Original Article

Long-term changes in abundance of *Calanus finmarchicus* south and north of Iceland in relation to environmental conditions and regional diversity in spring 1990–2013

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A 24-year time series of the abundance of *Calanus finmarchicus* from two standard sections differing in hydrographical conditions (Atlantic Water south of Iceland, Subarctic Water north of Iceland) was examined in relation to hydrography, phytoplankton dynamics, and large-scale climatic forcing (North Atlantic Oscillation, NAO). In the sea area around Iceland, *C. finmarchicus* is the most abundant mesozooplankter. The long-term variations were evaluated using multivariate statistics, principal component analyses, redundancy analyses (RDA), and principal response curves. Both south and north of Iceland, significant (RDA, $p < 0.05$, Monte-Carlo permutation tests) fluctuations in abundance and stages structure of *C. finmarchicus* between years were observed. The variations were, however, not in tune in south and north, indicating that the *C. finmarchicus* abundance may be influenced by different forcing factors in the two regions. South of Iceland, the analyses failed to find an effect of any of the environmental variables tested, whereas in the north the year-to-year variability was related to freshwater thickness west of Iceland and temperature north of the island (RDA, $p < 0.05$, Monte-Carlo permutation tests), indicating that advection of animals with currents from the south is important. In neither of the two regions was it possible to detect a unidirectional temporal trend in abundance of *C. finmarchicus* (RDA, $p < 0.05$, Monte-Carlo permutation tests). Based on a comparison with time series from nearby areas and the lack of a relationship with NAO, it is hypothesized that the growth and development of *C. finmarchicus* in Icelandic waters is more affected by local conditions than large-scale climatic forcing.

Keywords: *Calanus finmarchicus*, icelandic waters, long-term changes, north atlantic.

Introduction

The oceanic area around Iceland is divided into different oceanic regions or hydrographic domains by submarine ridges, upon which Iceland rests. The main division is formed by the Greenland-Iceland-Scotland Ridge that acts as a barrier that constrains flow between the relatively warm waters to the south and west of Iceland and the cold waters to the north and east of Iceland. Oceanographically, as well as biologically, the waters south and north of Iceland are therefore very different (Stefansson and Olafsson, 1991; Astthorsson and Gislason, 1995; Gudmundsson, 1998; Valdimarsson and Malmberg, 1999; Gislason *et al.*, 2009).

The Marine Research Institute's monitoring programme on the state of the marine ecosystem around Iceland started in the 1960s with sampling at transects to the north and east of the island. In the 1970s, transects were added to the south and north of Iceland. Standardized methods for sampling and analysis are applied with an annual cruise that starts in mid-May and ends in early June. The present study is based on material sampled on two transects, i.e. a part of these investigations.

Several earlier studies have addressed the results of the hydrography, chemistry and phytoplankton monitoring (e.g. Stefansson and Olafsson, 1991; Malmberg and Kristmannsson, 1992; Gudmundsson, 1998; Valdimarsson and Malmberg, 1999). Previous studies on zooplankton have mainly focused on spatial and long-term variability in biomass and relative composition (Astthorsson *et al.*, 1983, 2007; Astthorsson and Gislason, 1995), while Gislason and Astthorsson

(2004) and Gislason *et al.* (2009) reported on the spatial and long-term distribution patterns of zooplankton communities around Iceland in spring.

In Icelandic waters, as elsewhere in the North Atlantic, the copepod *Calanus finmarchicus* dominates the zooplankton in terms of numbers (Astthorsson *et al.*, 1983; Gislason, 2005). Being primarily a herbivore, it occupies a key trophic position between the phytoplankton and higher levels, such as fish larvae and pelagic fish. Its role in the diet of fish larvae has stimulated several studies on its ecology in Icelandic waters (Thorisson, 1989; Astthorsson and Gislason, 1999; Gislason and Astthorsson, 2000; Gislason *et al.*, 2000; Gislason, 2005). Investigations on the biomass distribution and egg production rates of *C. finmarchicus* around Iceland indicate that the warmer waters of the south and west coasts provide a more favourable environment for the growth and development of *C. finmarchicus* than the colder waters off the north coast (Gislason, 2005). In addition to this spatial variability, long-term monitoring of zooplankton around Iceland has shown that the biomass of zooplankton fluctuates markedly from 1 year to another. While there are no previous studies specifically addressing long-term changes of *C. finmarchicus* in Icelandic waters, it has been suggested, based on the dominant contribution of *C. finmarchicus* to the biomass, that the observed variations in total biomass may to a large extent reflect changes in the abundance and productivity of this species (Astthorsson and Gislason, 1995; Beare *et al.*, 2000).

