefánsson, 1961; Friðgeirsson, 1979; Brickman *et al.*,

2007) suggest that the larvae surviving in August could not have originated exclusively from the main spawning grounds off the south and west coasts. Spawning off the north coast must also have contributed to the larval population. Only part of the hatch-date distributions of larvae observed in August overlapped with the distributions from the main spawning grounds in the south, where the hatching was mostly from March to early May, whereas hatching of the surviving larvae in August reached into late June (Figure 9a, c, and e). The results indicate that the contribution of spawning sites off the north coast to the surviving population of 0-group capelin may, at least in some years, be considerably greater than previously assumed. There are indications of an earlier and/or more northerly spawning in 2007 relative to findings from the year 1904 (Jespersen, 1920). This may be a consequence of the elevated temperatures in Icelandic waters from ~1997 on (Anon., 2011). The relatively warm water may also be a factor contributing to increased larval capelin concentrations north of 68°N in August in recent years (MRI annual 0-group reports 1970–2003; Anon., 1970; Sveinbjörnsson and Hjörleifsson, 2002), most notably in 2007 (Figure 8a) and 2008 (not shown, Pálsson et al. 2012). It has also been reported that during the warm period of the mid-20th century, the main centre of capelin spawning was off the north coast (Sæmundsson, 1934).

The pelagic fish fauna of the Iceland Sea consisted primarily of juvenile and adult capelin and transient quantities of a number of larval species as well as adult blue whiting and herring, in terms of species occurrence. The summer distribution of adult capelin (age 2+) was mostly limited to western areas of the Iceland Sea, reaching far south along the East Greenland shelf. This indicates a marked westward, spatial displacement relative to previous findings (Vilhjálmsson, 1994, 2002). A recent acoustic survey, conducted in September/October 2010 by the MRI, to locate and measure the abundance of the capelin stock for management purposes, revealed a western and southern distribution of juvenile (age 1) and adult capelin (age 2+) located mainly in shelf or near-shelf waters off East Greenland, bounded by longitude 37°W to the west and latitude 72°N to the north (S. Sveinbjörnsson, pers. comm.). Previously, the capelin were, as a rule, distributed in offshore north Icelandic waters in autumn between 67 and 68°N (Vilhjálmsson, 1994). Therefore, the current, autumn distribution pattern indicates a pronounced change in distribution from offshore waters north of Iceland to those off East Greenland.

The mean annual biomass was estimated for primary and secondary production and pelagic fish. Phytoplankton wet-weight biomass was similar to that in the Norwegian Sea (Rey, 2004). It should be noted that the zooplankton biomass values illustrated in Figure 7d are only for the mesozooplankton fraction of the zooplankton. Macroplankton, especially euphausiids and amphipods, also contributed significantly to the zooplankton. Our results show that their numbers in the Iceland Sea are probably at least as high as in the Norwegian and Barents Seas (Dalpadado et al., 1998, 2001). In the latter area, the combined biomass of euphausiids and amphipods is estimated to be ~7 g dry weight m^{-2} (Melle, 2004). Assuming the biomass per m^2 of euphausiids and amphipods in the Iceland Sea to be similar, the combined dry weight of these groups in the Iceland Sea amounts to 1.7 million tonnes dry weight or 8.5 million tonnes wet weight. Therefore, the total zooplankton biomass in the Iceland Sea would amount to ~21 million tonnes wet weight.

The mean annual biomass of fish species was estimated to be 998 000 t. Much of the blue whiting was located at the southeast periphery of the Iceland Sea, i.e. off the east coast of Iceland, as well as outside the Iceland Sea proper in warmer waters along the shelf edge of East Greenland. The biomass within the Iceland Sea is therefore well below a million tonnes. The quantity of adult capelin during our study was low compared with previous years, and the mean annual biomass of pelagic fish was only a small fraction of what would be expected in view of zooplankton biomass and previous levels of pelagic fish stocks (Vilhjálmsson, 1994, 2002). The quantity of fish species other than herring, blue whiting, and capelin was small and may be considered as negligible in terms of biomass.

