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

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### Abstract:

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 ( $\sim 200$ – $1000$  m) layers, and peaked during late summer ( $\sim 11$ – $18$  g dry weight  $\text{m}^{-2}$ ,  $\sim 300\,000$ – $400\,000$  ind.  $\text{m}^{-2}$ ), 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 for the fisheries around Iceland, mainly related to its role as food provider for the Icelandic capelin stock, which during its summer feeding period in the Iceland Sea mainly preys 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 the capelin have changed, hence one of the main motivations behind this study was to provide background information on zooplankton in the feeding area that can contribute to the understanding of the factors affecting the capelin migrations.

The 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). These studies were, however, mainly restricted to the shelf areas or the regions over the shelf ridges, and to our knowledge there are no previous 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 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*. 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 better understand the factors that are influencing the capelin growth and feeding migrations.

## 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 northwards to the submarine ridge between Greenland and Jan Mayen divides the Iceland Sea into two main basins.

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

Sampling was conducted on 7 cruises 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) CTD. Seawater samples (0.5-2 l) for the measurement of chlorophyll *a* were collected from depths of 0, 5, 10, 20, 30 m and filtered through GF/C glass fibre 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 were collected using three types of gear (Table 2). At most stations a standard WP2 net (0.25 m<sup>2</sup> mouth area, 200 µm mesh size) was towed with a speed of ~45 m min<sup>-1</sup> from 50 m depth up to the surface. In addition, on four stations (Figure 1B), depth stratified samples from the whole water column were taken with a Multinet from HydroBios (0.25 m<sup>2</sup> mouth area, 200 µm mesh size). 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<sup>-1</sup>. By deploying the sampler three times, a total of 10 depth layers (50-400 m wide) were sampled from 1800 m and to the surface (Table 2). During August 2007 and 2008, macrozooplankton were collected at selected stations with a Tucker trawl (4 m<sup>2</sup> mouth area, 1000 µm mesh size). The trawl was towed obliquely from the surface to 100 m depth (200 m on one station) and back to the surface, while the ship cruised at ~1-2 knots. Payout and retrieval rates were ~0.5 m s<sup>-1</sup>. 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, while for the Multinet, depth was monitored with the built-in depth sensor. The volume of water filtered by all net types (WP2, Multinet, Tucker) was measured with HydroBios flowmeters fitted in the mouth of the nets, and the numbers or biomasses were standardized accordingly.

In the laboratory aboard ship the WP2 net catches were usually divided into two parts with a Motoda splitter (Motoda, 1959). One part was preserved in 4% neutralized formalin, whereas the other part was frozen (-18°C). The frozen samples were analysed for total dry weight biomass after drying the samples in an oven at ~70 °C for 20 hours (Båmstedt, 1974). The Multinet and Tucker samples were usually placed in formalin. 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 larger than ~9 mm prosome length). Except when the samples were so small that whole samples could be counted, the remainder was then subsampled with a Motoda splitter and an aliquot containing at least ~500 individuals analysed for species composition. For the copepods, the numbers have been converted to biomass (dry weight) 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 dry mass was not available, weights of species similar in size and shape were used.

It should be noted that in order to examine seasonal patterns, the Multinet data collected at different times of year during a three year period were considered in the temporal sequence of 12-14 February 2007, 1-5 May 2008, 19-27 May 2007, 17-30 July 2006, 21-26 Nov 2006 and 11-26 August 2007, although the data were not sampled chronologically. While it would obviously have been desirable to survey the area chronologically, this was not possible due to several logistical and practical reasons. In spite of this limitation, we nevertheless believe that by examining the data in this way it provides an overall picture of the seasonal dynamics of zooplankton and how they relate to environmental factors. For this analysis, 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 only one station could be taken on each side of the Ridge.

In order to examine mesozooplankton diversity, 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, 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 2007 and 2008, the other using data collected with the Tucker trawl from the top 100 m (macrozooplankton) in August 2007 and 2008. For both data sets, the linear model (RDA) was preferred over the alternative unimodal one (Canonical Correspondence Analysis, CCA). This selection was after test runs of Detrended Correspondence Analysis (DCA) showed that the gradient length of the first axis was 1.661 and 2.950 standard deviations for the mesozooplankton and macrozooplankton datasets, respectively, indicating that for both datasets most of the species had linear species-environment responses (ter Braak and Smilauer, 2002).

The mesozooplankton data matrix used as input in the RDA included 48 zooplankton species or groups in 73 samples, whereas the macrozooplankton data included 10 species or groups in 36 samples. The environmental variables were temperature and salinity (means from 0-50 m (mesozooplankton) or 0-100 m (macrozooplankton)), chlorophyll *a* ( $\text{mg m}^{-2}$ , 0-30 m), bottom depth, latitude, longitude and year. Date (day number) was included in the analysis as covariable to remove variability in the data that may have been caused by the samples not being sampled on the same dates during the three year period (July 2006, August 2007 and 2008). The environmental variables were centered and standardized to zero mean and unit variance, and species data were centered but not standardized to avoid over-weighting of 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. Prior to 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 (VIF) 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 (chlorophyll *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. 4.5ter Braak.

## Results

### *Seasonal variability - mesozooplankton*

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

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

deeper layers (~200-1000 m) at low temperatures (~0°C) and salinities ~34.9 (Figure 3). In May most of the animals were found in surface waters (<100 m) where they stayed until July (*C. hyperboreus*) or August (*C. finmarchicus*) when the stocks descended again into deeper waters (Figure 3). It is noteworthy that during the winter period, *C. hyperboreus* was mostly concentrated in the 800-1000 m depth interval west of the Ridge, whereas east of it the species was more evenly distributed below ~200 m down to 1000-14 000 m. Figure 3 further illustrates that *C. hyperboreus* generally overwintered deeper than *C. finmarchicus*.

#### *Taxonomic composition*

A total of 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. Thus 24 species and groups were found in one sample only, and only one, *Calanus finmarchicus*, was present in them all (Table 3).

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

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

In July the mesozooplankton diversity, whether it was measured by 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 (~67% of the total number of amphipods and euphausiids) 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 euphausiids were caught by the Tucker trawl. *Thysanoessa longicaudata* was most abundant (~17%), *T. inermis* ranked second (~6%) and *Meganyctiphanes norvegica* third (2.1%).

#### *Zooplankton distribution in July-August*

The sampling coverage for mesozooplankton biomass was different between years making comparison between years difficult (Figure 5). However, in the areas between 10°W and 25°W where the sampling was similar, the total mesozooplankton biomass was more concentrated towards Greenland in 2006 compared to 2007 and 2008 (Figure 5). Except for one shelf station of the northeast coast of Iceland, the highest values in 2006 were thus observed in the cold waters in the northwestern parts of the Iceland Sea, whereas in 2007 and 2008 the biomass was distributed more to the east with only low values being recorded in the western and northwestern parts of the Iceland Sea..

Figure 6 shows the distribution of the biomass of dominant copepods in the surface layers. As explained in the Methods section, copepod biomass was only estimated for those samples that were analysed for species composition and as they were fewer than the ones that were analysed for total zooplankton biomass (Table 1), the spatial coverage shown in Figures 5 and

6 is not identical. *C. hyperboreus* were most abundant in the relatively cold waters in the northwest and west and the abundance was higher in 2006 than in 2007 and 2008 (Figure 6). *C. finmarchicus* were most abundant in the northwestern (2006) or northeastern (2007, 2008) regions of the Iceland Sea, and were more abundant in 2007 than the preceding and succeeding years. *M. 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 mainly caught in the eastern and northeastern parts of the Iceland Sea, whereas for euphausiids as a group there was no clear spatial trend (Figure 7). *T. abyssorum* were distributed more in the east than *T. libellula*, while *G. wilkitzkii* was mainly caught 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 mainly caught 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 northwestern parts of the Iceland Sea (Figure 7).