The present paper seeks to remedy the lack of long-term studies on *C. finmarchicus* in Icelandic waters by presenting data on the interannual variation in abundance and stage composition of *C. finmarchcius* 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. The research questions asked are if the year-to-year variability in abundance and stage structure of *C. finmarchcius* is significant in the two regions, if the variability is in tune in south and north, if there is a unidirectional long-term trend in abundance, and finally how environmental factors are affecting the variability.

Material and methods
Zooplankton sampling

Although sampling for zooplankton monitoring began in the 1970s, to date, only samples collected since 1990 on Selvogsbanki transect in south (5 stations) and Siglunes transect in north (8 stations) have been analysed with respect to species composition (Figure 1). In this paper, we deal with this material.

In 1990 and 1991, the zooplankton samples were collected with a standard Hensen net (0.42 m^2 mouth area, 200 μm mesh size), while after that all the zooplankton samples were collected using a WP2 net (0.25 m^2 mouth area, 200 μm mesh size). The nets were towed from 50 m and to the surface with a speed of ~45 m min^{-1}. As the bottom depth on the shallowest station on the Selvogsbanki transect is only 46 m, there the net could only be towed from c. 40 m depth. 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. Samples containing <400 *C. finmarchicus* were counted from whole samples. Otherwise, they were subsampled with a Motoda splitter (Motoda, 1959) and an aliquot containing at least 200 individuals of *C. finmarchicus*
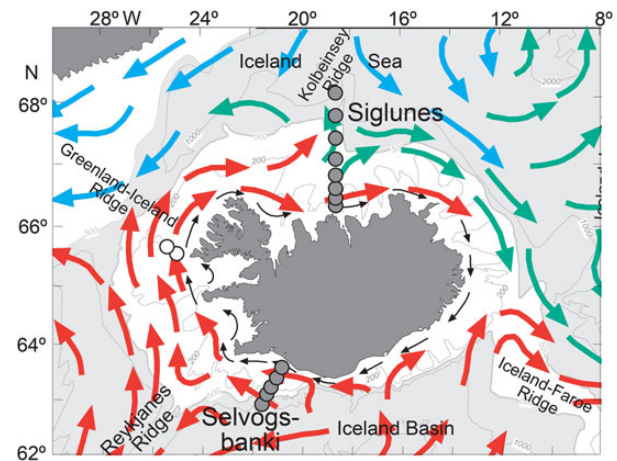

Figure 1. Map showing the location of the time-series stations. Inserted on the figure are the main ocean currents adapted from Valdimarsson and Malmberg (1999) and Stefansson and Olafsson (1991). Red arrows: Atlantic Water; blue arrows: Polar Water; green arrows: mixed water. The stations at are indicated by grey dots. Names of transects is also given. The stations used for the calculation of freshwater thickness are indicated by white dots.

counted and classed to developmental stages. Abundance (numbers per m^3) was calculated using the data from the flowmeters.

Environmental conditions and phytoplankton

At every station, vertical profiles of salinity and temperature were obtained with a CTD (Sea Bird Electronics SBE-9). Water samples for analysis of nutrients were collected from 0, 20, and 50 m depth, and analysed on-board using a Chemlab Auto Analyser. Further, samples were collected for chlorophyll *a* analysis from 10 and 30 m depth. The samples were filtered on-board onto GF/C glassfibre filters and stored in freezer until extracted in 90% acetone and analysed spectrophotometrically according to the method described by UNESCO/SCOR (1966), or fluorometrically (Holm-Hansen *et al.*, 1965).

In accordance with the data on *C. finmarchicus*, sampled between 0 and 50 m depth, indices for the environmental variables mentioned above were 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 subtracted from the appropriate winter values for nitrate at each location (Olafsdottir, 2006) and the difference integrated for each depth interval as a measure of nitrate used for phytoplankton growth. An index of freshwater thickness, used as a measure of the strength of the coastal current and the amount of freshwater in the coastal-zone west of Iceland, was calculated based on data from two stations off the west coast (Olafsson, 1985). The normalized winter (December–March) index of the North Atlantic Oscillation (NAO) was obtained from the National Center for Atmospheric Research (http://www.cgd.ucar.edu/cas/jhurrell/indices.html).

