



Abundance, composition, and development of zooplankton in the Subarctic Iceland Sea in 2006, 2007, and 2008

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A large-scale study of zooplankton from surface waters and depth-stratified sampling at selected sites in the Iceland Sea was conducted during the years 2006–2008. The abundance of mesozooplankton was low during winter, when animals were mostly confined to the colder ($\sim 0^{\circ}\text{C}$) and deeper (~ 200 – 1000 m) layers, and peaked during late summer (~ 11 – 18 g dry weight m^{-2} , $\sim 300\,000$ – $400\,000$ ind. m^{-2}), when animals resided mainly above the 50–100-m depth range. Diversity was greatest near the shelf edges and least in the central Iceland Sea. Around 32% of mesozooplankton variability was explained by six variables [longitude, year 2008, temperature, bottom depth, chlorophyll *a* (Chl *a*), and salinity]. Three main mesozooplankton communities were identified: (i) an Atlantic community in the east, with *Calanus finmarchicus* and *Pseudocalanus* spp. most abundant, (ii) an Arctic community at high latitudes, with large numbers of *C. hyperboreus* and *C. glacialis*, and (iii) a community with coastal affinities at lower latitudes, with large numbers of *Temora longicornis* and *Acartia* spp. Longitude and Chl *a* explained $\sim 43\%$ of macrozooplankton variability (euphausiids and amphipods). Results show that the region is a meeting place of Arctic and Atlantic species, with the copepods *C. finmarchicus* and *C. hyperboreus*, the amphipod *Themisto abyssorum*, and the euphausiid *Thysanoessa longicaudata* the key players.

Keywords: Iceland Sea, seasonal variability, zooplankton.

Introduction

The Iceland Sea, located between Iceland, Greenland, and Jan Mayen, has historically played an important role in the fisheries around Iceland, mainly related to its role as a food provider for the Icelandic capelin (*Mallotus villosus*) stock, which during its summer feeding in the Iceland Sea preys mainly on the rich copepod and euphausiid stocks in the area (Sigurdsson and Astthorsson, 1991; Astthorsson and Gislason, 1997a). During recent years, the feeding migration routes of capelin have changed, so one of the main motivations behind this study was to provide background information on zooplankton in the feeding area that can contribute to an understanding of the factors affecting capelin migrations.

Earlier investigations on zooplankton north of Iceland include long-term investigations in spring (Astthorsson *et al.*, 1983; Astthorsson and Gislason, 1995; Gislason *et al.*, 2009) and seasonal studies off the north and northeast coasts (Astthorsson and Gislason, 1997b; Gislason and Astthorsson, 1998; Astthorsson

and Gislason, 2003). Those studies were restricted mainly to the shelf areas or the regions over shelf ridges, and to our knowledge, there are no other studies on the seasonal abundance and composition of zooplankton in the oceanic part of the Iceland Sea north of 68°N . Zooplankton investigations were, however, included in the Icelandic participation in the International Greenland Sea Project (GSP) during the years 1987–1991, but were restricted to studies on abundance and distribution in autumn along two transects at the fringes of the Iceland Sea (Astthorsson *et al.*, 1995).

The aim of the present investigation is to describe the distribution, diversity, and seasonal variability of zooplankton in the Iceland Sea and to relate this to the hydrography and to chlorophyll *a* (hereafter Chl *a*). The investigation forms a part of a research effort known as the Iceland Sea Ecosystem Project, with field activity in 2006–2008 aimed at exploring the general structure and functioning of the Iceland Sea ecosystem so as to understand better the factors that are influencing capelin growth and feeding migrations (Pálsson *et al.*, 2012a).

Methods

The Iceland Sea is bounded by Iceland and the Iceland–Greenland Ridge in the south, Greenland in the west, the submarine ridge between Greenland and Jan Mayen in the north, and the Jan Mayen Ridge in the west (Stefansson, 1962; Figure 1a). The Kolbeinsey Ridge that stretches from the middle of the north coast of Iceland and north to the submarine ridge between Greenland and Jan Mayen divides the Iceland Sea into two main basins.

Relatively warm, saline Atlantic water enters the Iceland Sea from both the southwest as a branch of the Irminger Current and in the east from the Norwegian Sea through and over the Jan Mayen Ridge. The East Greenland Current carries cold, low-salinity water from the Greenland Sea in the north into the Iceland Sea (Stefansson, 1962; Valdimarsson and Malmberg, 1999). In the Iceland Sea, these water masses mix, and the proportion of warm and cold water varies by region and season. Where

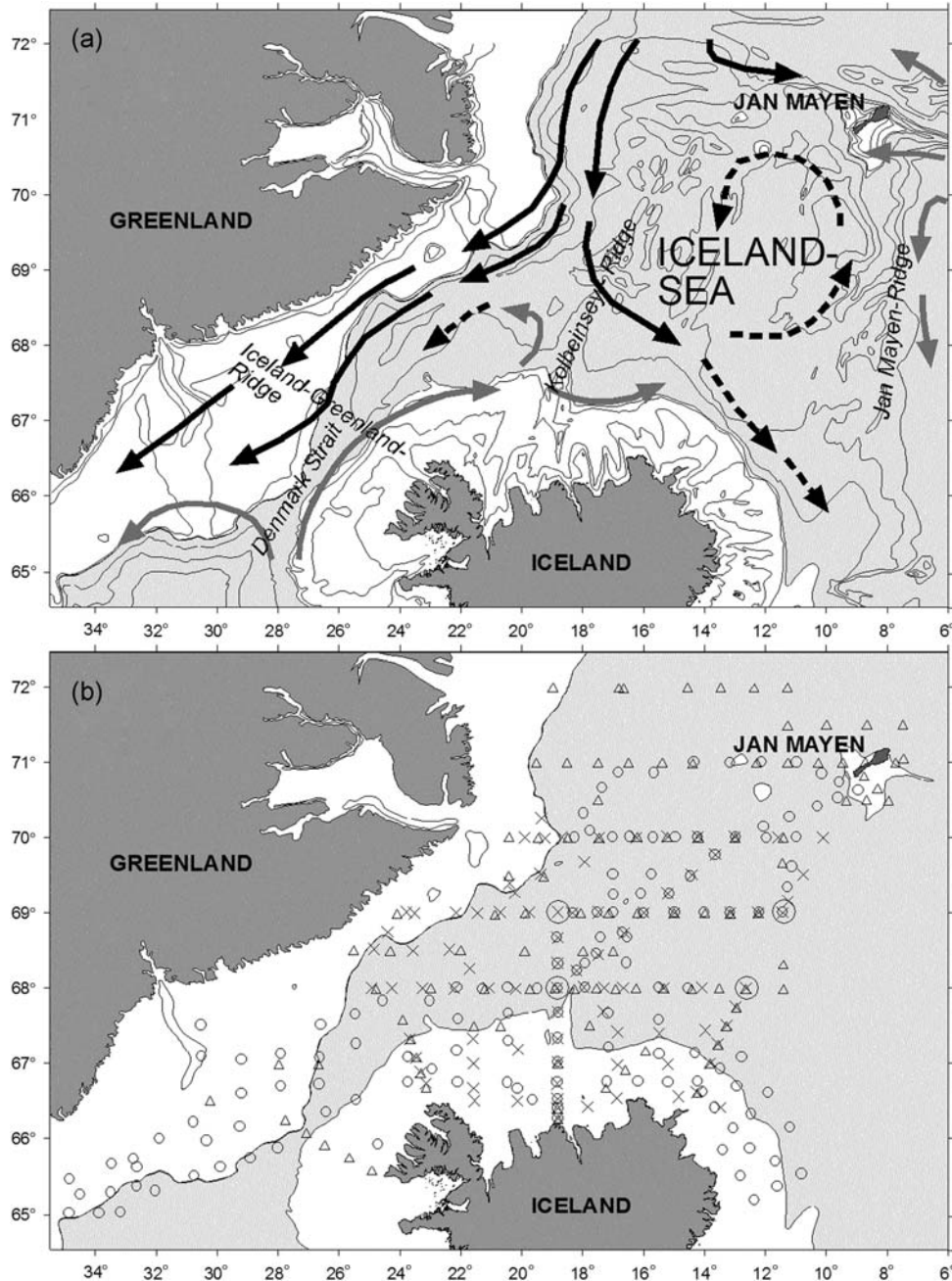


Figure 1. (a) Map of the study area showing schematically the main ocean currents in the upper layers. The 500-m bottom contour separates the shelf (white) from the off-shelf (grey). Grey arrows, Atlantic water; black arrows, Polar water; dashed black arrows, mixed water. Currents modified from Valdimarsson and Malmberg (1999), Blindheim and Österhus (2005), and Hunegnaw *et al.* (2009). (b) Map showing the location of stations occupied, 2006–2008. The small circles denote the stations occupied in July 2006, crosses the stations occupied in August 2007, and triangles the stations occupied in August 2008. The four larger circles denote the stations where the Multinet was used to sample the whole water column. The 500-m bottom contour is also shown.