#### *Distribution in relation to the environment in July-August*

RDA analysis showed that longitude, temperature, bottom depth, chlorophyll *a* and salinity significantly influenced the mesozooplankton species composition in late summer ( $p < 0.05$ , forward model selection using Monte-Carlo permutation test) (Figure 8). Further, the year 2008 had a significant effect on the ordination and thus the community structure, when the abundance of *Acartia* spp., *Podon leuckarti*, Cirripede larvae, Ophiuroidea, *Temora longicornis* and *Limacina* spp. was relatively higher 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 explained an additional 6% each. Depth, chlorophyll *a* and salinity were weaker contributors to the RDA model, explaining only 2-3% of the overall variability (Table 5). Latitude and the years 2006 and 2007 did not significantly contribute 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 explained variability (32%), while the gradient along the second axis explains ~24%. The first axis described a gradient from species that were mainly found in relatively deep waters in the eastern parts of the study area where salinity was relatively high (*C. finmarchicus*, *Pseudocalanus*, chaetognaths) towards species that were distributed more in the west and where it was shallower and the salinity also lower (*Acartia* spp., *C. glacialis*, *C. hyperboreus*, *Podon leuckarti*). It is also very evident 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 analysis (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 high abundances of species with coastal affinities was located in the south (e.g. *T. longicornis*, *Acartia* spp., *Podon leuckarti* and cirripede larvae) where temperature and salinities were relatively high but chlorophyll *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 chlorophyll *a* values relatively high (Figure 8).

A separate RDA analysis was carried out for the macrozooplankton data (euphausiids and amphipods) (Figure 9). The analysis showed that longitude and chlorophyll *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 the macrozooplankters ( $p < 0.05$ , forward

model selection using Monte-Carlo permutation test), longitude however, 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 chlorophyll *a*, 43%), and described a gradient from the west with relatively high chlorophyll *a* values (negative end) to the east with lower chlorophyll *a* values (positive end) (Figure 9). The second canonical axis explained only a very small part of the variation (~2%).

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

## Discussion

### *Seasonal variability - mesozooplankton*

The seasonal changes of zooplankton in the oceanic Iceland Sea were characterized by one main maximum in numbers in July and August (Figure 2). Earlier studies on the shelf areas north and northeast of Iceland also showed one main peak in zooplankton abundance, however it occurred earlier (June and July, Gislason and Astthorsson, 1998; Astthorsson and Gislason, 2003) than we observed in the offshore area. The earlier studies further 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 mainly caused by capelin predation (Gislason and Astthorsson, 1998). This was not an unreasonable assumption since the capelin are plankton feeders that normally migrate in large numbers to the area north of Iceland to feed during the summer months (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 (Palsson et al., 2012a). Thus, in the present study, capelin were only caught in very low quantities in the central Iceland Sea (Palsson 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 dry weight of mesozooplankton were greater east of the Kolbeinsey Ridge than west of the Ridge (Figure 2). This may reflect the greater biological production east of the Ridge than west of it, 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 waters and rose to the surface sometime between February and May (Figure 3). This is in accordance 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 waters appeared to start earlier in *C. hyperboreus* (July) than *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 to *C. finmarchicus* also accounts for the generally much lower biomass of *C. hyperboreus* in July and August in the surface layers compared to *C. finmarchicus* (Figure 6), in spite of 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 among the most abundant ones 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 the Barents Sea (Hassel, 1986).

The 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 somewhat different zooplankton fauna than the more offshore areas. Regions where these two systems interact/meet may therefore be inhabited by species from both regions/systems, which will be reflected in higher species diversity in these areas. In our study it may also be significant that near the shelf edges north of Iceland, currents from different sources meet (Figure 1A) that carry zooplankton species, thus contributing to higher diversity in these areas.

#### *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 favorable for phytoplankton growth (Sakshaug, 1997), which in turn may have led to higher zooplankton growth and biomass near to the ice edge and in areas where the ice recently retreated.

The northeastern distribution of *C. hyperboreus* in all three years indicates that it is 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 first named 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 affected the community structure of mesozooplankton in the Iceland Sea were longitude, the year 2008, temperature, depth, chlorophyll *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 to 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 be dependent 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 significant influence of east-west location on mesozooplankton distribution. It should be noted here 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 RTD diagram suggesting close relationship among them (Figure 8).

In our study the salinity in the upper 50 m varied from 30.8-34.9, 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 the salinity signifies some of 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 thus influence distribution (McLaren et al., 1968; Kinne, 1970). However, like salinity, the temperature variations may also indicate water masses of different origin, and thus the effects of temperature on the species composition may be indirect rather than direct and indicate advective transport of species. While we do not have detailed data or models of current patterns in the area it is difficult to evaluate if temperature is influencing the species composition directly or indirectly.



In the Iceland Sea, water masses of different origin mix. These water masses carry different zooplankters, i.e. warm water species from the south and east and cold water species from the north. The fact that both temperature and salinity influenced the zooplankton community similarly (the arrows point in the same direction in ordination space, Figure 7) suggests that water mass distribution is of major importance in structuring the plankton communities and that the Iceland Sea is a highly advective ecosystem.

It is noteworthy that the year 2008 was the second most important factor in explaining the mesozooplankton distribution and abundance (Table 5, Figure 8), meaning that the mesozooplankton assemblages were different in 2008 compared with 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 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 may influence the distribution of zooplankton species that live on the bottom during a part of the life cycle, like meroplankters and copepods that spend the winter as resting eggs on the bottom. These groups tend to be most abundant in coastal areas. Several of the groups that were most negatively correlated with bottom depth (e.g. *Podon leuckarti*, Cirripedia larvae, *Temora 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, it should be noted that with ~90% of the samples being taken at greater depth than 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 rather signify advection of animals from the coastal areas..

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

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

With regard to the macroplankton, the RDA analysis revealed that longitude explained by far the greatest part of the variability in community structure, with chlorophyll *a* biomass explaining the second most of the variability (Table 6, Figure 9). Sea temperature thus had no effect on the distribution according to the RDA analysis. From the RDA biplot (Figure 9) and the distribution maps illustrating the amphipods (Figure 7) it can be inferred that more *T. libellula* were found in the west than *T. abyssorum*. *T. libellula* is an arctic species while *T. abyssorum* are found in Atlantic and mixed subarctic water masses (Dalpadado et al., 2001; Melle, 2004). In the northern parts of the Norwegian Sea, *T. libellula* are thus mainly found in cold waters in the western parts, whereas *T. abyssorum* are more abundant in warmer waters in the southeast (Dalpadado et al., 2001). The distributions from this study (Figure 7) indicate that the Arctic *T. libellula* are advected into the Iceland Sea from the Greenland Sea with the

East-Greenland Current, while 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 Sea and the Norwegian Sea, amphipods are important components of the ecosystems (Dalpadado et al., 2001, 2008; Melle, 2004). They are both carnivores, feeding on small zooplankton such as copepods, while being themselves fed on by plantivorous fish and seabirds (Dalpadado et al., 2008; Skjoldal et al., 2004). Their relatively high numbers in the Iceland Sea ( $\sim 0.02\text{--}2$  individuals  $\text{m}^{-3}$ , 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 food web of the Iceland Sea. Our unpublished results indicate that both species reproduce in the area.

The amphipod *Gammarus wilkitzkii* was found in the westernmost parts of the Iceland Sea (Figures 7). This species usually lives attached to the underside of Arctic sea ice (Werner et al., 1999), where it predominately feeds 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 at least 4 days (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 receded from these stations only recently when we were there or that the animals were advected to the stations from nearby sea ice regions.

The euphausiids are also important in the area 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* are able to reproduce in Arctic waters (Siegel and Nicol, 2000; Dalpadado et al., 2008). In our study we found many larvae (mainly furcilia) from both species in August (*Thysanoessa* spp. in Figure 7). These may have been advected to the area from regions where temperature conditions were more favourable rather than 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 some spawning activity in the Iceland Sea. In this context it may be noted that a close inspection of adult individuals of the *Thysanoessa* species showed that they had fully developed external sexual organs at the time of sampling (August), thus 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). Thus, increased stratification in cold years when there is less inflow may lead to an 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 the 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 onto the sea areas north of Iceland (Anonymous, 2010). The results of the present investigation suggest that during such conditions the season of high biomass in the surface layers lasts about 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 frontal zone of mixing 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 amongst the zooplankters

were the copepods *C. finmarchicus* and *C. hyperboreus*, the amphipod *T. abyssorum* and the euphausiid *T. longicaudata*.

