Interannual variability in abundance and community structure of zooplankton south and north of Iceland in relation to environmental conditions in spring 1990-2007

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A 18-year zooplankton time series from two standard sections differing in hydrographical conditions (Subarctic Water north of Iceland, Atlantic water south of Iceland), was examined in relation to hydrography and phytoplankton dynamics, and large scale climatic changes in the North Atlantic Ocean (NAO). The long-term mean zooplankton abundance was higher south (~160 000 individuals m^{-2}) than north of Iceland (~120 000 individuals m⁻²). Abundance fluctuated markedly between years. Copepods (mainly *Calanus finmarchicus* and *Oithona* spp.) dominated the zooplankton, comprising >60-70% of the plankton in most years. Among the copepods, C. finmarchicus was more abundant south of Iceland (~20-70%) than to the north (~10-60%). Abundance and community structure were related to environmental variables using regression and multivariate techniques (PCA, RDA). Temperature and salinity were the most important environmental variables in explaining the differences in species composition north and south of Iceland, with species like Temora longicornis and Evadne nordmanni being relatively abundant to the south, and Metridia longa and C. hyperboreus to the north of Iceland. A significant yearto-year variability in community structure was observed both south and north of Iceland, with salinity and used Nitrogen dictating the variability south of Iceland and temperature to the north (Monte Carlo permutation tests, p<0.01). In neither region a unidirectional temporal trend in species composition was detected.

Keywords: Long-term changes, community structure, zooplankton, Icelandic waters

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Introduction

The system of submarine ridges, on which Iceland rests, divides the oceanic area around Iceland into different oceanic regions or hydrographic domains (Astthorsson and Gislason 1995, Beare et al. 2000, Gislason 2005). The main division is formed by the Greenland-Iceland-Scotland Ridge, that divides the cold waters to the north and east of Iceland from the warmer waters to the south and west. The different hydrographical domains have significant impact on the structure of plankton communities around Iceland.

The Icelandic monitoring programme for hydrography, nutrients, phyto- and zooplankton consists of a series of transects perpendicular to the coastline all around Iceland. Sampling of the transects to the north and east of Iceland was started in the 1960s. Additional section lines to the south and west were added in the 1970s. Currently, there are approximately 90 stations. The monitoring programme uses standardized methods and is taking place every year during late May and early June. The present study is based on material sampled during these investigations.

The results of the hydrography, chemistry and phytoplankton monitoring has been dealt with in several earlier reports (e.g. Malmberg and Kristmannsson 1992, Valdimarsson and

Malmberg 1999, Stefánsson and Olafsson 1991, Gudmundsson 1998). Previous analyses of the sampled zooplankton material has mainly dealt with the analyses of biomass and relative composition (Astthorsson et al. 1983, Astthorsson and Gislason 1995, Astthorsson et al. 2007), while Gislason and Astthorsson (2004) reported on the distribution patterns of zooplankton communities around Iceland in spring. In this paper we analyze data on species composition and community structure at two of the sampled transects, differing greatly in hydrographic conditions, one in the north where the water mass is characterized by a mixture of Atlantic and Polar Water (Subarctic Water), and the other in the south where Atlantic Water is predominant.

Several studies indicate that changes are taking place in the abundance and community structure of zooplankton in the North Atlantic as a result of climate change (e.g. Beaugrand 2003, Planque and Froementin 1996, Pershing et al. 2004, Hays et al. 2005, Reid and Beaugrand 2002, Valdes et al. 2007). A shift in zooplankton assemblages, with the distribution of warm water species being shifted northwards as the more northern waters warm up and the cold water ones receding to more northerly areas is particularly evident (Beaugrand et al. 2002, Beaugrand 2005). A similar change in distribution of fish species has been observed in Icelandic waters (Astthorsson and Palsson 2006). With all this in mind it is of particular interest to address if similar biogeographical changes in distribution and composition are taking place in the zooplankton communities around Iceland.

The main aim of this paper is thus to answer the following two questions:

1) How are the zooplankton communities south and north of Iceland influenced by environmental factors?