The low estimated fish biomass relative to comparable geographic areas is interesting and raises the question about the fate of the production at lower trophic levels. Although a fraction of the secondary and primary production would undoubtedly settle ungrazed to the bottom, a fraction would be advected away from the Iceland Sea proper into the ecosystems of adjacent waters, as suggested by the current pattern (Figure 1). Although data on the seasonal abundance of zooplankton are lacking from the period of larger capelin stocks in the Iceland Sea, it seems likely that predation by capelin had a greater impact then on growth and development of the zooplankton.

The changes observed in the distribution pattern of Iceland capelin since the late 1990s have been hypothesized to be related to climate change and a resulting change in hydrographic conditions, i.e. a warming of the upper and intermediate layers of the Iceland Sea (Vilhjálmsson, 2002). Those changes have been further substantiated within the current project, but not fully explained in causal terms. However, the available data suggest some warming in recent years. In the absence of other relevant, environmental factors, it is concluded that the large change in capelin distribution seems to have resulted from a rather modest warming in the Iceland Sea, which displaced the capelin stock into the western and southwestern waters of the Iceland Sea, i.e. East Greenland waters and the Denmark Strait. Corresponding spatial changes in the prey species of capelin can neither be ruled out nor verified because of a lack of long-term zooplankton data.

The present project is the first general ecosystem programme to be conducted in the Iceland Sea. The results provide a basic insight into the ecology of this Subarctic area, and an important benchmark for further studies. Similarities to adjacent areas in ecosystem structures were identified, e.g. in terms of species richness, trophic structure, and spring-bloom seasonality. To achieve a deeper understanding of the ecological interactions of capelin, further efforts are required with particular focus on capelin habitats and ecosystem factors of relevance in the life history of capelin.

References

Anon. 1970. Preliminary report on joint Icelandic–Norwegian investigation in the area between Iceland and East Greenland in August 1970. Annales Biologiques, 27: 196–202.

Anon. 2011. Environmental conditions in Icelandic waters 2010. Marine Research in Iceland, 158. 80 pp.

Astthorsson, O. S., and Gislason, A. 1995. Long-term changes in zooplankton biomass in Icelandic waters in spring. ICES Journal of Marine Science, 52: 657–668.

Blindheim, J., and Østerhus, S. 2005. The Nordic Seas, main oceanographic features. Geophysical Monograph, 158: 11–38.

Brickman, D., Marteinsdottir, G., Logeman, K., and Harms, I. H. 2007. Drift probabilities for Icelandic cod larvae. ICES Journal of Marine Science, 64: 49–59.

Buch, E., Malmberg, S-Aa., and Kristmannson, S. S. 1996. Arctic Ocean deep water masses in the western Iceland Sea. Journal of Geophysical Research, 103: 11965–11973.

Dale, T., Rey, F., and Heimdal, B. R. 1999. Seasonal development at high latitude oceanic site. Sarsia, 84: 419–435.

Dalpadado, P., Borkner, N., Bogstad, B., and Mehl, S. 2001. Distribution of *Themisto* spp. (Amphipoda) in the Barents Sea and predator–prey interactions. ICES Journal of Marine Science, 58: 867–895.

Dalpadado, P., Ellertsen, B., Melle, W., and Skjoldal, H. R. 1998. Summer distribution patterns and biomass estimates of macrozooplankton and micronekton in the Nordic Seas. Sarsia, 83: 103–116.

Fisk, A. T., Hobson, K. A., and Norstrom, R. J. 2001. Influence of chemical and biological factors on trophic transfer of persistent organic pollutants in the Northwater Polynya marine food web. Environmental Science and Technology, 35: 732–738.

Foote, K. G., Knudsen, H. P., Vestnes, G., MacLennan, D. N., and Simmonds, E. J. 1987. Calibration of acoustic instruments for fish density estimation: a practical guide. ICES Cooperative Research Report, 144. 69 pp.