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## References

- Anonymous 2010. Þættir úr vistfræði sjávar 2009. Environmental Conditions in Icelandic Waters 2009. (In Icelandic, English summary). Hafrannsóknir, 152: 1-53.
- 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.
- Astthorsson, O. S., and Gislason, A. 1997a. On the food of capelin in the subarctic waters north of Iceland. Sarsia, 82: 81-86.
- Astthorsson, O. S., and Gislason, A. 1997b. Biology of euphausiids in the subarctic waters north of Iceland. Marine Biology, 129: 319-330.
- Astthorsson, O. S., and Gislason, A. 2003. Seasonal variations in abundance, development and vertical distribution of *Calanus finmarchicus*, *C. hyperboreus* and *C. glacialis* in the East Icelandic Current. Journal of Plankton Research, 25: 843-854.
- Astthorsson, O. S., Hallgrímsson, I., and Jonsson, G. S. 1983. Variations in zooplankton densities in Icelandic waters in spring during the years 1961-1982. Rit Fiskideildar, 7: 73-113.
- Astthorsson, O. S., Gislason, A., and Jonsson, G. S. 1995. Zooplankton biomass and composition in the western Iceland Sea during autumn. Extended Abstracts Volume from a Symposium on Nordic Seas, Hamburg. Arctic Ocean Science Board and Sonderforschungsbereich "Processes relevant to climate", 21-24.
- Auel, H. 1999. The ecology of Arctic deep-sea copepods (Euchaetidae and Aetideidae). Aspects of their distribution, trophodynamics and effect on the carbon flux. Berichte zur Polarforsch, 319: 1-97.
- Båmstedt, U. 1974. Biochemical studies on the deep-water pelagic community of Korsfjorden, western Norway. Methodology and sample design. Sarsia, 56: 71-86.
- Blachowiak-Samolyk, K. 2008. Contrasting zooplankton communities (Arctic vs. Atlantic) in the European Arctic Marginal Ice Zone. Oceanologia, 50: 363-389.
- Blindheim, J., and Østerhus, S. 2005. The Nordic Seas, main oceanographic features. In Geophysical Monograph 158, pp. 11-38. Ed. By H. Drange, T.M. Dokken, T. Furevik, R. Gerdes, and W. Berger. American Geophysical Union, Washington DC.
- Dalpadado, P., Borkner, N., Bogstad, B., and Mehl, S. 2001. Distribution of *Themisto* (Amphipoda) spp. in the Barents Sea and predator-prey interactions. ICES Journal of Marine Science, 58: 867-895.
- Dalpadado, P., Ellertsen, B., and Johannessen, S. 2008. Inter-specific variations in distribution, abundance and reproduction strategies of krill and amphipods in the marginal ice zone of the Barents Sea. Deep-Sea Research, 55: 2257-2265.
- Davis, C. S. 1984. Predatory control of copepod seasonal cycles on Georges Bank. Marine Biology, 82: 31-40.
- 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 Astthorsson, O. S. 2004. Distribution patterns of zooplankton communities around Iceland in spring. Sarsia, 89: 467-477.
- Gislason, A., Petursdóttir, H., Astthorson, O.S., Gudmundsson, K., and Valdimarsson, H. 2009. Interannual variability in abundance and community structure of zooplankton south and north of Iceland in relation to environmental conditions in spring 1990-2007. Journal of Plankton Research, 31: 541-551.
- Hassel, A. 1986. Seasonal changes in zooplankton composition in the Barents Sea, with special attention to *Calanus* spp. (Copepoda). Journal of Plankton Research, 8: 329-339.

- Head, E. J. H., Harris, L. R., Yashayaev, I. 2003 Distributions of *Calanus* spp. and other mesozooplankton in the Labrador Sea in relation to hydrography in spring and summer (1995–2000). *Progress in oceanography*, 59: 1-30.
- Heath, M. R., Boyle, P. R., Gislason, A., Gurney, W. S. C., Hay, S. J., Head, E. J. H., Holmes, S., Ingvarsdottir, A., Jónasdóttir, S. H., Lindeque, P., Pollard, R. T., Rasmussen, J., Richards, K., Richardson, K., Smerdon, G., Speirs, D. 2004. Comparative ecology of overwintering *Calanus finmarchicus* in the northern North Atlantic, and implications for life-cycle patterns. *ICES Journal of Marine Science*. 61: 698-701.
- Hirche, H.-J., and Kosobokova, K. 2003. Early reproduction and development of dominant calanoid copepods in the sea ice zone of the Barents Sea - need for a change of paradigms? *Marine Biology*, 143: 769-781.
- 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*, Vol. 114, C02022: 1-15.
- Kinne, O. 1970. Temperature, animals: invertebrates. *In Marine Ecology*, Vol 1. Environmental Factors, Part 1, pp. 407–514. Ed. by O. Kinne. Wiley-Interscience, London.
- Kinne, O. 1971. Salinity, animals: invertebrates. *In Marine Ecology*, Vol 1. Environmental Factors, Part 2, pp. 821–995. Ed. by O. Kinne. Wiley-Interscience, London.
- Krebs, C. 1989. *Ecological Methodology*. Harper Collins, New York.
- Longhurst, A., and Williams, R. 1992. Carbon flux by seasonal vertical migrant copepods is a small number. *Journal of Plankton Research*, 11: 1495-1509.
- Mauchline, J. 1998. The biology of calanoid copepods. *Advances in Marine Biology*, 33: 1-710.
- McLaren, I. A., Walker, D. A., and Corkett, C. J. 1968. Effects of salinity on mortality and development rate of eggs of the copepod *Pseudocalanus minutes*. *Canadian Journal of Zoology*, 46: 1267–1269.
- 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. Færnø, O. A. Misund, and I. Röttingen. Tapir Academic Press.
- Motoda, S. 1959. Devices of simple plankton apparatus. *Memories of the Faculty of Fisheries, Hokkaido University*, 7: 73-94.
- Norrbin, M. F., Olsen, R.-E., and Tande, K. S. 1990. Seasonal variation in lipid class and fatty acid compositions of two small copepods in Balsfjorden, northern Norway. *Marine Biology*, 105: 205-211.
- Östvedt, O. J. 1955. Zooplankton investigations from weathership M in the Norwegian Sea. *Hvalrådets Skrifter*. 40: 1-93.
- Palsson, O. K., Gislason, A., Gudfinnsson, H., Gunnarsson, B., Olafsdóttir, S. R., Petursdóttir, H., Sveinbjörnsson, S., Thorisson, K., Valdimarsson, H. 2012a. Ecosystem structure in the Iceland Sea. *ICES Journal of Marine Science*, this volume.
- Palsson, O. K., Sveinbjörnsson, S., Valdimarsson, H., Gislason, A., Vilhjalmsón, H. 2012b. Lífshættir loðnu í Íslandshafi. Capelin life-history traits in the Iceland Sea. (In Icelandic, English summary). *Hafrannsóknir*, in press.
- Richter, C. 1994. Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. *Berichte zur Polarforschung*, 154: 1-87.
- Richter, C. 1995. Seasonal changes in the vertical distribution of mesozooplankton in the Greenland Sea Gyre (75°N): distribution strategies of calanoid copepods. *ICES Journal of Marine Science*, 52: 533-539.
- Sakshaug, E. 1997. Biomass and productivity distributions and their variability in the Barents Sea. *ICES Journal of Marine Science*, 54: 341-350.