Table 1. Number of stations and samples (in parenthesis) analysed for dw and species composition (S) for this study by cruises and gear type.

Year	Month	Cruise	WP2		Multinet		Tucker	
			dw	S	dw	S	dw	S
2006	17–30 July	bs062006	139 (139)	–	–	21 (54)	–	–
	21–26 November	af112006	–	–	–	2 (18)	–	–
2007	12–14 February	bs032007	–	–	–	4 (35)	–	–
	19–27 May	bs082007	–	–	–	2 (18)	–	–
	11–26 August	bs112007	71 (71)	19 (19)	–	4 (37)	–	12 (12)
2008	1–5 May	bs062008	–	–	–	4 (37)	–	–
	12–31 August	af112008	86 (86)	29 (29)	–	–	–	14 (14)
Total			296 (296)	48 (48)	–	37 (199)	–	26 (26)

Table 2. Overview of zooplankton net specifications (opening area, mesh size), towing mode, and depth layers sampled.

Sampling gear (m)	Opening area (m ²)	Mesh size (µm)	Towing mode	Sampling depth
WP2	0.25	200	Vertical tow	0–50
Multinet	0.25	200	Vertical tow	0–50–100–200–300–400–600–800–1 000–1 400–1 800
Tucker	4.00	1 000	U-tow	0–100 ^a

^aAt one station, sampling was from the surface to 200 m.

the warm and cold water masses meet off the northwest and north coasts of Iceland, a frontal area is formed. Another front stretches from the middle of Denmark Strait northeastwards towards the west of Jan Mayen.

Sampling was conducted during seven cruises made during 2006, 2007, and 2008 (Table 1). The number of stations occupied varied between cruises. At most stations, temperature and salinity were recorded with a Sea Bird Electronics (SBE) conductivity–temperature–depth. Seawater samples (in 0.5–2 l water bottles) for measuring Chl *a* were collected from depths of 0, 5, 10, 20, and 30 m and filtered through GF/C glassfibre filters. The filters were then homogenized in 90% aqueous acetone and the extract measured in a spectrophotometer according to the method described by Strickland and Parsons (1968). Zooplankton were sampled at most stations. Their biomass was estimated and species and stage composition determined (Table 1).

The zooplankton was collected using three types of gear (Table 2). At most stations, a standard WP2 net (0.25 m² mouth area, 200 µm mesh) was towed at a speed of ~45 m min⁻¹ from 50 m to the surface. In addition, at four stations (Figure 1b), depth-stratified samples from the whole water column were taken with a Multinet from HydroBios (0.25 m² mouth area, 200 µm mesh). The sampler was placed at the lower limit of the deepest depth-interval to be sampled, and five nets were opened and closed on command from the ship, as the sampler was hauled vertically at a speed of ~45 m min⁻¹. By deploying the sampler three times, ten depth layers (50–400 m wide) were sampled from 1800 m to the surface (Table 2). During August of 2007 and 2008, macrozooplankton was collected at selected stations with a Tucker trawl (4 m² mouth area, 1000 µm mesh). The trawl was towed obliquely from the surface to 100 m (to 200 m at one station) and back to the surface, while the ship cruised at ~1–2 knots. Payout and retrieval rates were ~0.5 m s⁻¹. The depth of the WP2 net and the Tucker trawl was monitored with a SCANMAR acoustic depth recorder fitted on the wire just above the net-frame, whereas for the Multinet, depth was monitored with the built-in depth sensor. The

volume of water filtered by all net types (WP2, Multinet, and Tucker) was measured with HydroBios flowmeters fitted in the mouth of each net, and the numbers or biomasses were standardized accordingly.

In the laboratory aboard ship, WP2 net catches were usually divided into two parts with a Motoda splitter (Motoda, 1959). One part was preserved in 4% neutralized formalin, and the other part was frozen (–18°C). The frozen samples were analysed for the total dry weight (dw) biomass after drying the samples in an oven at ~70°C for 20 h (Båmstedt, 1974). The Multinet and Tucker samples were usually placed in formalin, and at a later date in the laboratory ashore, the formalin samples were analysed for species composition. As a rule, the entire sample was counted for the larger plankton (euphausiids, amphipods, mysids, decapods, chaetognaths, and copepods >~9 mm prosome length). When the samples were very small, the whole samples were counted, whereas for the remainder, they were subsampled with a Motoda splitter and an aliquot containing at least ~500 individuals was analysed for species composition. For the copepods, the numbers have been converted to biomass (dw) using stage-specific dry mass from various sources (Davis, 1984; Norrbin *et al.*, 1990; Longhurst and Williams, 1992; Richter, 1994; Auel, 1999; Hirche and Kosobokova, 2003). When mean individual dw was not available, weights of species similar in size and shape were used.

Note that to examine seasonal patterns, the Multinet data collected at different times of year during a 3-year period were considered in the temporal sequence 12–14 February 2007, 1–5 May 2008, 19–27 May 2007, 17–30 July 2006, 11–26 August 2007, and 21–26 November 2006, although the data were not sampled chronologically. Although it would obviously have been desirable to survey the area chronologically, this was not possible for logistical and practical reasons. Despite this limitation, by examining the data in this way, we provide an overall picture of the seasonal dynamics of zooplankton and how they relate to environmental factors. For this analysis, the average values were calculated for the two stations west of the Kolbeinsey Ridge and the two stations east of it, except for 19–27 May 2007 and

21–26 November 2006, when just one station could be occupied on each side of the Ridge.

To examine mesozooplankton diversity, the Shannon–Wiener diversity indices were calculated (Krebs, 1989). For this analysis, only samples from the top 50 m collected during July (2006) and August (2007 and 2008) with the WP2 net or Multinet were considered.

Redundancy analysis (RDA) was used to examine the distribution of zooplankton in relation to environmental variables. RDA is a direct gradient analysis of taxon data, in which the axes are constrained by a linear model, i.e. by linear combinations of environmental variables. Two RDA analyses were carried out, one using data collected from the top 50 m with the Multinet or WP2 net (mesozooplankton) in July 2006 and August of 2007 and 2008, the other using data collected with the Tucker trawl from the top 100 m (macrozooplankton) in August of 2007 and 2008. For both datasets, the linear model (RDA) was preferred over the alternative unimodal one (canonical correspondence analysis). This selection was after test runs of detrended correspondence analysis showed that the gradient length of the first axis was 1.661 and 2.950 s.d. for the mesozooplankton and macrozooplankton datasets, respectively, indicating that for both datasets, most species had linear species–environment responses (ter Braak and Smilauer, 2002).

The mesozooplankton data matrices used as input in the RDA included 48 zooplankton species or groups in 73 samples, whereas the macrozooplankton data included ten species or groups in 36 samples. The environmental variables were temperature and salinity (means from 0 to 50 m for mesozooplankton or 0–100 m for macrozooplankton), Chl *a* (mg m^{-2} , 0–30 m), bottom depth, latitude, longitude, and year. Date (day number) was included in the analysis as a covariable to remove variability in the data that may have been caused by the samples not being sampled on the same dates during the 3-year period (July 2006 and August of 2007 and 2008). The environmental variables were centred and standardized to zero mean and unit variance, and species data were centred but not standardized to preclude overweighting rare species (ter Braak and Smilauer, 2002). The environmental variables were all used as continuous variables in the analysis, except from years that were put into the analysis as a categorical variable and are represented as centroids of the samples belonging to each category. Before analyses, the abundance data were transformed using $\ln(x + 1)$ transformation so as to allow the less important taxa to influence the species patterns (ter Braak and Smilauer, 2002). Monte Carlo permutation tests with 499 permutations were carried out to find out which environmental variables significantly ($p < 0.05$) explained the species composition. The analysis ranks the environmental variables according to their quantitative importance by forward selection. Only those variables that significantly ($p < 0.05$) explained the ordination were included in the ordination models. Multicollinearity among the environmental variables was checked for by calculating variance inflation factors (VIFs) for all the variables that were statistically significant (ter Braak and Smilauer, 2002). For the RDA analysis carried out on the mesozooplankton data, the highest VIF was 6.3 (salinity), and for the one carried out on the macrozooplankton data, it was 1.4 (Chl *a*). These low values are clearly acceptable and indicate that multicollinearity does not represent a problem for the interpretation of the results (ter Braak and Smilauer, 2002). The analyses were carried out using the program Canoco v. 4.5.