2) Has the community structure changed with time, and if so how is the change related to environmental factors?

Materials and methods

As stated in the introduction, zooplankton sampling north of Iceland started in the 1960s, while in the south in the 1970s. However, only a part of the sampled material has been analyzed with respect to species composition. In this paper we only deal with this material, namely samples that have been collected since 1990 on two transects, one in the north (Siglunes, 8 Stns), and the other in the south (Selvogsbanki, 5 Stns) (Figure 1). The transects were occupied from mid to end of May in all years.

In 1990 and 1991 the zooplankton samples were collected with a standard Hensen net $(0.42 \text{ m}^2 \text{ mouth area, } 200 \,\mu\text{m} \text{ mesh size})$, while after that all the zooplankton samples were collected using a WP2 net $(0.25 \text{ m}^2 \text{ mouth area, } 200 \,\mu\text{m} \text{ mesh size})$. The nets were towed from 50 m and to the surface with a speed of ~1 m s⁻¹. As the bottom depth on the shallowest station on the Selvogsbanki transect is only 46 m, the net could only be towed from c. 40 m depth there. The volume of water filtered by the net was measured with HydroBios flowmeters fitted in the mouth of the net.

The zooplankton samples were preserved in 4% neutralized formalin until analysis in the laboratory. As a rule, the entire sample was counted for the larger plankton (euphausiids, amphipods, mysids, decapods, chaetognaths and copepods >1 mm prosome length). Except when the sample was very small the remainder was then subsampled with a Motoda splitter (Motoda 1959) and an aliquot containing at least 500 individuals analyzed for species composition. Further, the copepods *Calanus finmarchicus, C. hyperboreus*, and *C. glacialis* were classed to developmental stages. Abundance (numbers per m⁻²) was

calculated using the data from the flowmeters and the depth of sampling.

At every station, vertical profiles of salinity and temperature were obtained with a CTD (Sea Bird Electronics SBE-9). Nutrient samples (~250 ml) were collected from 0, 20 and 50 m depth, and analyzed on board using a Chemlab Auto Analyzer. Further, water samples (1 or 2 l) were collected for chlorophyll *a* analysis from 10 and 30 m depth. The seawater samples were filtered onto GF/C glass fibre filters which were analyzed spectrophotometrically according to the method described by UNESCO/SCOR (1968).



Figure 1. Map showing the location of the time series stations. Inserted on the figure are the main ocean currents adapted from Valdimarsson and Malmberg (1997) and Stefánsson and Olafsson (1991). Red arrows: Atlantic Water, blue arrows: Polar Water,

In accordance with the zooplankton data, sampled between 0 and 50 m depth, an index for the environmental variables mentioned above was calculated for the same depth interval. Values for temperature, salinity and chlorophyll *a* were simply averaged down to 50 m depth. The measured nitrate concentrations (0-50 m) were, on the other hand, subtracted from the appropriate winter values for nitrate at each location (Olafsdottir 2006) and the difference integrated for each depth interval as an index of used nitrate for phytoplankton growth.

Multivariate methods were used to examine the distribution of zooplankton in relation to environmental variables. The data matrice included 68 zooplankton species or groups in 234 samples (~13 stations x 18 years). The environmental variables were temperature, salinity, chlorophyll *a*, year, used N, and the normalized winter (December-March) index of the North Atlantic Oscillation (NAO) obtained from the National Center for Atmospheric Research (http://www.cgd.ucar.edu/cas/jhurrell/indices.html). The analyses were carried out using the program Canoco v. 4.5 (ter Braak and Smilauer 2002). Prior to analyses the abundance data were transformed using ln(x+1) transformation (ter Braak and Smilauer 2002).

Principal Component Analysis (PCA) was used to examine relationships among the stations as to species composition. The data set may be viewed as influenced by a number of variables and the PCA will present the data as influenced by a reduced number of axes of greatest variability, thereby reducing the dimensionality of the data, and thus help in revealing the internal structure of data in an unbiased way. This is a linear model and it was preferred for the alternative unimodal model (Correspondence Analysis, CA) after a

test run of Detrended Correspondence Analysis (DCA), showing that the gradient length of the first axis was 2.248 standard deviations, indicating that most of the species had linear species-environment responses (ter Braak and Smilauer 2002).