- Siegel, V., and Nicol, S. 2000. Population parameters. *In* Krill Biology, Ecology and Fisheries, pp. 103-149. Ed. by I. Everson. Blackwell Science Publication, UK.
- Sigurdsson, T., and Astthorsson, O. S. 1991. Aspects of the feeding of capelin (*Mallotus villosus*) during autumn and early winter in the waters north of Iceland. ICES Council Meeting 1991/H:49, 16 pp.
- Skjoldal, H. R., Dalpadado, P., and Dommasnes, A. 2004. Food web and trophic interactions. *In* The Norwegian Sea ecosystem, pp. 447-506. Ed by H. R. Skjoldal, R. Sætre, A. Færnø, O. A. Misund, I. Röttingen. Tapir Academic Press.
- Stefansson, U., and Olafsson, J. 1991. Nutrients and fertility of Icelandic waters. Rit Fiskideildar, 7: 1-56.
- Stefansson, U. 1962. North Icelandic Waters. Rit Fiskideildar, 3: 1-269.
- Stefansson, U., and Jakobsson, J. 1989. Oceanographical variations in the Iceland Sea and their impact on biological conditions, a brief review. *In* Proceedings of the sixth conference of the Comité Arctique International, 13-15 May 1985, pp. 427-455. Ed. by L. Rey, and V. Alexander. E.J. Brill, Leiden.
- Strickland, J. D. H., and Parsons, T. R. 1968. A practical handbook of seawater analysis. Bulletin of the Fisheries Research Board of Canada, 167. 311 pp.
- ter Braak, C. J. F., and Smilauer, P. 2002. CANOCO Reference manual and CanoDraw for Windows User's guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power (Ithaca, NY, USA), 500 pp.
- 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. International Council for the Exploration of the Sea, Committee Meeting (Biological Oceanography Committee), L:20: 1-17.
- Valdimarsson, H., and Malmberg, S. A. 1999. Near-surface circulation in Icelandic waters derived from satellite tracked drifters. Rit Fiskideildar, 16: 23-39.
- Vilhjalmsson, H. 2002. Capelin (*Mallotus villosus*) in the Iceland–East Greenland–Jan Mayen ecosystem. ICES Journal of Marine Science 216: 870-883.
- Werner, I. 1997. Grazing of the Arctic under-ice amphipods on sea-ice algae. Marine Ecology Progress Series, 160: 93-99.
- Werner, I., Auel, H., Garrity, C., and Hagen, W. 1999. Pelagic occurrence of the sympagic amphipod *Gammarus wilkitzkii* in ice-free waters of the Greenland Sea – dead end or part of the life cycle? Polar Biology, 22: 56-60.

## Tables

Table 1. Number of stations and samples (in parentheses) analysed for dry weight (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 Jul	bs062006	139 (139)	-	-	21 (54)	-	-
	21-26 Nov	af112006	-	-	-	2 (18)	-	-
2007	12-14 Feb	bs032007	-	-	-	4 (35)	-	-
	19-27 May	bs082007	-	-	-	2 (18)	-	-
	11-26 Aug	bs112007	71 (71)	20 (20)	-	4 (37)	-	12 (12)
2008	1-5 May	bs062008	-	-	-	4 (37)	-	-
	12-31 Aug	af112008	86 (86)	29 (29)	-	-	-	14 (14)
Total			296 (296)	49 (49)	-	37 (199)	-	26 (26)

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

Sampling gear	Opening area (m <sup>2</sup> )	Mesh size (µm)	Towing mode	Sampling depth (m)
WP2	0.25	200	Vertical tow	0-50
Multinet	0.25	200	Vertical tow	0-50-100-200-300-400-600-800-1000-1400-1800
Tucker	4.00	1000	U-tow	0-100*

\*At one station the sampling was made 0-200 m.

Table 3. Mesozooplankton species collected in the Iceland Sea by the WP2- and Multinets during 2006, 2007 and 2008 and number of samples in which the species occurred. Total number of samples analysed was 247.

Taxon	Samples	Taxon	Samples
<b>PROTOZOA</b>		<b>COPEPODA (Cntd)</b>	
<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
<b>CNIDARIA</b>		<i>Metridia longa</i>	189
<i>Aglantha digitale</i>	37	<i>Metridia lucens</i>	2
Cnidaria indet.	75	<i>Metridia</i> spp.	3
<b>SIPHONOPHORA</b>		<i>Microcalanus</i> spp.	149
<i>Lensia conoidea</i>	1	<i>Microsetella norvegica</i>	12
Siphonophora indet.	13	<i>Oithona</i> spp.	226
<b>CTENOPHORA</b>		<i>Oncaea</i> spp.	215
Ctenophora indet.	3	<i>Phaennidae</i> spp.	2
<b>NEMTODA</b>		<i>Pleuromamma robusta</i>	1
Nematoda indet.	1	<i>Pseudaetidis armatus</i>	13
<b>POLYCHAETA</b>		<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
<b>GASTROPODA</b>		<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	<b>OSTRACODA</b>	
<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	<b>CIRRIPEDIA</b>	
<b>BIVALVIA</b>		Cirripedia indet.	10
Bivalvia indet.	18	<b>ISOPODA</b>	
<b>CLADOCERA</b>		Isopoda indet.	36
<i>Evadne nordmanni</i>	5	<b>AMPHIPODA</b>	
<i>Podon leuckarti</i>	5	<i>Apherusa</i> spp.	4
<b>COPEPODA</b>		<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	<b>EUPHAUSIACEA</b>	
<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	<b>MYSIDACEA</b>	
<i>Chiridus armatus</i>	8	<i>Boreomysis arctica</i>	1
<i>Chiridus obtusifrons</i>	4	<b>DECAPODA</b>	
<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	<b>CHAETOGNATHA</b>	
<i>Euchaeta barbata</i>	27	Chaetognatha indet.	229
<i>Euchaeta barbata</i> f. <i>farrani</i>	13	<b>ECHINODERMATA</b>	
<i>Euchaeta glacialis</i>	78	Ophiuroidea indet.	25
<i>Euchaeta hanseni</i>	2	<b>LARVACEA</b>	
<i>Euchaeta norvegica</i>	48	Larvacea indet.	89



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

Taxon	%
<i>AMPHIPODA</i>	
<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
<i>EUPHAUSIACEA</i>	
<i>Thysanoessa longicaudata</i>	16.8
<i>Thysanoessa inermis</i>	6.5
<i>Meganyctiphanes norvegica</i>	2.1

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

Explanatory variable	Explained variability	p	F
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
Chlorophyll a (0-30 m)	0.02	0.014	2.45
Salinity (0-50 m)	0.02	0.032	1.91
Total	0.32		

Table 6. Macrozooplankton. Ranking of environmental variables that significantly (Monte Carlo permutation test in RDA,  $p < 0.05$ ) influenced distribution of mesozooplankton in the Iceland Sea in 2006 (July) and 2007 and 2008 (August). The proportion of explained variability by each variable and the p- and F-values are also given.

Explanatory variable	Explained variability	p	F
Longitude	0.33	0.002	12.77
Chlorophyll a (0-30 m)	0.10	0.036	4.48
Total	0.43		