Results

Seasonal variability of mesozooplankton

Both the west and east of the Kolbeinsey Ridge, the seasonal variability in total numbers was characterized by low winter values ($< 50\,000 \text{ ind. m}^{-2}$), higher values in spring (May, $\sim 70\,000$ – $100\,000 \text{ ind. m}^{-2}$), and one main peak during summer in July and August ($\sim 300\,000$ – $400\,000 \text{ ind. m}^{-2}$; Figure 2). After August, the numbers decreased and, in November, relatively small numbers were recorded ($\sim 50\,000 \text{ ind. m}^{-2}$). The east of the Kolbeinsey Ridge, the annual mean mesozooplankton abundance was ~ 1.5 times greater ($\sim 200\,000 \text{ ind. m}^{-2}$) than the west of the Ridge ($\sim 135\,000 \text{ ind. m}^{-2}$).

Copepods dominated the zooplankton, constituting $> 85\%$ of all mesozooplankton on most sampling dates (Figure 2). The copepod biomass fluctuated from relatively low winter values in February (~ 4 – 8 g dw m^{-2}) to high summer values in July/August (~ 11 – 18 g dw m^{-2} ; Figure 2). As with the annual mean mesozooplankton abundance, the annual mean biomass of copepods was higher in the east ($\sim 12 \text{ g m}^{-2}$) than the west ($\sim 9 \text{ g m}^{-2}$) of the Kolbeinsey Ridge.

During winter (November–February), the bulk of the copepod biomass was observed in the deeper layers (~ 200 – 1000 m) at low temperatures ($\sim 0^\circ\text{C}$) and salinities ~ 34.9 (Figure 3). In May, most of the animals were found in surface waters ($< 100 \text{ m}$), where they stayed until July (*C. hyperboreus*) or August (*C. finmarchicus*), when the stocks descended again into deeper water (Figure 3). It is of note that during the winter, *C. hyperboreus* was mostly concentrated in the 800–1000-m depth range west of the Ridge, whereas in the east of it, the species was more evenly distributed below $\sim 200 \text{ m}$ down to 1000–1400 m. Figure 3 also shows that *C. hyperboreus* generally overwintered deeper than *C. finmarchicus*.

Taxonomic composition

In all, 101 species and taxonomic groups were identified in the 247 WP2 and Multinet samples, which were identified to species (Table 3). Several species were rare, with 24 species and groups found in one sample only, whereas only one, *Calanus finmarchicus*, was present in all samples (Table 3).

The Multinet samples that were collected through the whole water column and during all seasons provide the most complete information on annual relative numbers and biomass of the mesozooplankton. As stated previously, copepods constituted $> 85\%$ of the mesozooplankton by number on most sampling dates. Six species constituted $\sim 92\%$ of all copepods found in the samples: *Oithona* spp. (mainly *O. similis*; $\sim 36\%$ of all copepods), *C. finmarchicus* ($\sim 18\%$), *Pseudocalanus* spp. ($\sim 16\%$), *Oncaea* spp. (mainly *O. conifer*; $\sim 12\%$), *M. longa* ($\sim 7\%$), and *C. hyperboreus* ($\sim 4\%$).

Calanus hyperboreus clearly dominated the annual copepod biomass ($\sim 45\%$), followed by *C. finmarchicus* ($\sim 28\%$), *M. longa* ($\sim 17\%$), *Pseudocalanus* spp. ($\sim 3\%$), *Oithona* spp. ($\sim 2\%$), and *Pareuchaeta glacialis* ($\sim 1\%$). Together these six copepod species made up $\sim 95\%$ of the total copepod biomass.

In July, the mesozooplankton diversity, whether measured by a number of species and groups or by the Shannon–Wiener diversity index, was highest over the shelf edges north of Iceland and east of Greenland (Figure 4).

Seven species of amphipods were caught by the Tucker trawl (Table 4). *Themisto abyssorum* was the most common amphipod ($\sim 67\%$ of the total number of amphipods and euphausiids),

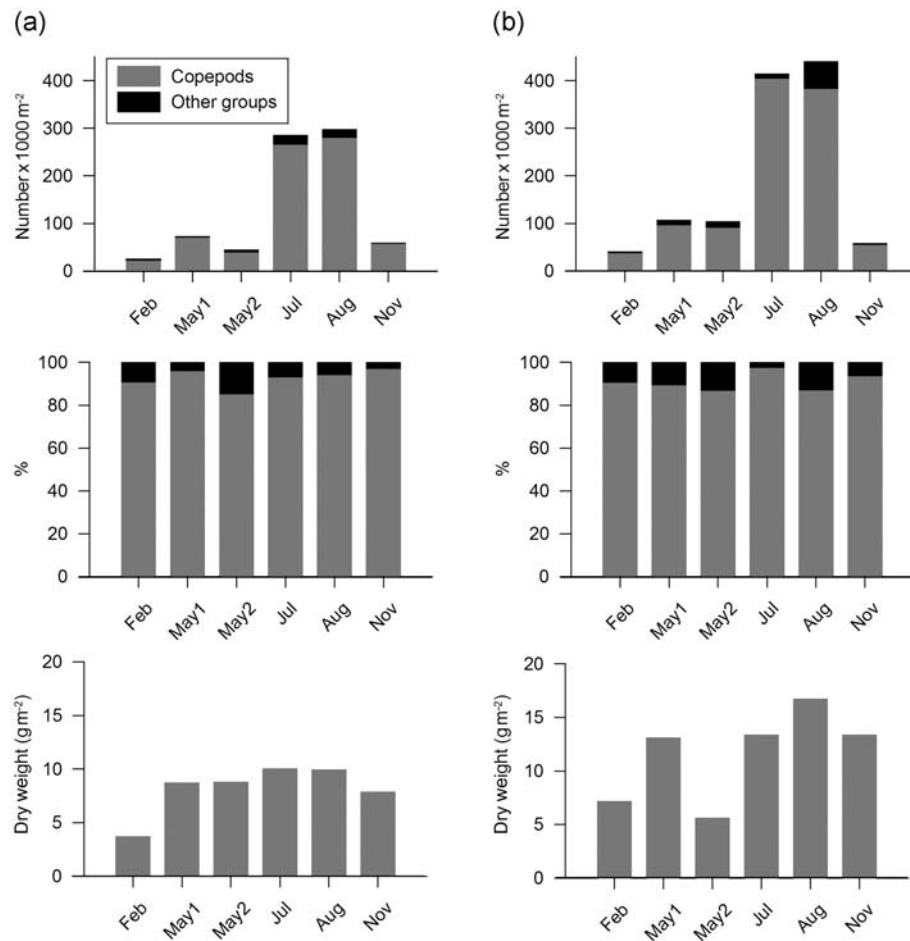


Figure 2. Seasonal changes in the numbers of mesozooplankton in the Iceland Sea from February to November. May1 and May2 denote the first and the second half of May, respectively. Values are means from (a) two stations west of the Kolbeinsey Ridge and (b) two stations east of the Ridge, except for the second half of May and November, when only one station could be sampled on each side of the Ridge. The samples were collected with a Multinet during 2006, 2007, and 2008 (Table 1). The top panels show total numbers (whole water column), the centre panels are relative composition, and the bottom panels are the biomass of copepods (whole water column). Light grey shading, copepods; black shading, other groups. For the location of the stations, refer to Figure 1b.

with *T. libellula* also important (~8%). The other amphipods caught by the Tucker trawl (*Gammaracanthus loricatus*, *Gammarus wilkitzkii*, *Hyperia galba*, *Hyperoche medusarum*, and *T. gaudichaudii*) contributed <0.5% of the total number of amphipods and euphausiids. Three species of euphausiid were caught by the Tucker trawl. *Thysanoessa longicaudata* was most abundant (~17%), *T. inermis* ranked second (~6%), and *Meganctiphanes norvegica* third (2.1%).

Zooplankton distribution in July/August

Comparison of mesozooplankton biomass between years is complicated by the different sampling coverage (Figure 5). However, in the areas between 10 and 25°W where the sampling was similar, the total mesozooplankton biomass was more concentrated towards Greenland in 2006 than in 2007 and 2008 (Figure 5). Except for one shelf station off the northeast coast of Iceland, the highest values in 2006 were in the cold waters in the northwestern Iceland Sea, whereas in 2007 and 2008 the biomass was distributed more to the east, with only low values recorded in the western and northwestern regions.

Figure 6 shows the distribution of the biomass of dominant copepods in the surface layers. As explained above, copepod biomass was estimated only for those samples that were analysed for species composition, and because they were fewer than the ones that were analysed for the total zooplankton biomass (Table 1), the spatial coverage shown in Figures 5 and 6 is not identical. *Calanus hyperboreus* were most abundant in the relatively cold waters in the northwest and west, and abundance was higher in 2006 than in 2007 and 2008 (Figure 6). *Calanus finmarchicus* were most abundant in the northwestern (2006) or northeastern (2007 and 2008) regions of the Iceland Sea and were more abundant in 2007 than in the preceding and succeeding years. *Metridia longa* were found mostly in the southeast in 2006, whereas in 2007 and 2008, they were more in the north or northeast (Figure 6).