Statistical analyses

One-way analysis of variance (ANOVA), with subsequent *post hoc* Tuckey's–Kramer tests when ANOVA results were significant ($p < 0.05$), was performed to test for differences in long-term

mean of total abundances between transects and between stations within transects. The ANOVA used $\log(x + 1)$ transformed data.

Principal component analyses (PCA) were carried out with the double purpose of examining relationships between the samples from the two sites, and identifying major long-term changes in total abundance of *C. finmarchicus* for the period 1990–2013. PCA is a linear unconstrained ordination model and it was preferred for the alternative unimodal model (correspondence analysis) after test runs of detrended correspondence analyses, showing that the gradient length of the first ordination axis was <2.3 SD always, indicating that *C. finmarchicus* had linear species-environment responses (ter Braak and Smilauer, 2002). As stated above, the data were sampled during the last days of May or during the first days of June. Nevertheless, there may be some variability due to differences in sampling dates from 1 year to another. In attempt to account for the possible effects of this on the analysed results, we included the day number of the year (day of the year) as a categorical covariable in the PCAs. Two sets of PCAs were run:

(i) To examine relationships among samples, the analysis was applied to the original data matrix of stage resolved *C. finmarchicus* abundance data (numbers per m^3) for the period 1990–2013 (matrix of 7 copepodite stages × 312 samples). There were seven instances, when a station could not be visited due to sea ice or bad weather. Values for these stations were obtained by interpolation using averages of values obtained at the same station the year before and the year after.

(ii) To extract the dominant pattern of long-term variability in total abundance, the sum of all stages was calculated for each year and the data analysed separately for the Selvogsbanki transect (matrix of 5 stations × 24 years) and the Siglunes transect (8 stations × 24 years).

Redundancy analysis (RDA) was used to model the relationship between the relative stage composition of *C. finmarchicus* and environmental variables. The RDA was run on the original dataset of seven copepodite stages (numbers per m^3) × 312 samples for the period 1990–2013. RDA is an ordination technique in which the ordination axes are constrained by linear combinations of environmental variables. The linear model (RDA) was preferred to the unimodal one (canonical correspondence analysis) for the same reasons as described above for the PCA (Verdonschot and ter Braak, 1994; ter Braak and Smilauer, 2002). All significant testing was assessed by Monte-Carlo permutation tests (999 permutations) under reduced model (ter Braak and Smilauer, 2002), and variables were only retained in the analysis if they explained a significant ($p < 0.05$) amount of variance in the *C. finmarchicus* data. Three sets of RDA were run, separately for the southern and northern areas:

(1) To test if there was a significant variability in stage composition of *C. finmarchicus* between years, RDA was performed with years as categorical environmental variable, and stations as categorical covariable (thereby removing from the analyses the effect that stations may have on the stage composition data). The Monte-Carlo permutations tests were performed within the blocks defined by the covariables (stations).

(2) To test for temporal trends (unidirectional change) in the data, RDA analyses were applied, with years as continuous environmental variable and stations as categorical covariable. Monte-Carlo permutation tests were restricted for split-plot design with stations as main-plots and years as split plots. No

permutations were applied on the main-plot levels, but freely exchangeable permutations dependent across main-plots were performed on the split-plot levels. This design ensures that the comparison is made for each station separately for the whole series 1990–2013.

(3) To test for what is causing the difference in stage composition between years, the RDA analyses were carried out with temperature, salinity, chlorophyll *a*, used N, NAO, and freshwater thickness as environmental variables. As in the last previous analysis, The Monte-Carlo permutation tests were performed restricted for split-plot design with stations as a categorical covariable defining the main-plot factor and years as the split-plot factor, thus ensuring that the year-to-year comparison is made for each station separately. Permutations were not performed for the main-plot factor (stations), whereas permutations for time series were performed for the split-plot factor (years) dependent across main-plots so as to account for possible autocorrelation in the time series data (ter Braak and Smilauer, 2002).

The principal response curve (PRC) method (van den Brink and ter Braak, 1999), which is a special case of RDA, was used to focus on how the stage structure of *C. finmarchicus* varied between sites and from year to year. The PRC method offers a technique to analyse and visualize temporal variability in compositional data as well as providing information on the groups (stages of *C. finmarchicus*, in the present study) that contribute to the observed variability (van den Brink *et al.*, 2008). The sampling years were put into the model as a set of covariables, and the interactions between sites and years were introduced as explanatory variables (van den Brink *et al.*, 2008). The PCR diagram plots the principal components of the variance explained by treatments (sites) against time (year) using a reference time series (Selvogsbanki transect, in present study) (van den Brink and ter Braak, 1999).