## Figures

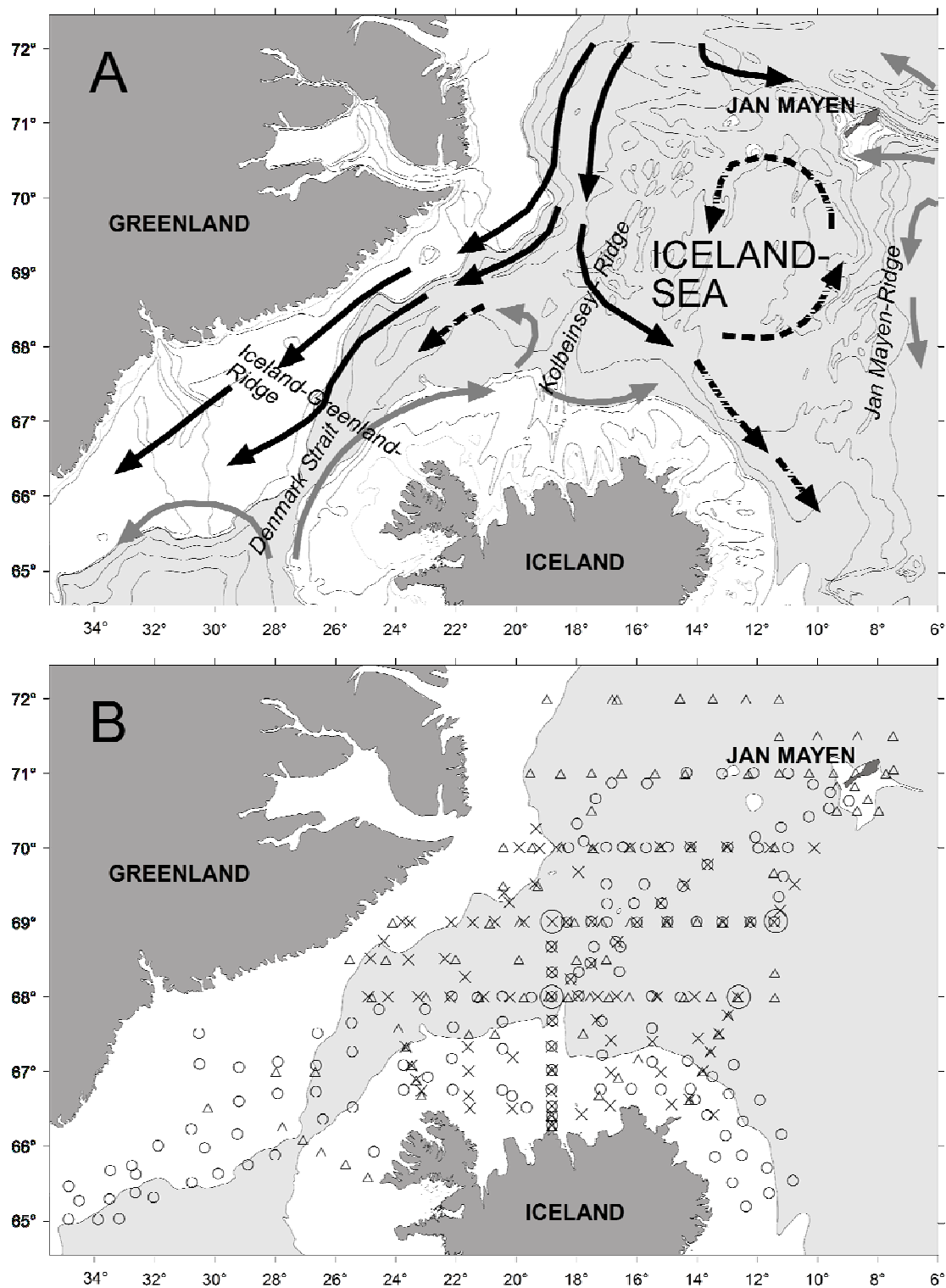


Figure 1. A. Map of the study area showing schematically the main ocean currents in the upper layers. The 500 m bottom contour separates the shelf (white) from the off-shelf (gray shading). Gray arrows: Atlantic Water, black arrows: Polar Water, broken black arrows: mixed water. (Currents modified from Valdimarsson and Malmberg, 1999; Blindheim and Österhus, 2005; Hunegnaw et al., 2009). B. Map showing location of stations occupied during 2006-2008. The small circles denote stations occupied in July 2006, crosses are stations

occupied in August 2007 and triangles are stations occupied in August 2008. The four larger circles denote stations where the Multinet was used to sample the whole water column. The 500 m bottom contour is also shown.

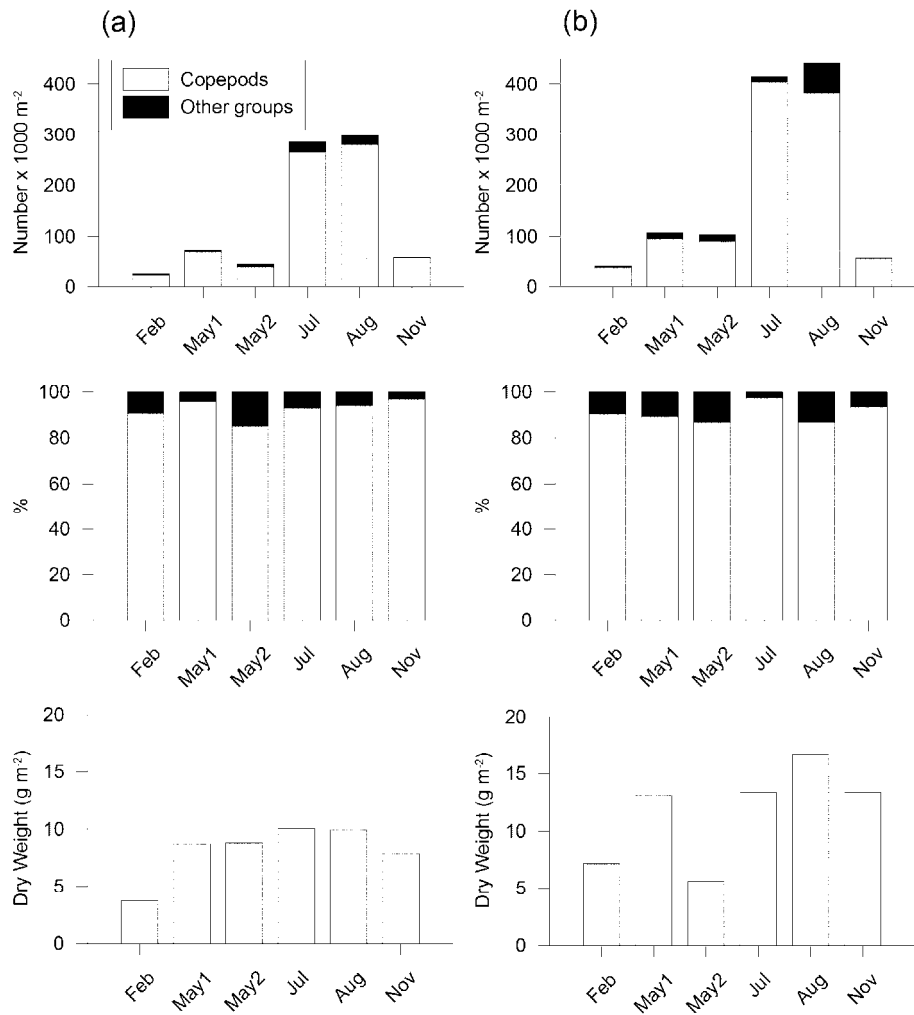


Figure 2. Mesozooplankton. Seasonal changes in numbers of mesozooplankton in Iceland Sea from February – November. May1 and May2 denote first and second half of May, respectively. The values are means from two stations west of the Kolbeinsey Ridge (A) and two stations east of the Ridge (B), except for 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 panel shows total numbers (numbers m<sup>-2</sup>, whole water column), the mid-panel is relative composition (%), and the bottom panel is biomass of copepods (dry weight g m<sup>-2</sup>, whole water column). Light grey shading: copepods; black shading: other groups. For location of the stations refer to Figure 1B.