Amphipods were caught mainly in the eastern and northeastern Iceland Sea, but for euphausiids as a group, there was no clear spatial trend (Figure 7). *Themisto abyssorum* were distributed more in the east than *T. libellula*, and *G. wilkitzkii* was caught mainly near the shelf edge on the Greenland side of the Iceland Sea (Figure 7). The euphausiids *T. longicaudata* and *T. inermis* were found more in the north than *M. norvegica*, which was

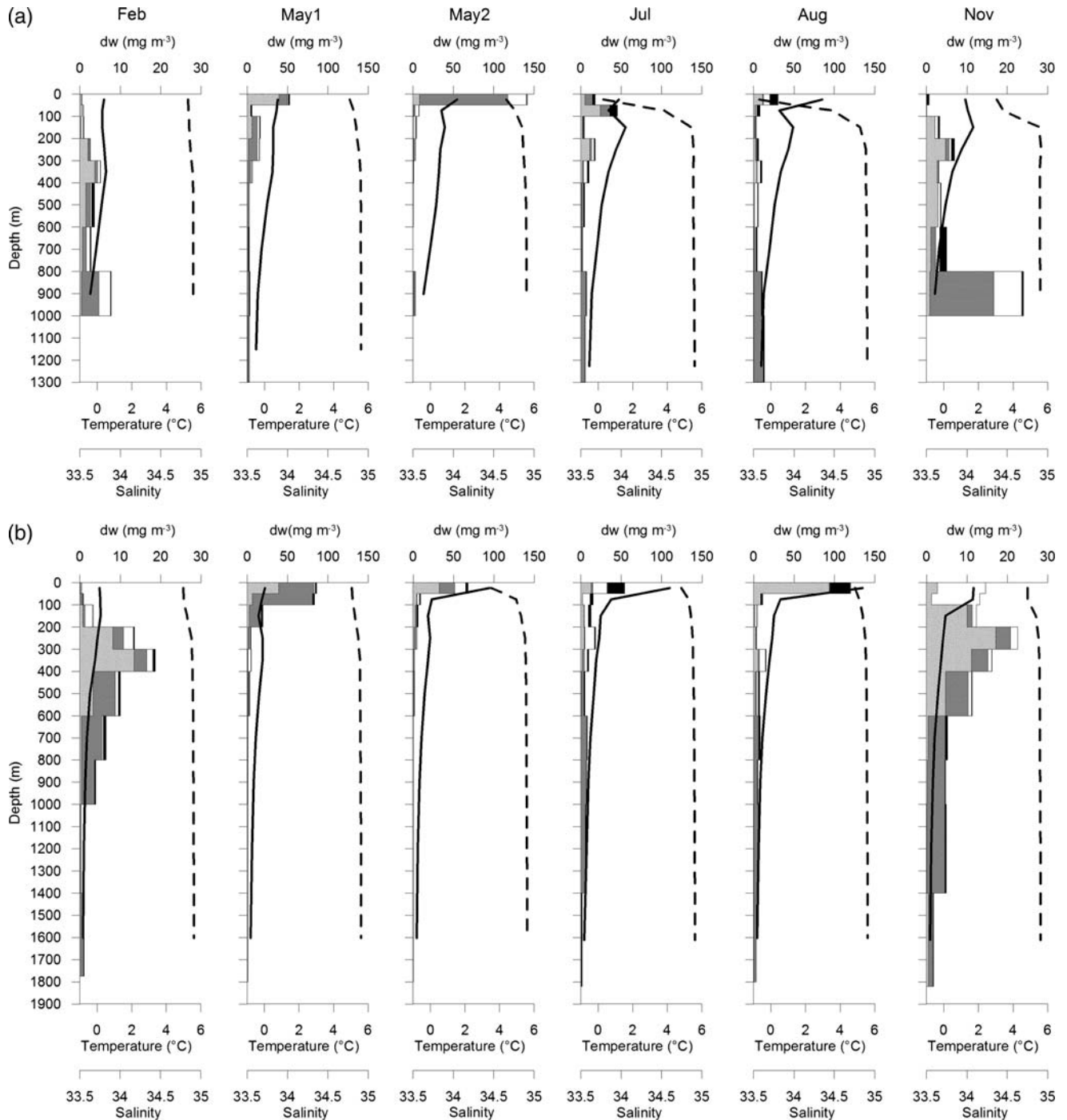


Figure 3. Vertical distribution of *Calanus hyperboreus* (dark grey), *C. finmarchicus* (light grey), *Metridia longa* (white), and other copepods (black) from February to November. May1 and May2 denote the first and the second half of May, respectively. Values (dw mg m^{-3}) are the means from two stations west of the Kolbeinsey Ridge (upper panels) and two stations east of the Ridge (lower panels), except for the second half of May and November, when only one station could be sampled on each side of the Ridge. Temperature and salinity profiles obtained by simultaneous conductivity–temperature–depth casts are also shown. The data were sampled during 2006, 2007, and 2008 (Table 1). Note the change in horizontal scales for dw between sampling times. For the location of the stations, refer to Figure 1b.

caught mainly in the southwest (Figure 7). Most of the *Thysanoessa* larvae (*Thysanoessa* spp. in Figure 7) were furcilia stages. They were mainly caught near the shelf edges north of Iceland and in the oceanic area in the northeastern parts of the Iceland Sea (Figure 7).

Distribution in relation to the environment in July/August

RDA showed that longitude, temperature, bottom depth, Chl *a*, and salinity significantly influenced the mesozooplankton species composition in late summer ($p < 0.05$, forward model selection

Table 3. Mesozooplankton species collected in the Iceland Sea by the WP2 and Multinet during 2006, 2007, and 2008, and the number of samples in which the species was found (the total number of samples analysed, 247).

Taxon	Samples	Taxon	Samples
Protozoa		Copepoda (Cntd)	
<i>Ellobiopsis</i> spp.	1	<i>Gaetanus affinis</i>	4
<i>Globorotalia truncatulinoides</i>	1	<i>Gaetanus brevispinus</i>	58
Foraminifera indet.	149	<i>Gaetanus tenuispinus</i>	40
Radiolaria indet.	44	<i>Haloptilus longicornis</i>	1
Tintinnida indet.	25	<i>Heterohabdus norvegicus</i>	63
Protozoa indet.	2	<i>Metridia brevicaudata</i>	3
Cnidaria		<i>Metridia longa</i>	189
<i>Aglantha digitale</i>	37	<i>Metridia lucens</i>	2
Cnidaria indet.	75	<i>Metridia</i> spp.	3
Siphonophora		<i>Microcalanus</i> spp.	149
<i>Lensia conoidea</i>	1	<i>Microsetella norvegica</i>	12
Siphonophora indet.	13	<i>Oithona</i> spp.	226
Ctenophora		<i>Oncaea</i> spp.	215
Ctenophora indet.	3	<i>Phaennidae</i> spp.	2
Nemtoka		<i>Pleuromamma robusta</i>	1
Nematoda indet.	1	<i>Pseudaetidus armatus</i>	13
Polychaeta		<i>Pseudocalanus</i> spp.	216
<i>Pelagobia</i> spp.	16	<i>Pseudochirella spectabilis</i>	1
<i>Tomopteris</i> spp.	2	<i>Pseudophaenna typica</i>	1
<i>Trousiopsis</i> spp.	1	<i>Scaphocalanus magna</i>	23
Aphroditoidea	1	<i>Scolecithricella minor</i>	12
Typhloscolecidae	1	<i>Spinocalanus</i> spp.	1
Polychaeta indet.	30	<i>Temora longicornis</i>	13
Gastropoda		<i>Xanthocalanus</i> spp.	2
<i>Clione limacina</i>	7	Idyaeidae	1
<i>Limacina balea</i>	1	Harpacticoida indet.	3
<i>Limacina helicina</i>	3	Mormonilla indet.	1
<i>Limacina lesururii</i>	1	Ostracoda	
<i>Limacina retroversa</i>	6	<i>Conchoecia borealis</i>	83
<i>Limacina</i> spp.	33	<i>Conchoecia</i> spp.	45
Gastropoda indet.	3	Ostracoda indet.	39
Pteropoda indet.	1	Cirripedia	
Bivalvia		Cirripedia indet.	10
Bivalvia indet.	18	Isopoda	
Cladocera		Isopoda indet.	36
<i>Evadne nordmanni</i>	5	Amphipoda	
<i>Podon leuckartii</i>	5	<i>Apherusa</i> spp.	4
Copepoda		<i>Eusirus holmi</i>	1
<i>Acartia</i> spp.	14	<i>Gammarus wilkitzkii</i>	2
<i>Aetidae</i> spp.	36	<i>Themisto abyssorum</i>	80
<i>Aetideopsis multiserrata</i>	13	<i>Themisto gaudichaudi</i>	2
<i>Aetideopsis rostrata</i>	18	<i>Themisto libellula</i>	59
<i>Aetideopsis serrata</i>	1	Astyridae	2
<i>Aetideopsis</i> spp.	8	Euphausiacea	
<i>Bradyidius similis</i>	7	<i>Meganyctiphanes norvegica</i>	11
<i>Calanus finmarchicus</i>	247	<i>Thysanoessa inermis</i>	26
<i>Calanus glacialis</i>	113	<i>Thysanoessa longicaudata</i>	98
<i>Calanus hyperboreus</i>	207	<i>Thysanoessa raschi</i>	3
<i>Centropages typicus</i>	1	Mysidacea	
<i>Chiridus armatus</i>	8	<i>Boreomysis arctica</i>	1
<i>Chiridus obtusifrons</i>	4	Decapoda	
<i>Chiridus</i> spp.	3	Galatheidea larvae	1
<i>Chiridus tenuispinus</i>	8	<i>Hymenodora glacialis</i>	14
<i>Clausocalanoidae</i>	1	Natantia indet.	8
<i>Euaugaptilus</i> spp.	1	Chaetognatha	
<i>Euchaeta barbata</i>	27	Chaetognatha indet.	229
<i>Euchaeta barbata farrani</i>	13	Echinodermata	
<i>Euchaeta glacialis</i>	78	Ophiuroidea indet.	25
<i>Euchaeta hanseni</i>	2	Larvacea	
<i>Euchaeta norvegica</i>	48	Larvacea indet.	89