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. The linear model (RDA) was preferred for the unimodal one (Canonical Correspondence Analysis, CCA), for the same reasons as described above for the PCA (ter Braak and Smilauer 2002, Verdonschot and ter Braak 1994).

Results

Figure 2 shows average sea surface (0-50 m) temperature and salinity at the Selvogsbanki and Siglunes transects during the latter half of May from 1990 to 2007. At both transects, these parameters fluctuated rather irregularly, especially at the Siglunes transect. At the Selvogsbanki transect, temperatures fluctuated between ~7.5-9.0°C with an increasing trend, from the beginning of the time series (~8°C) to its end (~8.5°C). At the Siglunes transect, temperatures were lower and fluctuated more than in the south, between ~0.5-5° C. In both environments, salinity fluctuated more or less in parallel with temperature (Figure 2).



Figure 2. Temperature (°C) and Salinity variations (means from 0-50 m) at Selvogsbanki (left panel) and Siglunes (right panel) transects from 1990 to 2007. The values are means from five and eight stations at the Selvogsbanki and Siglunes transects, respectively. Vertical lines show standard error. For location of transects see Figure 1. Linear regressions for the plots (only significant for the Selvogsbanki transect) are as follows: T = 0.0482Y - 88.088, $r^2 = 0.2699$, p=0.03 and S = 0.0121Y + 10.8, $r^2 = 0.4352$, p=0.03.

The long-term mean zooplankton abundance was higher south (Selvogsbanki transect, $\sim 160\ 000\ \text{individuals}\ \text{m}^{-2}$) than north of Iceland (Siglunes transect, $\sim 120\ 000\ \text{individuals}\ \text{m}^{-2}$) (Figure 3). South of Iceland (Selvogsbanki transect) zooplankton total abundance showed a peak in the beginning of the time series (around 1990) while a low was observed in 1992 (Figure 3). Peaks were also observed around 1993-1995 and in 2001 and 2005. Thus the time period between the zooplankton maxima on the Selvogsbanki transect was 4-7 years.

North of Iceland (Siglunes transect), relatively low values of zooplankton were observed in the beginning of the series, while maxima were observed in 1994, 1996, 2003 and 2005 (Figure 3).

Copepods were the most abundant group in both environments (60-80%) with *Calanus finmarchicus* as the most abundant species, and more dominating in the south (~20-70%) than north (~10-60%) (Figure 3). *Oithona* spp. was the second most abundant copepod in both environments (~20-40%).



Figure 3. Variations in total numbers (numbers m⁻², 0-50m), percentage of main zooplankton groups (% numbers, 0-50m) and percentage of copepods (% numbers, 0-50m) at Selvogsbanki (left panel) and Siglunes (right panel) transects from 1990 to 2007. The values are means from five and eight stations at the Selvogsbanki and Siglunes transects, respectively. Vertical lines show standard error.

In order to examine the relationship between the samples, a PCA was carried out (Figure 4). The PCA model used year, salinity, temperature, chlorophyll *a*, used N and NAO as supplementary variables. As one may expect the inter-annual variability in species composition to vary between regions, a year (as categorical) by area interaction term was introduced to the model, both as supplementary.