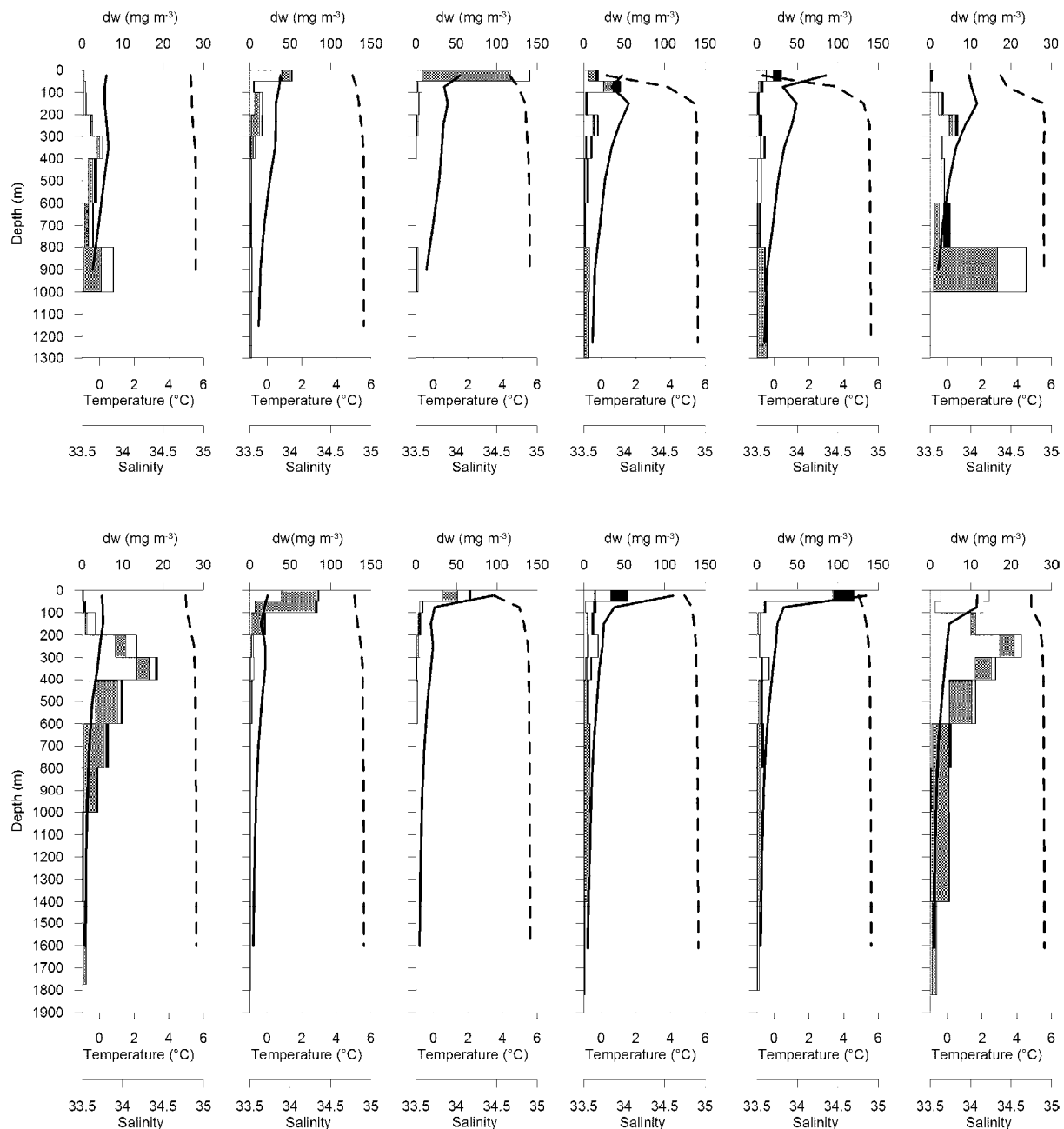


Figure 3. Mesozooplankton. Vertical distribution of *Calanus hyperboreus* (dark gray shading), *C. finmarchicus* (light gray shading), *Metridia longa* (white) and other copepods (black) (dry weight  $\text{mg m}^{-3}$ ) from February – November. May1 and May2 denote first and second half of May, respectively. The values are means from two stations west of the Kolbeinsey Ridge (upper panel) and two stations east of the Ridge (lower panel), except for 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 CTD casts are also shown. The data were sampled during 2006, 2007 and 2008 (Table 1). Note the change in horizontal scales between sampling times. For location of the stations refer to Figure 1B.

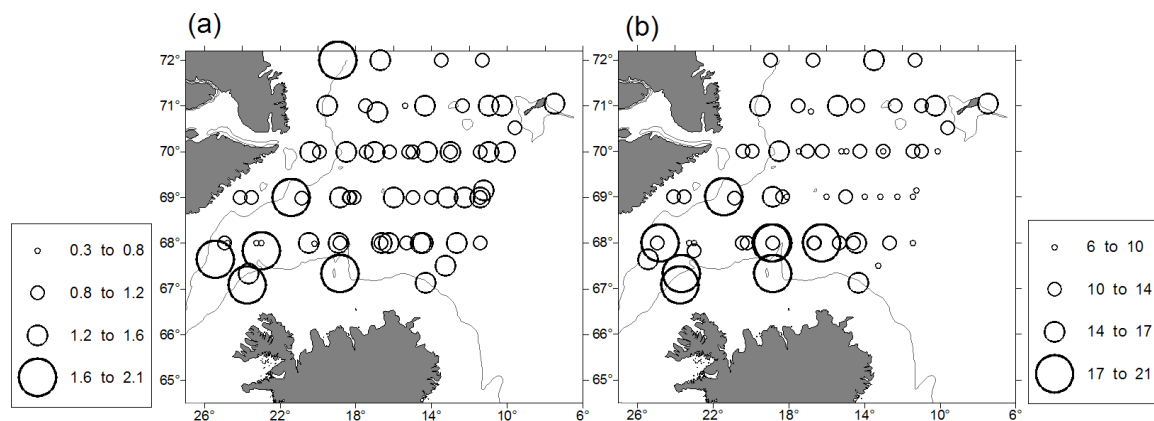


Figure 4. Mesozooplankton. Species diversity of zooplankton in surface layers (0-50 m) in July 2006 and August 2007, 2008, as assessed by the Shannon-Wiener diversity index (A) and number of species (B). The samples were collected with WP2 or Multinet. The 500 m bottom contour is shown.

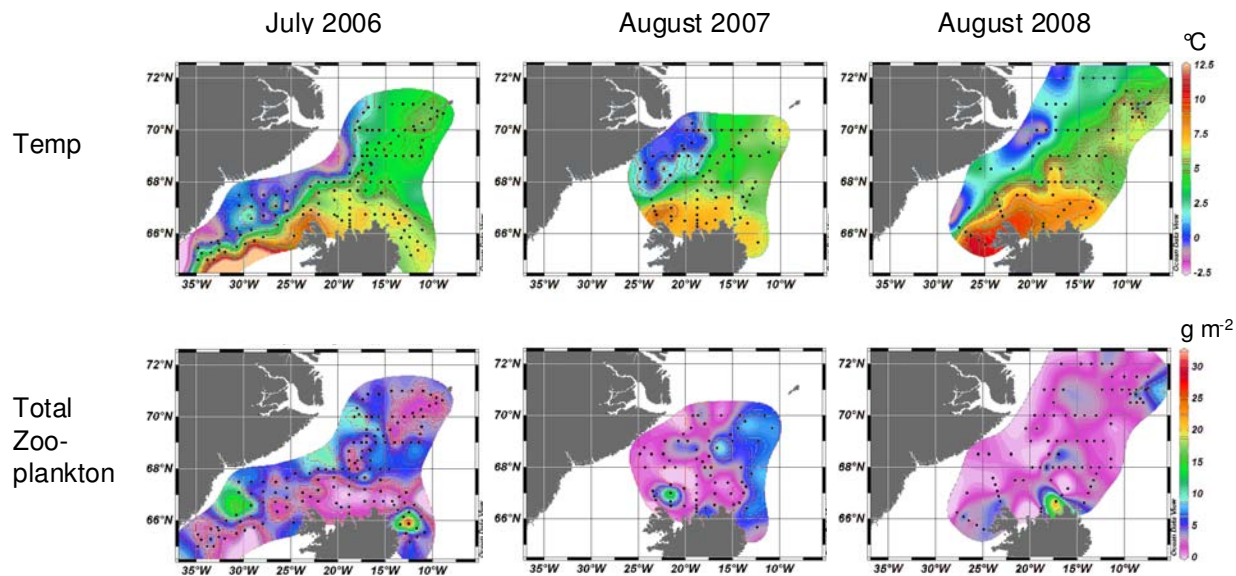


Figure 5. Sea temperatures (means from 0-50 m) (upper panel) and total mesozooplankton biomass (dry weight  $\text{g m}^{-2}$ , 0-50 m) (lower panel) in Iceland Sea during July 2006 and August 2007 and 2008.