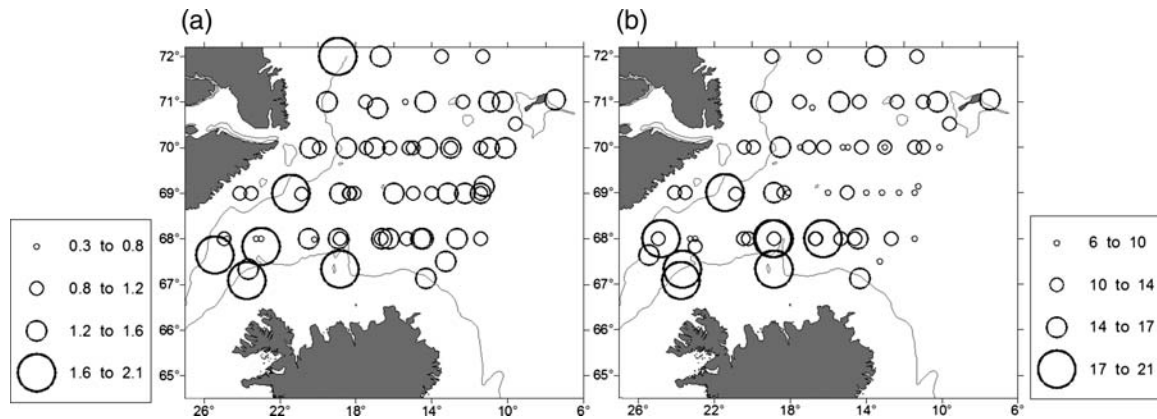


Figure 4. Species diversity of mesozooplankton in the surface layers (0–50 m) in July 2006 and August of 2007 and 2008, as assessed by (a) the Shannon–Wiener diversity index and (b) the number of species. The samples were collected with a WP2 or a Multinet. The 500-m bottom contour is shown.

Table 4. Macrozooplankton species (amphipods and euphausiids) in the Iceland Sea caught by the Tucker trawl, and the relative abundance (as a percentage of the total number of amphipods and euphausiids identified to species), based on samples collected in August 2007 and 2008.

Taxon	Per cent
Amphipoda	
<i>Themisto abyssorum</i>	66.7
<i>Themisto libellula</i>	7.8
<i>Gammaracanthus loricatus</i>	<0.5
<i>Gammarus wilkitzkii</i>	<0.5
<i>Hyperia galba</i>	<0.5
<i>Hyperoche medusarum</i>	<0.5
<i>Themisto gaudichaudii</i>	<0.5
Euphausiacea	
<i>Thysanoessa longicaudata</i>	16.8
<i>Thysanoessa inermis</i>	6.5
<i>Meganyctiphanes norvegica</i>	2.1

using the Monte Carlo permutation test; Figure 8). Further, the year 2008 had a significant effect on the ordination and hence the community structure, when the abundance of *Acartia* spp., *Podon leuckarti*, cirripede larvae, Ophiuroidea, *Temora longicornis*, and *Limacina* spp. was relatively greater than during 2006 and 2007 (Figure 8). Together these explanatory variables explained ~32% of the variability in mesozooplankton abundance and distribution (Table 5). Longitude explained by far the greatest part (13%), with the year 2008 and temperature explaining an additional 6% each. Depth, Chl *a*, and salinity were weaker contributors to the RDA model, explaining just 2–3% of the overall variability (Table 5). Latitude and the years 2006 and 2007 did not contribute significantly to the variation and are shown as passive variables in Figure 8.

Figure 8 further shows that the gradient along the first canonical axis explains ~56% of the variability explained (32%), whereas the gradient along the second axis explains ~24%. The first axis described a gradient from species that were found mainly in relatively deep water in the eastern parts of the study area, where salinity was relatively high (*C. finmarchicus*, *Pseudocalanus*, and chaetognaths), towards species distributed more in the west where it was shallower and salinity was lower (*Acartia* spp., *C. glacialis*, *C. hyperboreus*, and *P. leuckarti*). It is

also clear that both temperature and salinity were higher in eastern parts of the study area (at low longitudes) than in west.

Three main mesozooplankton communities or assemblages were identified by the RDA (Figure 8). An Atlantic community was observed in the east where *C. finmarchicus*, *Pseudocalanus*, chaetognaths, and foraminiferans were relatively abundant, and temperature and salinity were relatively high. A second community with relatively great abundances of species with coastal affinities was located in the south (e.g. *T. longicornis*, *Acartia* spp., *P. leuckarti*, and cirripede larvae), where temperature and salinity were relatively high but Chl *a* values low. This community was particularly apparent in 2008. The third community, represented by Arctic species (*C. hyperboreus* and *C. glacialis*, *Microcalanus* spp., *Oncaea* spp.), was in the north, where both temperature and salinity values were low and Chl *a* values relatively high (Figure 8).

A separate RDA was carried out for macrozooplankton data (euphausiids and amphipods; Figure 9). The analysis showed that longitude and Chl *a* had a significant effect on the species distribution. Together, these two explanatory variables explained 43% of the variability in the abundance and distribution of macrozooplankters ($p < 0.05$; forward model selection using the Monte Carlo permutation test), but longitude explained by far the greatest part (33%; Table 6).

The first canonical axes of the RDA explained ~98% of the explainable variation (the variation attributed to longitude and Chl *a*, 43%), and described a gradient from the west, with its relatively high Chl *a* values (negative end), to the east, with its lower Chl *a* values (positive end; Figure 9). The second canonical axis explained just a small part of the variation (~2%).

From the RDA (Figure 9), as from the distribution maps (Figure 7), it may be inferred that *M. norvegica* and *G. wilkitzkii* were mostly in the west (they were most closely correlated with increasing longitude), whereas *T. abyssorum* were mainly in the east (correlated with lower longitudes).

Discussion

Seasonal variability of mesozooplankton

The seasonal changes in zooplankton in the oceanic Iceland Sea were characterized by one main peak in numbers in July/August (Figure 2). Earlier studies on the shelf areas north and northeast

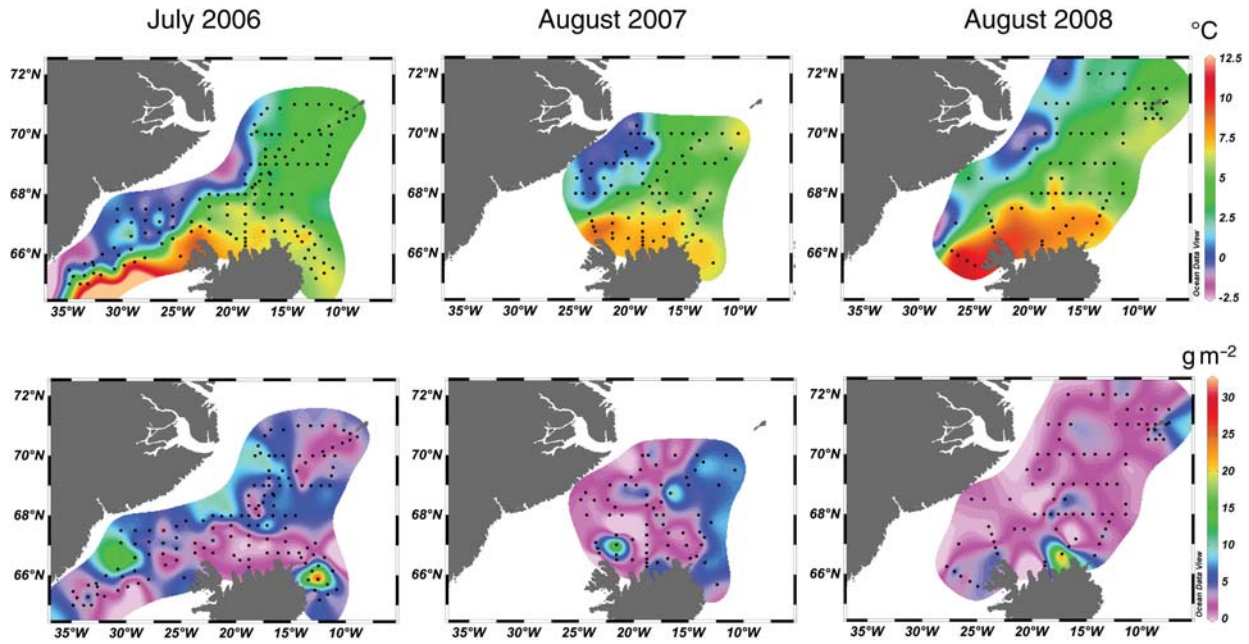


Figure 5. Sea temperatures (means 0–50 m; upper panels) and total mesozooplankton biomass (dw g m^{-2} , 0–50 m; lower panels) in the Iceland Sea during July 2006 and August of 2007 and 2008.