Frank, K. T., and Leggett, W. C. 1981. Prediction of egg development and mortality rates in capelin (*Mallotus villosus*) from meteorological, hydrographic and biological factors. Canadian Journal of Fisheries and Aquatic Sciences, 38: 1327–1338.

Friðgeirsson, E. 1979. Notes on capelin and sandeel larvae collected in Icelandic waters 1976–1979. ICES Document CM 1979/L: 28.

Gislason, A., and Astthorsson, O. S. 1998. Seasonal variations in biomass, abundance and composition of zooplankton in the Subarctic waters north of Iceland. Polar Biology, 20: 85–94.

Gislason, A., and Silva, T. 2012. Abundance, composition and development of zooplankton in the Subarctic Iceland Sea in 2006, 2007 and 2008. ICES Journal of Marine Science, 69: 000–000.

Gjøsæter, J., and Monstad, T. 1985. Primary growth rings in otoliths of the Barents Sea capelin. Fiskeridirektoratets Skrifter Serie Havundersøgelser, 17: 521–528.

Guðfinnsson, H. G., Debes, D., Falkenhaug, T., Gaard, E., Gislason, A., Petursdottir, H., Sigurðsson, Þ., et al. 2008. Abundance and productivity of the pelagic ecosystem along a transect across the northern Mid Atlantic Ridge in June 2003. ICES Document CM 2008/C: 13.

Guðmundsson, K. 1998. Long-term variation in phytoplankton productivity during spring in Icelandic waters. ICES Journal of Marine Science, 55: 635–643.

Guðmundsson, K., Gislason, A., Ólafsson, J., Thorisson, K., Björnsdóttir, R., Steingrímsson, S. A., Ólafsdóttir, S., et al. 2002. Ecology of Eyjafjördur project. Chemical and biological parameters measured in Eyjafjördur in the period April 1992–August 1993. Marine Research Institute Report, 89. 129 pp.

Guðmundsson, K., and Valsdóttir, K. 2004. Frumframleiðnimælingar á Hafrannsóknastofnuninni árin 1958–1999. Umfang, aðferðir og úrvinnsla. [Primary production measurements at the Marine Research Institute in Iceland 1958–1999.] Marine Research Institute Report, 107. 56 pp. (in Icelandic, with English abstract).

Hakkinen, S., and Rhines, P. B. 2009. Shifting surface currents in the northern North Atlantic Ocean. Journal of Geophysical Research, 114: C04005.

Hasle, G. R. 1978. The inverted-microscope method. In Phytoplankton Manual, pp. 88–96. Ed. by A. Sournia. UNESCO, Paris.

Hátún, H., Sandö, A. B., Drange, H., Hansen, B., and Valdimarsson, H. 2005. Influence of the Atlantic Subpolar Gyre on the thermohaline circulation. Science, 309: 1841–1844.

Hobson, K. A., Ambrose, W. G., and Renaud, P. E. 1995. Sources of primary production, benthic–pelagic coupling, and trophic relationships within the Northeast Water Polynya: Insights from $\delta^{13}C$ and $\delta^{15}N$ analysis. Marine Ecology Progress Series, 128: 1–10.

Hobson, K. A., and Welch, H. E. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Marine Ecology Progress Series, 84: 9–18.

Holliday, N. P., Hughes, S. L., Bacon, S., Beszczynska-Möller, A., Hansen, B., Lavin, A., Loeng, H., et al. 2008. Reversal of the 1960s to 1990s freshening trend in the northeast North Atlantic and Nordic Seas. Geophysical Research Letters, 35: L03614, doi:10.1029/2007GL032675.

Hughes, S. L., Holliday, N. P., and Beszczynska-Möller, A. (Eds). 2011. ICES Report on Ocean Climate 2010. ICES Cooperative Research Report, 209. 69 pp.

Hunegnaw, A., Siegismund, F., Hipkin, R., and Mork, K. A. 2009. Absolute flow field estimation for the Nordic Seas from combined gravimetric, altimetric, and in situ data. Journal of Geophysical Research, 114, C02022.