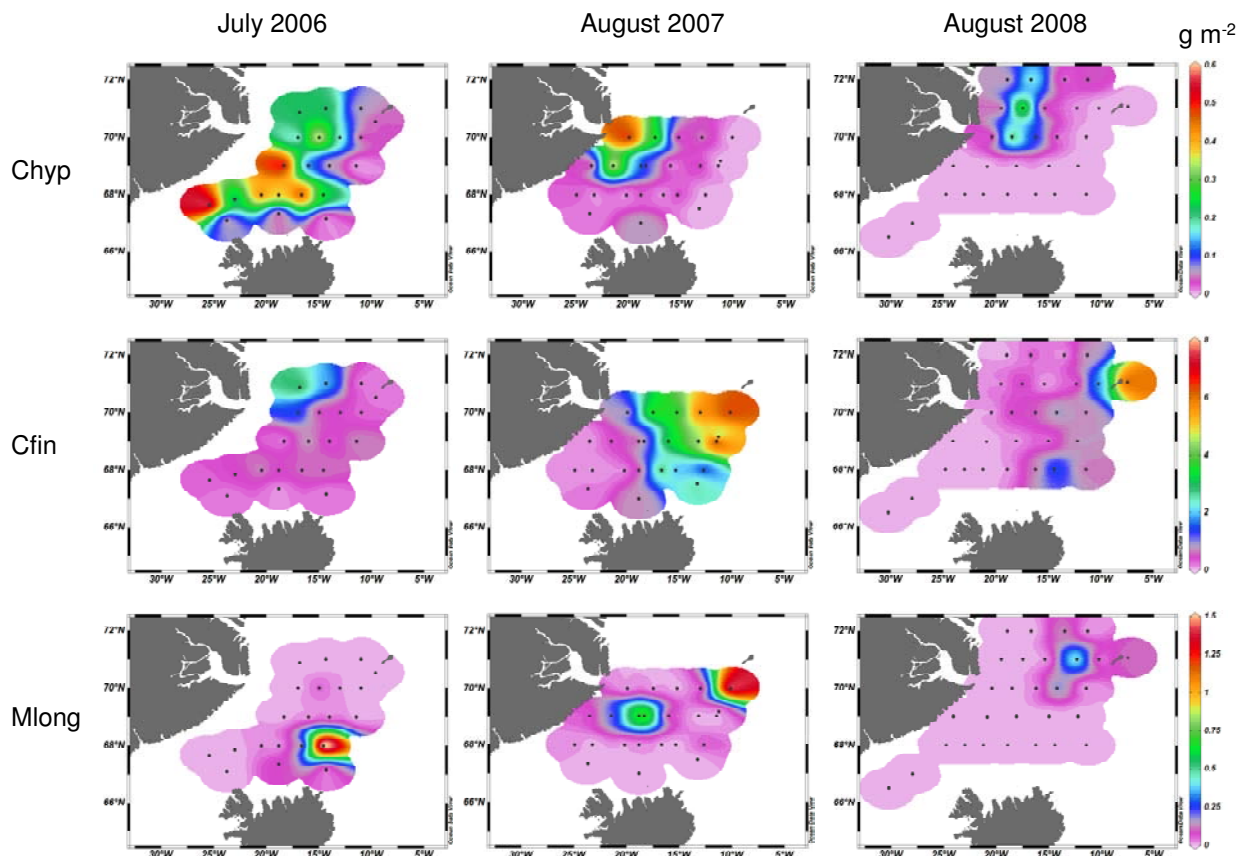


Figure 6. Distribution of *Calanus hyperboreus* (top panel) *C. finmarchicus* (mid-panel) and *Metridia longa* (bottom panel) (dry weight  $\text{g m}^{-2}$  0-50 m) in Iceland Sea during July 2006 and August 2007 and 2008.

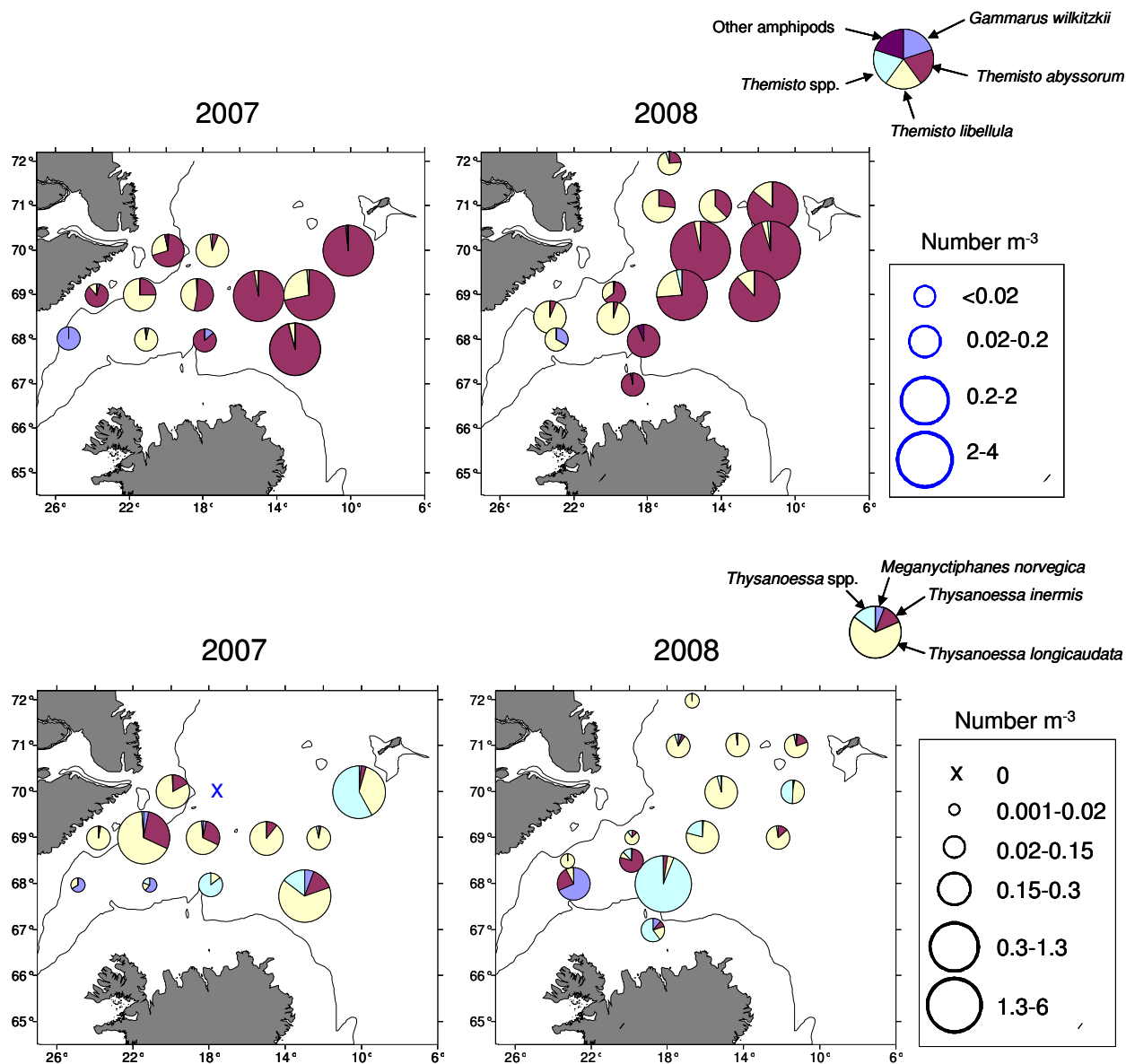


Figure 7. Macrozooplankton. Distribution of amphipods (upper panel) and euphausiids (lower panel) in Iceland Sea during August 2007 and 2008 (numbers  $m^{-3}$ , 0-100 m). The samples were collected with Tucker-trawls. *Thysanoessa* spp. are mainly larval stages that could not be identified beyond the genus level. The 500 m bottom contour is shown.