The multivariate analyses were carried out using the program Canoco v. 5.0. Before analyses, the abundance data were transformed using $\log(x + 1)$ transformation (ter Braak and Smilauer, 2002).

Results

Long-term sea surface (0–50 m) temperature variations for the Selvogsbanki and Siglunes transects during latter half of May is shown in Figure 2. Irregular fluctuations are apparent on both transects, and especially so for the Siglunes transect. At the Selvogsbanki transect, temperatures fluctuated between ∼6.5 and 9.0°C with an increasing trend, from the beginning of the time series (∼7.5°C) to its end (∼8.5°C). At the Siglunes transect, temperatures were lower, between ∼0.5 and 6°C.

Both north and south of Iceland, the average abundance of *C. finmarchicus* fluctuated greatly between years (Figure 3). South of Iceland, the highest values were observed in 1990 and 2008, whereas in the north, abundance was greatest in 1993 and 2005.

The long-term mean of *C. finmarchicus* abundance was more than two times higher in south (Selvogsbanki transect, ∼1600 individuals m^{-3}) than north of Iceland (Siglunes transect, ∼700 individuals m^{-3}) (Figures 3 and 4) ($p < 0.05$, one-way ANOVA). In south of Iceland (Selvogsbanki transect), the abundance appeared higher at Station 2 than at the other stations (Figure 4); however, the difference in mean numbers between the stations was insignificant according to one-way ANOVA test ($p > 0.05$). On the other hand for the Siglunes stations, north of
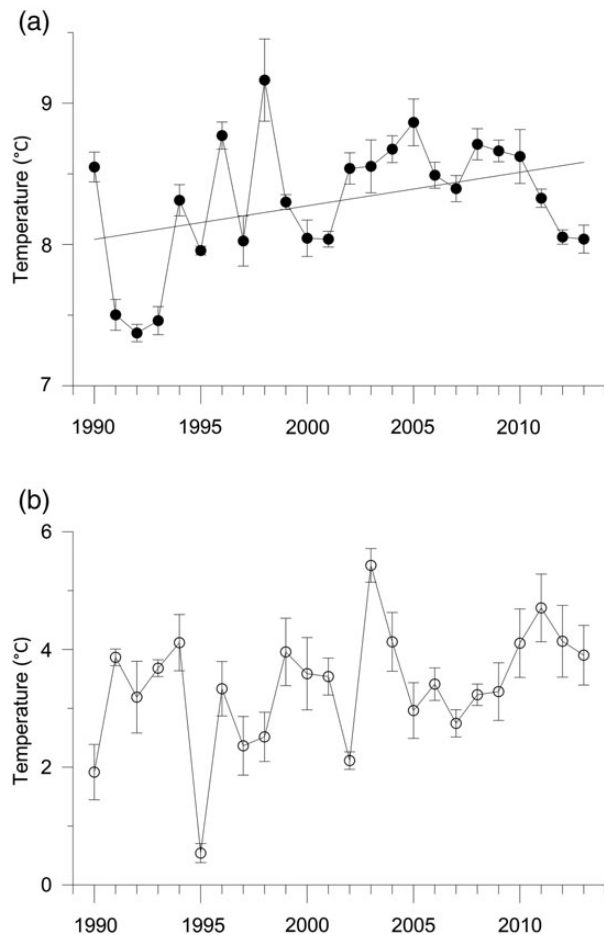
Figure 2. Temperature (°C) variations (means from 0 to 50 m) at Selvogsbanki (a) and Siglunes (b) transects during latter half of May from 1990 to 2013. The values are means from five and eight stations at the Selvogsbanki and Siglunes transects, respectively. Vertical lines show standard error. For location of transects, see Figure 1. Linear regression (only significant for the Selvogsbanki transect) is: $T = 0.024Y - 39.2$, $r^2 = 0.14$, $p = 0.05$.

Iceland, the ANOVA showed a significant difference in mean abundance along the transect ($p < 0.001$). A subsequent *post hoc* Tuckey−Kramer test showed that abundance was significantly lower at Station 1 than at Station 3, and at Station 8 compared with stations 2, 3, 4, and 6, whereas the test showed no difference in mean abundance between Stations 5 and 7 and any of the other stations.