Ivarjord, T., Pedersen, T., and Moksness, E. 2008. Effects of growth rates on the otolith increments deposition rate in capelin larvae (*Mallotus villosus*). Journal of Experimental Marine Biology and Ecology, 358: 170–177.

Jeansson, E., Jutterström, E. S., Rudels, B., Andersson, L. G., Olsson, K. A., Jones, E. P., Smethie, W. M., et al. 2008. Sources to the East Greenland Current and its contribution to the Denmark Strait Overflow. Progress in Oceanography, 78: 12–28.

Jespersen, P. 1920. On the occurrence of the postlarval stages of the herring and the "lode" (*Clupea harengus* L. and *Mallotus villosus* O.F.M.) at Iceland and the Færoes. Meddelelser fra Kommissionen for Havundersøgelser Serie Fiskeri, 6: 1–25.

Jónsson, S., and Valdimarsson, H. 2012. Hydrography and circulation over the southern part of the Kolbeinsey Ridge. ICES Journal of Marine Science, 69: 000–000.

Kosobokova, K. N., and Hirche, H-J. 2000. Zooplankton distribution across the Lomonosov Ridge, Arctic Ocean: species inventory, biomass and vertical structure. Deep Sea Research, 47: 2029–2060.

Malmberg, S-Aa., and Valdimarsson, H. 2003. Hydrographic conditions in Icelandic waters, 1990–1999. ICES Marine Science Symposia, 219: 50–60.

Melle, W. 2004. Zooplankton: the link to higher trophic levels. In The Norwegian Sea Ecosystem, pp. 137–202. Ed. by H. R. Skjoldal, R. Sætre, A. Fernö, O. A. Misund, and I. Röttingen. Tapir Academic Press, Trondheim.

Ólafsson, J. 2003. Winter mixed layer nutrients in the Irminger and Iceland Seas, 1990–2000. ICES Journal of Marine Science, 219: 329–332.

Ólafsson, J., Ólafsdóttir, S. R., Benoit-Cattin, A., and Takahashi, T. 2010. The Irminger Sea and the Iceland Sea time series measurements of sea water carbon and nutrient chemistry 1983–2008. Earth System Science Data, 2: 99–104.

Pálsson, Ó. K., Sveinbjörnsson, S., Valdimarsson, H., Gislason, A., and Vilhjálmsson, H. 2012. Capelin life-history traits in the Iceland Sea. Marine Research in Iceland, 162 (in print).

Petursdottir, H., Falk-Petersen, S., and Gislason, A. 2012. Trophic interactions of mesozooplankton and fish in the Iceland Sea as evaluated by fatty acid and stable isotope analysis. ICES Journal of Marine Science, 69: 000–000.

Rey, F. 2004. Phytoplankton: the grass of the sea. *In* The Norwegian Sea Ecosystem, pp. 97–136. Ed. by H. R. Skjoldal, R. Sætre, A. Fernö, O. A. Misund, and I. Röttingen. Tapir Academic Press, Trondheim.

Rey, F., Noji, T. T., and Miller, L. A. 2000. Seasonal phytoplankton development and new production in the central Greenland Sea. Sarsia, 85: 329–344.

Rudels, B., Fahrbach, E., Meincke, J., Budéus, G., and Eriksson, P. 2002. The East Greenland Current and its contribution to the Denmark Strait overflow. ICES Journal of Marine Science, 59: 133–1154.

Sakshaug, E. 1997. Biomass and productivity distributions and their variability in the Barents Sea. ICES Journal of Marine Science, 54: 341–350.

Sakshaug, E., Johnsen, G., Kristiansen, S., Von Quillfeldt, C., Rey, F., Slagstad, D., and Thingstad, F. 2009. Phytoplankton and primary production. *In* Ecosystem Barents Sea, pp. 167–208. Ed. by E. Sakshaug. Tapir Academic Press, Trondheim.

Sæmundsson, B. 1934. Probable influence of changes in temperature on the marine fauna of Iceland. Rapports et Procès-Verbaux des Réunions du Conseil Permament International pour l'Exploration de la Mer, 86: 1–6.