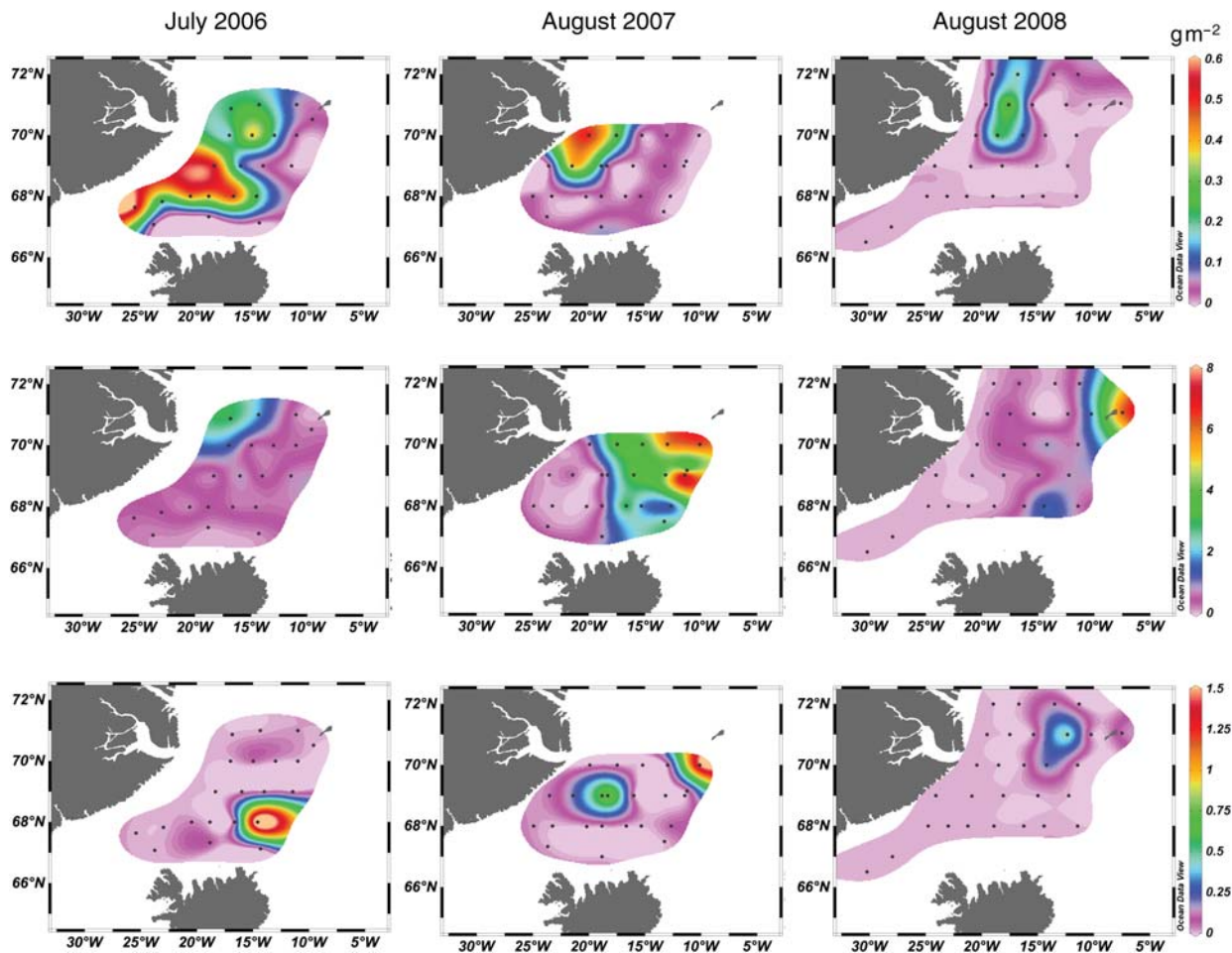


Figure 6. Distribution of *Calanus hyperboreus* (top panels), *C. finmarchicus* (centre panels), and *Metridia longa* (bottom panels) in terms of dw g m^{-2} ; 0–50 m) in the Iceland Sea during July 2006 and August of 2007 and 2008.

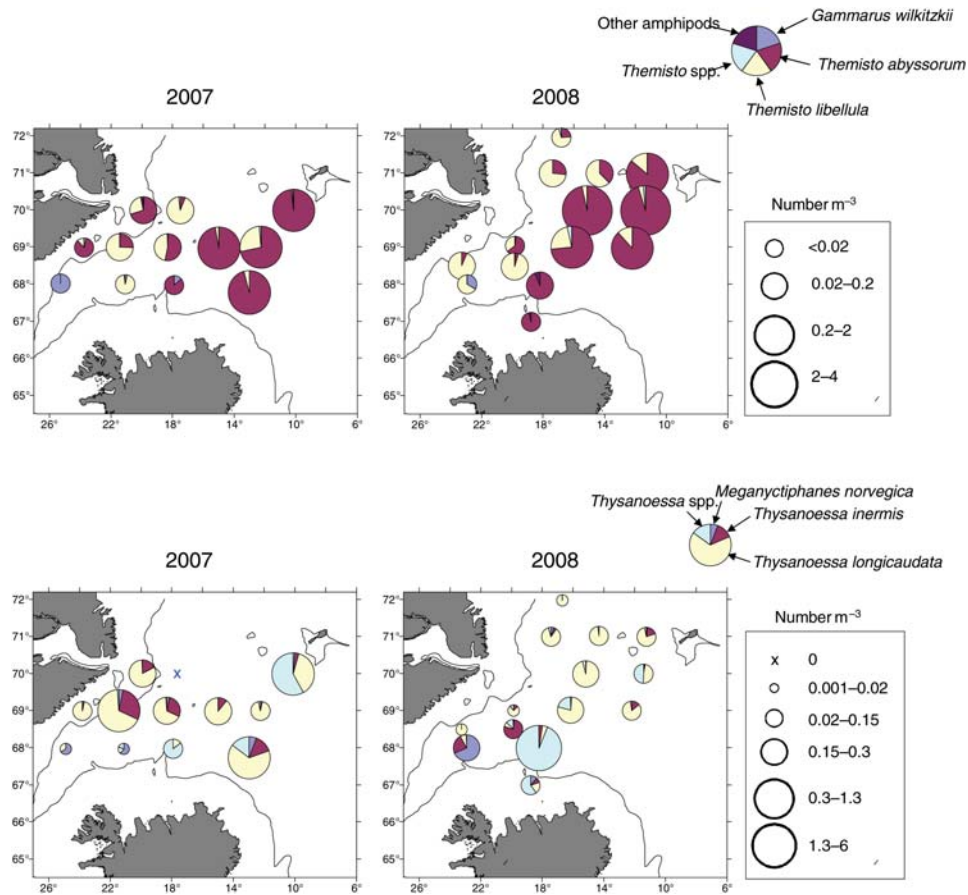


Figure 7. Distribution of amphipods (upper panels) and euphausiids (lower panels) in the Iceland Sea during August of 2007 and 2008 (0–100 m). The samples were collected with Tucker trawls. *Thysanoessa* spp. are mainly larval stages that could not be identified beyond the genus level. The 500-m bottom contour is shown.

of Iceland also showed one main peak in zooplankton abundance, but it was earlier (June and July; Gislason and Astthorsson, 1998; Astthorsson and Gislason, 2003) than we observed in the offshore area. The earlier studies also indicated a dramatic decline in zooplankton biomass in August, which we did not observe in the oceanic area, but which was hypothesized by the earlier workers to be caused mainly by capelin predation (Gislason and Astthorsson, 1998). This was not an unreasonable assumption because capelin are plankton-feeders that normally migrate in large numbers to the area north of Iceland to feed during summer (Vilhjalmsson, 2002). Since the earlier studies were made, a drastic decline in the stock size of the capelin has been observed, and the location of the feeding migrations has also changed markedly (Pálsson *et al.*, 2012a). Hence, in the present study, capelin were only caught in very low quantities in the central Iceland Sea (Pálsson *et al.*, 2012a, b), and it is unlikely that predation by capelin was affecting the growth and development of zooplankton there.