In both regions, most of the population consisted of the youngest copepodite stages (C1−3, Figures 3 and 4). South of Iceland, on average ∼70% of the population were young stages (C1−3), except closest to land (∼90%). North of Iceland the proportion of young copepodite stages was even higher (>80%), except at the stations closest to land (Station 1, ∼70%) and farthest from the shore (Station 8, 30%).

The PCA analysis carried out to examine relationships in abundance and stage structure of *C. finmarchicus* among stations showed a major separation between stations in south and north (Figure 5). The first (PC1) and second (PC2) axes accounted for 51.2 and 27.1% of the observed variance in stages composition of *C. finmarchicus*,

respectively (Figure 5). The covariable (day of the year) only contributed to a small proportion of the total variance (1%). The main gradient along the first PC axis separated stations located to the south of Iceland (on the left side in Figure 5) from those located to the north (on the right side in Figure 5). Station 8 in north (N8) and Station 2 in south (S2) are special and separated from the others by the gradient along the second (PC2) axis, with larger numbers of the older stages (C5, C6 females and males). The number of all stages tended to increase towards the south, thus confirming what is illustrated by Figures 3 and 4. The results further indicated that the difference between south and north was mainly dictated by temperature and salinity as both were much higher in south than north (Figure 5, see also Figure 2).

To analyse the major long-term changes in total abundance of *C. finmarchicus*, two PCAs were performed, one for each dataseries in south (Selvogsbanki) and north (Siglunes).

In south of Iceland (Selvogsbanki), the first axis (PC1) of the PCA accounted for 64.4% of the total variance of the data (Figure 6). The second axis (PC2) explained much less variability (16.5%). The first axis represented a gradient from low (low PCA scores) to high (high PCA scores) abundance of *C. finmarchicus* (Figure 6). The contribution of the covariable (day of the year) to the total variance was low (6.1%). From the scatter of the stations on the ordination plot, the variability was similar at all stations (the lines all point in the same direction and they are all closely related to the first axis). There was no obvious unidirectional temporal trend in abundance of *C. finmarchicus* as illustrated by the random arrangement of years on the ordination plot (Figure 6).

The right panel in Figure 6 shows the year-to-year variability of the first principal component as a measure of abundance of *C. finmarchicus* in south of Iceland (Selvogsbanki transect). Values of the first principal component were high (indicating high abundance of *C. finmarchicus* at all stations on Selvogsbanki transect) at the beginning of the time series (1990). Relatively high values were also observed around 1994−1995, 2000−2001, 2006, and 2008−2009. The lowest values (low abundance of *C. finmarchicus*) were observed in 1992, 1997, and 2003. As judged by the 3-year running means, the time period between maxima in *C. finmarchicus* abundance on Selvogsbanki transect was ∼5−8 years.