Sieracki, M. E., Verity, P. G., and Stoecker, D. K. 1993. Plankton community response to sequential silicate and nitrate depletion during the 1989 North Atlantic spring bloom. Deep Sea Research II, 40: 213–225.

Skjoldal, H. R., Dalpadado, P., and Dommasnes, A. 2004. Food webs and trophic interactions. *In* The Norwegian Sea Ecosystem, pp. 447–506. Ed. by H. R. Skjoldal, R. Sætre, A. Fernö, O. A. Misund, and I. Röttingen. Tapir Academic Press, Trondheim.

Søreide, J. E., Falk-Petersen, S., Hegseth, E. N., Hop, H., Carroll, M. L., Hobson, K. A., and Blachowiak-Samolyk, K. 2008. Seasonal feeding strategies of *Calanus* in the high-Arctic Svalbard region. Deep Sea Research II, 55: 2225–2244.

Søreide, J. E., Hop, H., Carroll, M. L., Falk-Petersen, S., and Hegseth, E. N. 2006. Seasonal food web structures and sympagic–pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. Progress in Oceanography, 71: 59–87.

Stefánsson, U. 1961. Hafið. Almenna bókafélagið, Reykjavík. 293 pp.

Strickland, J. D. H., and Parsons, T. R. 1972. A practical handbook of seawater analysis. Bulletin of the Fisheries Research Board of Canada, 167. 310 pp.

Sveinbjörnsson, S., and Hjörleifsson, E. 2002. Report on the 0-group fish survey in Icelandic waters in August 2002. ICES Document CM 2002/ACFM: 20.

Swift, J. H., and Aagaard, K. 1981. Seasonal transitions and water mass formation in the Iceland and Greenland Seas. Deep Sea Research, 28: 1107–1120.

Tamelander, T., Renaud, P. E., Hop, H., Carroll, M. L., Ambrose, W. G., and Hobson, K. A. 2006. Trophic relationships and pelagic–benthic coupling during summer in the Barents Sea marginaliIce zone, revealed by stable carbon and nitrogen isotope measurements. Marine Ecology Progress Series, 310: 33–46.

Taylor, A. H., Harbour, D. S., Burkhill, P. H., and Edwards, E. S. 1993. Seasonal succession in the pelagic ecosystem of the North Atlantic and the utilization of nitrogen. Journal of Plankton Research, 15: 875–891.

Thordardottir, Th. 1977. Primary production in North Icelandic waters in relation to recent climatic changes. *In* Polar Oceans. Proceedings of the Polar Oceans Conference held at McGill University, Montreal, May 1974, pp. 655–665. Ed. by M. J. Dunbar. Arctic Institute of America, Canada.

Thordardottir, Th. 1984. Primary production north of Iceland in relation to water masses in May–June 1970–1980. ICES Document CM 1984/L: 20. 17 pp.

Tomas, C. (Ed). 1997. Identifying Marine Phytoplankton. Academic Press, London. 858 pp.

Vaage, K., Pickart, R. S., Spall, M. A., Valdimarsson, H., Jónsson, S., Torres, D., Østerhus, S., *et al.* 2011. Significant role of the North Icelandic jet in the formation of Denmark Strait overflow water. Nature Geoscience, 5 pp. doi:10.1038/NGEO1234.

Valdimarsson, H., and Jónsson, S. 2007. Time series and hydrographic variability in Icelandic waters. CLIVAR Exchanges, 12: 23–24.

Vilhjálmsson, H. 1994. The Icelandic capelin stock. Capelin (*Mallotus villosus*) in the Iceland–East Greenland–Jan Mayen ecosystem. Rit Fiskideildar, 13. 281 pp.

Vilhjálmsson, H. 2002. Capelin (*Mallotus villosus*) in the Iceland–East Greenland–Jan Mayen ecosystem. ICES Journal of Marine Science, 59: 870–883.

Walczowski, W., and Piechura, J. 2011. Influence of the West Spitsbergen Current on the local climate. International Journal of Climatology, 31: 1088–1093.

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