Both the annual mean numbers and mean dw of mesozooplankton were greater in the east than the west of the Kolbeinsey Ridge (Figure 2). This may reflect the greater biological production in the east than the west of the Ridge, but also possibly a greater inflow of animals into the eastern basin from the Norwegian Sea.

In the Iceland Basin, the biomass-dominant copepods *C. hyperboreus*, *C. finmarchicus*, and *M. longa* all overwintered in deep water and rose to the surface sometime between February and

May (Figure 3). This is in accord with the general behaviour of the species in other northern regions (Östvedt, 1955; Richter, 1995; Heath *et al.*, 2004). The seasonal return migration into deep water appeared to start earlier in *C. hyperboreus* (July) than in *C. finmarchicus* (August), probably reflecting differences in life-history strategies between the annual *C. finmarchicus* and the longer-living *C. hyperboreus*. The earlier descent of *C. hyperboreus* compared with *C. finmarchicus* also accounts for the generally much smaller biomass of *C. hyperboreus* in July and August in the surface layers compared with *C. finmarchicus* (Figure 6), despite the higher annual biomass of the former species.

Taxonomic composition

As in most other marine systems, copepods dominated the mesozooplankton. The most numerous copepod species in the present study were also reported as among the most abundant in earlier investigations at the northern and southeastern fringes of the Iceland Sea (Astthorsson *et al.*, 1995) as well as in the Labrador Sea (Head *et al.*, 2003), Greenland Sea (Richter, 1994), and Barents Sea (Hassel, 1986).

Species diversity was usually greatest over the shelf edges, i.e. off East Greenland and north Iceland (Figure 4). It is well known that pelagic shelf areas tend to contain a rather different zooplankton fauna than the more offshore areas. Regions where these two systems meet and interact, therefore, are inhabited by species from both systems, which is reflected in a greater species diversity

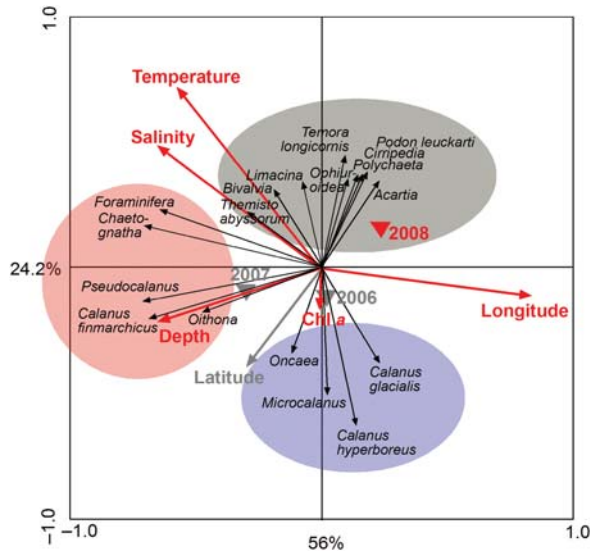


Figure 8. RDA biplot of mesozooplankton species abundances (numbers m^{-3} , 0–50 m, thin black arrows) and environmental variables (red and grey arrows) in the Iceland Sea during 2006 (July) and 2007 and 2008 (both August). Environmental variables are Chl *a*, temperature, and salinity (means from 0 to 50 m), bottom depth, and year. The first canonical axis explains 56% of the species–environment relationship, and the second axis explains 24.2%. Year is put into the analysis as a categorical variable and denoted as triangles (centroids). Day of the year is a covariable to subtract the variability attributable to different sampling times. Red arrows or triangles explain significant variation in the zooplankton community structure. Insignificant variables (grey arrows and triangles) are passive and do not influence the analysis. The arrows point in the direction of the steepest increase in the respective variables, and the angles between them reflect their correlations. Taxa with < 10 fit value to the first axis are not shown (i.e. taxa for which the first axis roughly explains < 10% of the variance; ter Brak and Smilauer, 2002). For the RDA model design and further explanation, see text. Zooplankton communities are indicated by colour shading as red (Atlantic), blue (Arctic), and grey (coast-associated).

Table 5. Mesozooplankton: ranking of environmental variables that significantly (Monte Carlo permutation test in RDA; $p < 0.05$) influenced the distribution of mesozooplankton in the Iceland Sea in 2006 (July) and 2007 and 2008 (August), and the proportion of variability explained by each variable along with the p - and F -values.

Explanatory variable	Variability explained	p -value	F -value
Longitude	0.13	0.002	10.73
2008	0.06	0.002	5.78
Temperature (0–50 m)	0.06	0.002	5.77
Bottom depth	0.03	0.010	2.54
Chl <i>a</i> (0–30 m)	0.02	0.014	2.45
Salinity (0–50 m)	0.02	0.032	1.91
Total	0.32		

in these boundary areas. In our study, it may also be significant that near the shelf edges north of Iceland, currents from different sources meet (Figure 1a), carrying different zooplankton species, and hence contributing to greater diversity in those areas.

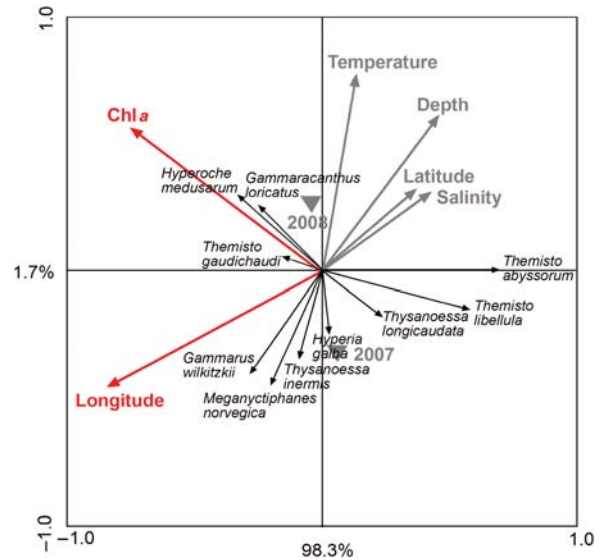


Figure 9. RDA biplot of euphausiid and amphipod abundances (numbers m^{-3} , 0–100 m, thin black arrows) and environmental variables (black and grey arrows) in the Iceland Sea during 2006 (July) and 2007 and 2008 (both August). Environmental variables are Chl *a*, temperature, and salinity (means from 0 to 100 m), bottom depth, and year. The first canonical axis explains 98.3% of the species–environment relationship, and the second axis explains 1.7%. Year is put into the analysis as a categorical variable and denoted as triangles (centroids). Day of the year is a covariable to subtract the variability attributable to different sampling times. Red arrows explain significant variation in the zooplankton community structure. Insignificant variables (grey arrows and triangles) are passive and do not influence the analysis. The arrows point in the direction of the steepest increase in the respective variables, and the angles between them reflect their correlations. Taxa with < 10 fit value to the first axis are not shown (ter Brak and Smilauer, 2002). For the RDA model design and further explanation, see text.

Table 6. Macrozooplankton: ranking of environmental variables that significantly (Monte Carlo permutation test in RDA; $p < 0.05$) influenced the distribution of macrozooplankton in the Iceland Sea in 2006 (July) and 2007 and 2008 (August), and the proportion of variability explained by each variable along with the p - and F -values.

Explanatory variable	Variability explained	p -value	F -value
Longitude	0.33	0.002	12.77
Chl <i>a</i> (0–30 m)	0.10	0.036	4.48
Total	0.43		

Mesozooplankton distribution in July and August

The mesozooplankton total biomass was generally distributed more to the west or northwest in 2006 than in 2007 and 2008 (Figure 5). We do not know the reason for this, but it may be related to the large amount of sea ice in the western parts of the study area in 2006, but not in 2007 and 2008. Melting sea ice may have created conditions favourable for phytoplankton growth (Sakshaug, 1997), which in turn may have led to greater zooplankton growth and biomass near the ice edge and in areas from where the ice had recently retreated.

The northeastern distribution of *C. hyperboreus* in all 3 years indicates that they are being advected into the Iceland Sea from the Greenland Sea via the East Greenland Current (Figure 6). The picture is not as clear with respect to *C. finmarchicus* and *M. longa*, but for the former species, the results suggest that at least in some years, animals could be advected into the Iceland Basin from the Norwegian Sea.