The first (PC1) and second (PC2) axes explained 17.2 and 10.8% of the observed variance in species composition, respectively (Figure 4). There was a clear grouping of stations into two groups with the main gradient being from stations located north of Iceland to stations south of Iceland, thus indicating a clear difference in community structure between the two regions. The results further indicated that while the year-to-year variation seems to be similar in both regions (the magnitude of the scatter is similar) the differences between south and north were mainly dictated by hydrography, with both the temperature and salinity being much lower in the north than south. There was no obvious unidirectional temporal trend in species composition as illustrated by the random arrangement of years on the ordination plot. In the species plot (Figure 4), only the species at the edge of the plot are shown, as they are the most important for indicating difference between sites, whereas the ones near the centre are of minor importance (ter Braak and Prentice 1988). From the first PCA axis we see a gradient from relatively high abundance of stages C2-C6 of *C. hyperboreus* (low PCA scores) at the northern stations to high abundances of *Podon leuckarti*, cirripedes, bivalves, polychaetes and *Centropages hamatus* (high PCA scores) at the southern stations. The variability along the second PCA axis is mainly driven by variability in the abundances of *Oncaea* spp., echinoderms larvaceans and the youngest stages of *Calanus* spp. (*Calanus* nauplii, and stages C2 and C3 of *C. finmarchicus*) and juvenile euphausiids (calyptopis stage).



Figure 4. Selvogsbanki and Siglunes transects combined. Results of Principal Component Analysis (PCA) of mesozooplankton abundance data (numbers m^{-2} , 0-50m) collected in May-June 1990-2007. For clarity, the left panel shows centroids of the nominal supplementary environmental variable (interaction of year by area), the centroid representing the (weighted) average location of samples collected in a given year in ordination space, i.e. along all ordination axes simultaneously. Other suplementary variables are shown with green arrows. The right panel only shows the species at the edge of the plot, i.e. those species that are most important for indicating difference between sites (ter Braak and Prentice 1988). In the left panel, the red and blue lines connect centroids for the Selvogsbanki, and Siglunes transects, respectively. The two axes of the PCA plot explain 28% of total species variation. For PCA model design refer to main text.

In order to test if the variability in community structure between years apparent in Figure 4 is significant, RDA analyses were performed for the two areas separately with years as categorical environmental variables, and stations as categorical covariables (thereby removing from the analysis the effect that stations may have on the abundance data). Monte Carlo permutation tests (499 permutations) were performed under reduced model (ter Braak and Smilauer 2002). The permutations wee unrestricted and the blocks defined by covariables (Stns).

For the southern area, the results showed a significant difference in species composition between years (p=0.002), with 36.6% of the variation in species composition being explained by year, and 19% explained by covariables (Stns). However, from the random arrangement of the data points no unidirectional temporal trend was evident (Figure 5). Similarly, for the northern area, 36.5% of the species composition could be explained by year, and 12% by the covariable (P=0.002), while there was no temporal trend in the

species composition as evidenced by the scatter of the data points showing no obvious unidirectional temporal pattern (Figure 5). For the southern area, the triplot further indicates a grouping of years into two categories, with taxa like *Calanus* nauplii, *Oncaea* spp., *Centropages hamatus* and echinoerms being relatively abundant in 1993, 1994, 2001 and 2005 (when used N values were also relatively high) and low in the other years. It is also noteworthy that in 1990 the juvenile stages of *C. finmarchicus* were relatively abundant (Figure 5). In the north, the grouping of years was less evident. However, the triplot indicates that the variability in species composition between years is mainly dictated by the variability in the relative abundance of *C. finmarchicus*, *Oithona* spp., larvaceans and echinoderms (Figure 5).



Figure 5. RDA ordination plot of the centroids of the nominal environmental variable year (red triangles). Taxa with <5 fit value to the first axis are not shown (ter Brak and Smilauer 2002). Supplemetary environmental variables not influencing the ordination are shown in green. The two axes of the RDA plot explain 38.9% and 43% of the explainable variation for the Selvogsbanki and Siglunest transects, respectively. For RDA model design see text.

To test formally for temporal trend (unidirectional) in the data, RDA analyses were applied for the two areas separately, with year as continuous environmental variable and stations as categorical covariable. Monte Carlo permutation tests (499 permutations) were used under reduced model restricted for split-plot design with years as split-plots and stations as whole plots (ter Braak and Smilauer 2002). No permutations were applied on whole plot levels, but freely exchangeable permutations dependent across whole plots were performed on split-plot levels. For both areas, no temporal trends were detected in species composition (Monte Carlo permutation tests, p>0.2).