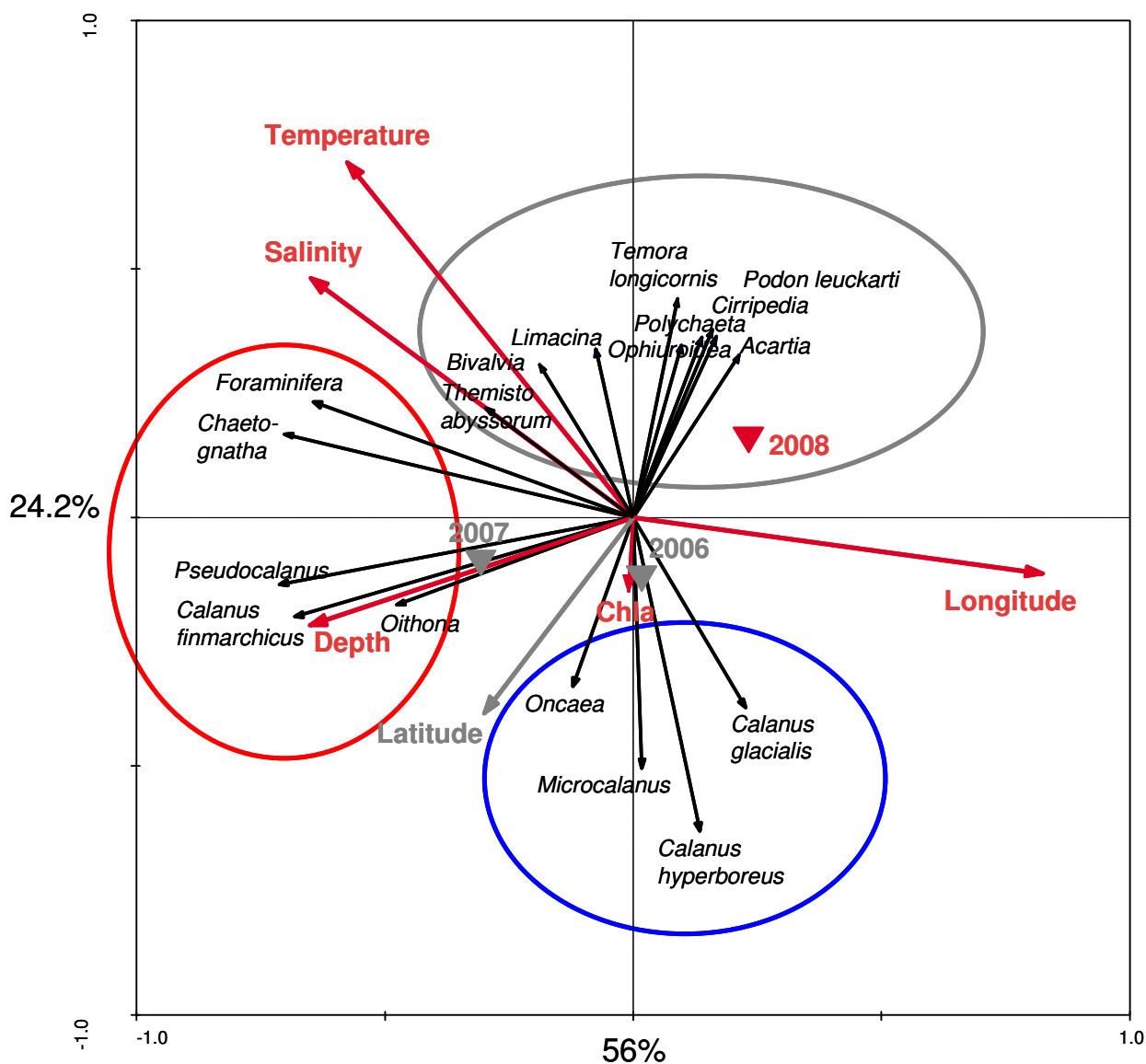


Figure 8. Mesozooplankton. RDA biplot of mesozooplankton species abundances (numbers  $m^{-3}$ , 0-50 m) (thin black arrows) and environmental variables (red and grey arrows) in the Iceland Sea during 2006 (July), 2007 and 2008 (August). Environmental variables are chlorophyll *a*, temperature and salinity (means from 0-50 m), bottom depth and year. First canonical axis explains 56% of species-environment relationship, second axis explains 24.2%. Year is put into the analysis as categorical variable and denoted as triangles (centroids). Day of the year is covariable to subtract variability due to different sampling times. Red arrows or triangles significantly explain variation in zooplankton community structure. Insignificant variables (grey arrows and triangles) are passive and do not influence the analysis. The arrows point in the direction of steepest increase of the respective variables. 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 Braak and Smilauer, 2002). For RDA model design and further explanation see text. Zooplankton communities are indicated by color shading, red (Atlantic), blue (Arctic) and gray (coastal associated).

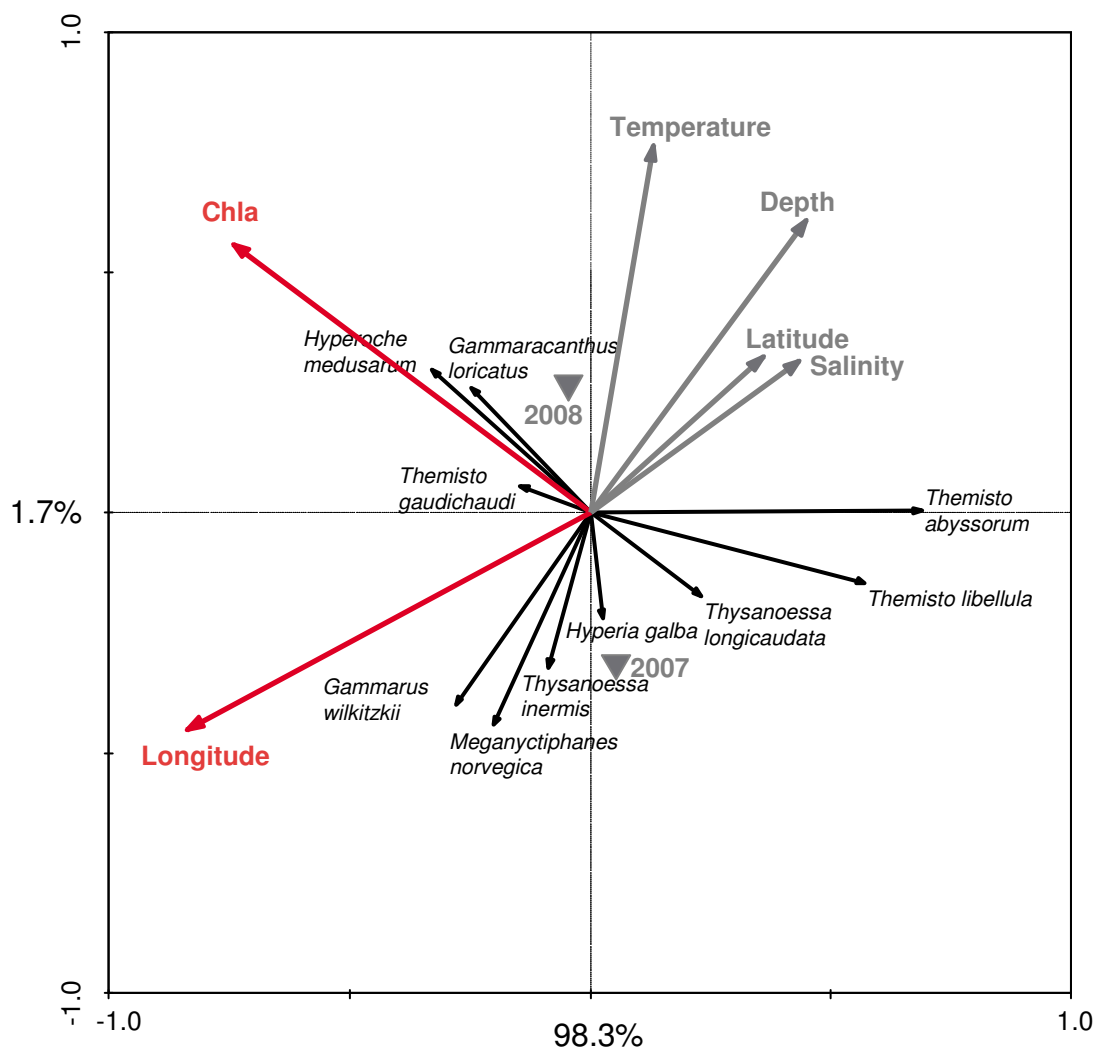


Figure 9. Macrozooplankton. RDA biplot of euphausiid and amphipod abundances (numbers  $\text{m}^{-3}$ , 0-100 m) (thin black arrows) and environmental variables (black and grey arrows) in the Iceland Sea during 2006 (July), 2007 and 2008 (August). Environmental variables are chlorophyll *a*, temperature and salinity (means from 0-50 m), bottom depth and year. First canonical axis explains 98.3% of species-environment relationship, the second axis 1.7%. Year is put into the analysis as categorical variable and denoted as triangles (centroids). Day of the year is covariable to subtract variability due to different sampling times. Red arrows significantly explain variation in zooplankton community structure. Insignificant variables (grey arrows and triangles) are passive and do not influence the analysis. The arrows point in the direction of steepest increase of the respective variable. 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 RDA model design and further explanation see text.