Distribution in relation to the environment

The explanatory factors that significantly influenced the community structure of mesozooplankton in the Iceland Sea were longitude, the year 2008, temperature, depth, Chl *a*, and salinity, together explaining ~32% of the variability in abundance and distribution of the mesozooplankton species (Table 5, Figure 8). This is a low value, but comparable with values that have been found in similar studies in the Barents Sea and Fram Strait (Blachowiak-Samolyk, 2008). Comparing results from different studies of this kind is made difficult by the fact that the outcome will depend on the extent of the study in time and space, and the number and nature of the explanatory factors used in the analysis.

In the present study, longitude was the most important explanatory variable, reflecting the significant influence of the east–west location on the mesozooplankton distribution. Note that longitude is not a forcing factor in itself, but rather represents the effects of hydrography and advection on zooplankton community structure, as discussed below. The longitudinal gradient was generally in good agreement with salinity and temperature, which both also significantly affected the community structure. Temperature and salinity were located close to each other on the RDA diagram, demonstrating the close relationship between them (Figure 8).

In our study, salinity in the upper 50 m varied from 30.8 to 34.9, which would be unlikely to affect the physiology of zooplankters in the open ocean (McLaren *et al.*, 1968; Kinne, 1971). It is therefore more likely that salinity signifies the advective processes that are at work in the system. On the other hand, small changes in temperature may have direct effects on growth and mortality rates of zooplankton and hence influence distribution (McLaren *et al.*, 1968; Kinne, 1970). However, like salinity, temperature variations may also indicate water masses of different origin, so the effects of temperature on species composition may be indirect rather than direct, and indicate advective transport of species. As we do not have detailed data or models of current patterns in the area, it is difficult to evaluate whether temperature is influencing species composition directly or indirectly.

In the Iceland Sea, water masses of a different origin mix. These water masses carry different zooplankters, i.e. warm-water species from the south and east, cold-water species from the north. The fact that temperature and salinity influenced the zooplankton community similarly (the arrows point in the same direction in ordination space; Figure 8) suggests that water-mass distribution is of primary importance in structuring plankton communities and that the Iceland Sea is a highly advective ecosystem.

Note that the year 2008 was the second-most important factor in explaining mesozooplankton distribution and abundance (Table 5, Figure 8), meaning that mesozooplankton assemblages were different in 2008 than in the two preceding years. An inspection of the RDA diagram reveals that during 2008, the abundance of species with coastal affinities (*Acartia* spp., *T. longicornis*, benthic larvae) was relatively high (Figure 8), which suggests

that the advection of animals from nearby coastal areas in the south was likely relatively important in 2008, which further underlines the importance of advection in the ecosystem.

Bottom depth also had a significant effect on the community structure of mesozooplankton in the Iceland Sea (Table 5, Figure 8). It is well known that bottom depth can influence the distribution of zooplankton species that live on the seabed during a part of their life cycle, such as meroplankters and copepods that spend winter as resting eggs on the seabed. These groups tend to be most abundant in coastal areas. Several of the groups that were most negatively correlated with bottom depth (e.g. *P. leuckarti*, Cirripedia larvae, *T. longicornis*, *Acartia* spp.; Figure 8) are all reported in the literature as having coastal affinities (Mauchline, 1998; Gislason and Astthorsson, 2004). In this regard, however, note that with ~90% of the samples being taken at depths >500 m (depth range of all stations 224–2240 m), it is unlikely that bottom depth was directly influencing the community structure in the way described above, but that the results instead signify advection of animals from coastal areas.

Although only relatively low values of Chl *a* were observed in our study during late summer (range 3.25–75 mg m⁻², 0–30 m), they nevertheless significantly affected the ordination (Table 5, Figure 8). It may be assumed that Chl *a* at least partly reflects the primary productivity so these results may be taken to indicate that primary production is affecting the abundance and composition of mesozooplankton communities.

Three mesozooplankton assemblages were identified by the RDA, with the division being both affected by the geographic position (longitude and depth) and water masses (temperature and salinity; Figure 8). When considering these results, it should be borne in mind that the data used in the analysis were collected in 3 years during a 2-month period, and therefore it is likely that the results do not merely represent snapshots of the structure, but that they are more or less characteristic of general mesozooplanktonic structure in the Iceland Sea during late summer.

With regard to macroplankton, the RDA revealed that longitude explained by far the greatest part of the variability in community structure, with Chl *a* biomass explaining the second greatest part of the variability (Table 6, Figure 9). Sea temperature therefore had no effect on the distribution according to the RDA. From the RDA biplot (Figure 9) and the distribution maps illustrating the amphipods (Figure 7), it may be inferred that more *T. libellula* than *T. abyssorum* were found in the west. *Themisto libellula* is an Arctic species, whereas *T. abyssorum* is found in Atlantic and mixed Subarctic water masses (Dalpadado *et al.*, 2001; Melle, 2004). In the northern Norwegian Sea, *T. libellula* is found mainly in cold waters in the west, whereas *T. abyssorum* is more abundant in warmer waters in the southeast (Dalpadado *et al.*, 2001). The distributions from this study (Figure 7) indicate that Arctic *T. libellula* are advected into the Iceland Sea from the Greenland Sea with the East Greenland Current, and that the Atlantic–Subarctic *T. abyssorum* are carried into the region from the Norwegian Sea by a branch of the Atlantic current (see also Figure 1a).

In the Barents and Norwegian Seas, amphipods are important components of these ecosystems (Dalpadado *et al.*, 2001, 2008; Melle, 2004). They are both carnivores, feeding on small zooplankton such as copepods and themselves are fed on by plantivorous fish and seabirds (Skjoldal *et al.*, 2004; Dalpadado *et al.*, 2008). Their relatively large numbers in the Iceland Sea (~0.02–2 ind. m⁻³; Figure 7), which are even higher than those observed

in the Barents Sea (Dalpadado *et al.*, 2001), and their importance as food for capelin and other plankton-eating species in the Iceland Sea (Astthorsson and Gislason, 1997a), underlines their importance in the foodweb of the Iceland Sea. Our unpublished results indicate that both species reproduce in the area.

The amphipod *G. wilkitzkii* was found in the westernmost parts of the Iceland Sea (Figure 7). It usually lives attached to the underside of Arctic sea ice (Werner *et al.*, 1999), where it feeds largely on detritus, animal remains, and ice algae (Werner, 1997), but it has also been caught by ordinary plankton nets in ice-free waters previously occupied by sea ice (Werner *et al.*, 1999). It is not clear for how long the species may be able to survive in ice-free waters, probably for at least 4 d (Werner *et al.*, 1999). Its presence in our samples taken on the westernmost stations in both 2007 and 2008 indicates that the sea ice had recently receded before our occupation of these stations or that the animals were advected into the area from nearby sea-ice regions.

Euphausiids are important as conveyors of energy between trophic levels, especially the most abundant species, *T. longicaudata* (Astthorsson and Gislason, 1997a). It is generally considered unlikely that *T. longicaudata* and *T. inermis* can reproduce in Arctic waters (Siegel and Nicol, 2000; Dalpadado *et al.*, 2008). In the current study, we found many larvae (mainly furcilia) from both species in August (*Thysanoessa* spp. in Figure 7). These may have been advected into the area from regions where temperature conditions were more favourable rather than them being locally produced. However, the presence of a few euphausiid nauplii in the WP2 and Multinet net samples taken in May and August (unpublished results) indicates at least some spawning activity in the Iceland Sea. In this context, close inspection of adult *Thysanoessa* spp. showed that they had fully developed external sexual organs at the time of sampling (August), suggesting that they can mature in the Arctic waters.

Previous studies in waters off north Iceland have shown that the biological production in the region is to a large extent governed by the inflow of Atlantic water to the area (Thordardottir, 1977, 1984; Astthorsson *et al.*, 1983; Stefansson and Jakobsson, 1989; Stefansson and Olafsson, 1991; Astthorsson and Gislason, 1995). Therefore, increased stratification in cold years when there is less inflow may lead to early depletion of nutrients in the surface layers and reduced primary production and, ultimately, reduced growth of zooplankton. Conversely, by maintaining mixing and renewal of nutrients to surface layers in warm years, the Atlantic influx may prolong the growth season of the phytoplankton. The years 2006, 2007, and 2008 have been defined as warm years with relatively high inflow of warm Atlantic water into the sea areas north of Iceland (Anon., 2010). The results of the present investigation suggest that, during such conditions, the season of high biomass in the surface layers lasts ~4 months (Figure 3), with greatest total numbers of zooplankton in July and August (Figure 2). The species composition in the Iceland Sea, as revealed by the present study, clearly shows that the area may be considered a broad zone of mixing of Atlantic and Arctic water masses by which zooplankton from different regions are advected into the area. The results demonstrate the close association between the abiotic environment and biotic factors in the Iceland Sea. The key players in the system among the zooplankters were the copepods *C. finmarchicus* and *C. hyperboreus*, the amphipod *T. abyssorum*, and the euphausiid *T. longicaudata*.

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