In order to test statistically for what is causing the differentiation in species composition between years, the RDA analyses were carried out with temperature, salinity, chlorophyll *a*, used N and NAO as environmental variables. Only environmental variables that significantly explained some of the variation were included in the model and the rest added to the plots as supplementary variables thus not influencing the analyses, The analyses were carried out for the two transects separately. For these analyses, Monte Carlo permutation tests (499 permutations) were performed restricted for a repeated measures design (i.e. split-plot design) with stations as the main plot factor (whole-plots) and years as the within plot factor (split-plots). Permutations were not performed for the main plot factor (stations), while permutations for time series were performed for the within plot factor (years) dependent across whole plots so as to account for possible autocorrelation in the time series data (ter Braak and Smilauer 2002).



Figure 6. Selvogsbanki transect. RDA triplot of species (black arrows) and environmental variables (red and green arrows). Red arrows significantly explain variation in species composition. Insignificant variables (green) are passive and do not influence the analysis. Taxa with <5 fit value to the first axis are not shown (ter Brak and Smilauer 2002). For the Selvogsbanki transect, the two axes of the RDA plot explain 100% of the explainable variation. For the Siglunes transect, Axis 1 of the RDA plot explains 100% of the explainable variation, the second axis being the first "residual" axis. For RDA model design see text.

For the southern transect (Selvogsbanki), the analysis showed that salinity and used N contributed significantly (p=0.05) to the year-to-year variation explaining 10.5% and 6.7%, respectively, of the variation (Figure 6). Environmental variables correlated with the 1st RDA axis described a gradient from stations with high salinity and low used N values at the negative end (oceanic) to stations with low salinity and high used N values at the positive end (coastal). At the negative end (high salinity) euphausiid eggs and were relatively abundant, whereas coastal species (*Evadne nordmanni, Podon leuckarti,* cirripedes, *Temora longicornis*, and *Centropages hamatus*) were relatively abundant at the positive end (low salinity, high values of used N).

For the northern area (Siglunes transect), only temperature contributed significantly (p=0.03) to the year to year variation in species composition explaining 9.5% of the variation (Figure 6). In the northern area, juvenile stages of *C. finmarchicus* (nauplii and C1-3) and euphausiids (eggs and nauplii) were relatively abundant when temperature was high, whereas amphipods and *Calanus hyperboreus* were more abundant with lower temperatures.

Discussion

The long-term mean zooplankton abundance was higher south than north of Iceland (Figure 3). This is in line with previous findings with the mean annual biomass in the

surface layers being more than two times higher in the Atlantic Water south of Iceland than in the subarctic waters north of the island (Gislason 2002). As discussed by Gislason (2002), this may possibly be reflecting the higher production of zooplankton in the warm waters south of Iceland as compared to the relatively colder waters off the north coast.

There was a clear difference in community structure between the two regions, with relatively high abundance of stages C2-C6 of *Calanus hyperboreus* at the northern stations and high abundances of *Podon leuckarti*, cirripedes, bivalves, polychaetes and *Centropages hamatus* at the southern stations (Fig. 4), whereas *C. finmarchicus* and *Oithona* spp, are dominant in both regions. Similarly, previous investigations have shown the overall dominance of *C. finmarchicus* in Icelandic waters, with species of arctic origin being relatively abundant in the northern regions and species with coastal affinities on the southern shelves (Jespersen 1940; Astthorsson et al. 1983; Gislason and Astthorsson 2004).

The results further indicated that while the year-to-year variation seems to be similar in both regions (Figures 3,4), the differences between south and north were mainly dictated by hydrography, which accords with previous findings (Astthorsson and Gislason 1995).

Even though both regions showed a significant difference in species composition between years, no unidirectional temporal trend in species composition could be detected for neither transect (Figure 5). Thus, in spite of the general warming of surface waters south of Iceland, no parallel zooplankton community change could be detected there. North of Iceland, the warming of surface waters is not as evident as in the south (Figure 2), so the lack of unidirectional zooplankton community change is not as surprising for that area. However, these findings are at odds with what Beaugrand et al. (2002) found for a wider region of the north Atlantic, namely that with increasing regional sea temperatures in recent decades, extensive biogeographical shifts of the zooplankton communities have taken place in the North Atlantic basin, with species of warmer-water affinities having moved northwards. Zooplankton populations around Iceland are being influenced by influx of populations both from the north and south and it may be hypothesized that in the long-term this could lead to a greater stability of the zooplankton populations around Iceland as compared to other marine ecosystems that may depend more on one main offshore source of animals.

For the southern transect (Selvogsbanki), salinity and used N contributed significantly to the year-to-year variation in zooplankton community structure (Figure 6). Particularly evident was that low salinity values and high used N values were associated with high abundance of coastal species (Figure 6). Used N is probably a more conservative index of phytoplankton growth than chlorophyll *a*, high values of used N indicating that substantial phytoplankton growth has taken place. Thus the results presented here indicate that low salinity is associated with relatively high phytoplankton growth (Figure 6). This accords with the findings of previous studies showing that southwest of Iceland the growth and development of phytoplankton are heavily influenced by freshwater efflux from rivers (Gudmundsson 1998). The growth of phytoplankton and key zooplankters are closely related, and the present results thus demonstrate that the year-to year variability in zooplankton community structure southwest of Iceland is related to timing and magnitude of the primary productivity, which are in turn heavily influenced by freshwater efflux from rivers.

For the northern area (Siglunes transect), only temperature contributed significantly to the year-to-year variation in species composition, with juvenile stages of *C. finmarchicus* and euphausiids being relatively abundant when temperature is high, whereas amphipods and

Calanus hyperboreus were more associated with lower temperatures (Figure 6). The waters north of Iceland are characterized by large hydrographic fluctuations, which depend largely on the influences of northerly and southerly winds north of the island (Stefánsson 1962, Stefánsson and Gudmundsson 1969, Jonsson 1992, Olafsson 1999). Astthorsson and Gislason (1995, 1998) showed that these hydrographic variations do influence the productivity of the zooplankton north of Iceland, with zooplankton biomass being almost two times higher in warm years than in cold years. As discussed by Astthorsson and Gislason (1995, 1998) the reason for this may be the better feeding conditions of the zooplankton due to increased primary production, advection of zooplankton with the Atlantic Water from the south, and faster temperature dependent growth of the zooplankton in warm years. The present results of a relatively high incidence of juvenile stages of *C. finmarchicus* and euphausiids when temperatures are high indicates that recruitment of these two important zooplanktonic groups is indeed relatively high in warm years.

Several workers have successfully linked changes in the abundance and distribution of plankton to the North Atlantic Oscillation (NAO) (e.g. Planque and Froementin 1996, Pershing et al 2004, Hays et al. 2005). It was therefore somewhat surprising that no significant effect of NAO on interannual zooplankton community structure off Iceland was detected in the present study. The reason may be related to the fact that Iceland is at one end of the NAO dipole. In this connection it may be mentioned that Olafsson (1999) found no relationship between the frequency of northerly and southerly winds north of Iceland on one hand and the NAO-index on the other. He concluded that hydrographic variability north of Iceland could not be explained by the NAO index, but that the variability was rather related to regional meteorological conditions off the north coast.

To summarize, the analyses presented here show a clear difference in zooplankton community structure south and north of Iceland, mainly determined by hydrography. South of Iceland, long term changes in zooplankton composition are mainly dictated by salinity and used N, whereas north of Iceland temperature is most important. In the south, the species or groups that are most strongly associated with the variables affecting the year-to-year variability are coastal species (*Acartia, Temora*, cladocerans), whereas in the north juvenile stages of oceanic groups (*C. finmarchicus* and Euphausiids) have a parallel position. Thus suggesting that long term variability in zooplankton abundance and community structure is to a considerable degree affected by coastal processes south of Iceland and oceanic ones in the north. Finally, no unidirectional trend was observed in zooplankton community structure, neither in north or south.

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