A corresponding PCA for the Siglunes transect, north of Iceland, revealed similar result as described for the south, i.e. most of the variation in abundance of *C. finmarchicus* was represented by the first axis (PC1) of the PCA (43.6%) (Figure 7). However, in contrast to the southern area where the second axis (PC2) only explained a small part of the variability, the second axis for the northern time series explained a much greater fraction of the variability (25.3%). Furthermore, the ordination shows that the pattern of long-term variability was quite similar at stations 2−7, i.e. mainly represented by a gradient along the first axis from low (low PCA scores) to high (high PCA scores) abundance of *C. finmarchicus* (Figure 7). The variability at Station 1 was represented by both axes almost equally (Figure 7), whereas the long-term variability at Station 8 was more closely associated with the second axis of the PCA than to the first one (Figure 7). The second principal component can thus be regarded as the best possible single representation of the long-term changes of *C. finmarchicus* at Station 8, low scores indicating high abundance of *C. finmarchicus* at Station 8 and low abundance at Station 1 and *vice versa*. As in the southern region, the contribution of the categorical covariable day of the year to the total variance was low (4.5%), and there was no obvious pattern in the arrangement of years on the ordination plot, suggesting
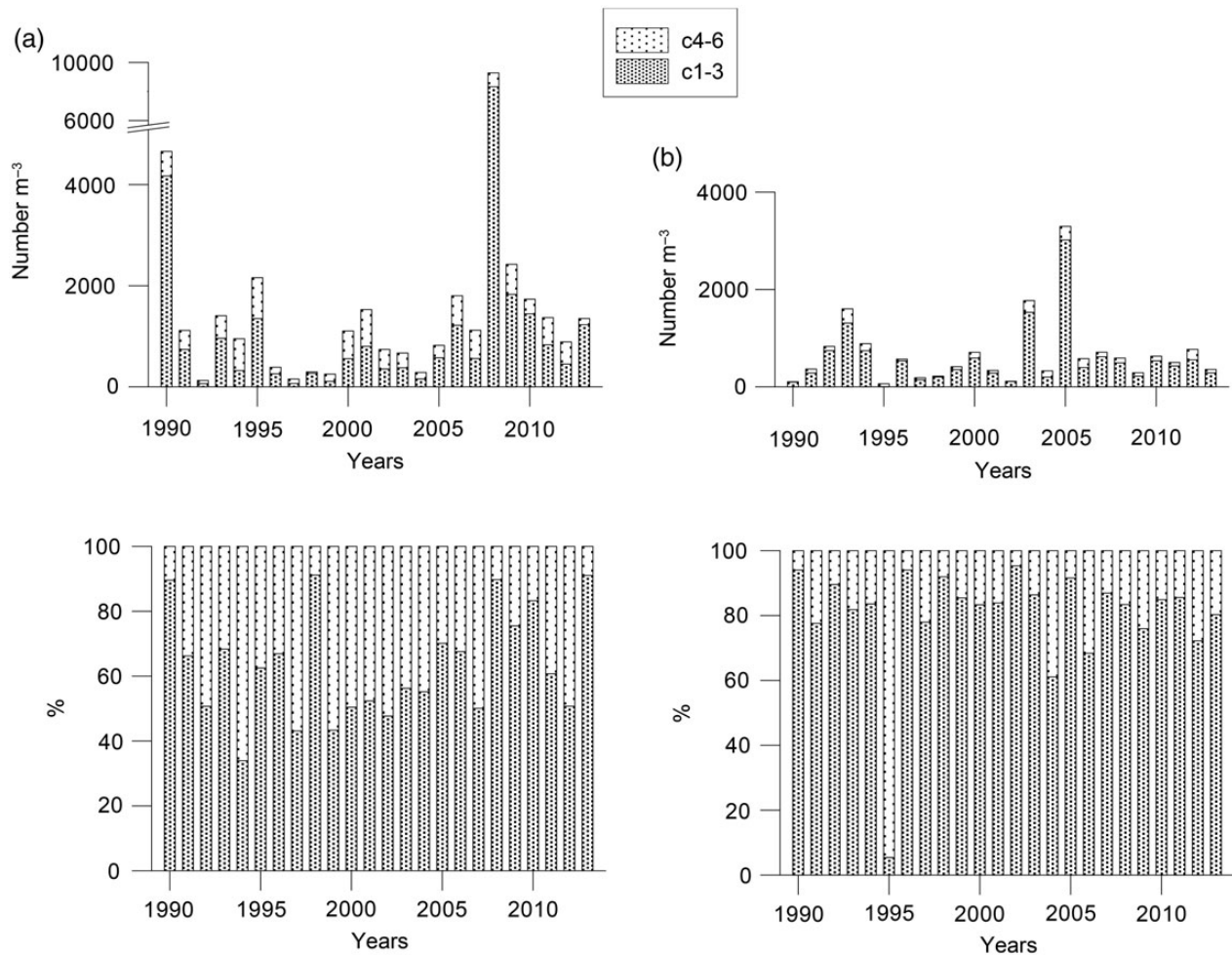
Figure 3. Interannual variation in average abundance (numbers per m³) and percentage compositon of *C. finmarchicus* at Selvogsbanki (a) and Siglunes (b) transects in spring.

that a unidirectional temporal trend in abundance was absent from the time series (Figure 7).

North of Iceland, the first principal component showed low values (indicating low abundance of *C. finmarchicus* at Stations 2–7) in 1995 and 2002, whereas the highest values (high abundance of *C. finmarchicus* at Stations 2–7) were observed in 1994, 2003, and 2005 (Figure 7a). As evaluated by the 3-year running means, ∼4–7 years passed between maxima in abundance.

The second principal component showed high values (high abundance of *C. finmarchicus* at Station 1) near the beginning of the time series (1991 and 1993), in 1998 and 2001–2002, whereas low values (high abundance of *C. finmarchicus* at Station 8) were observed in 1994–1997, 2000, 2003, and near the end of the series (2011 and 2013, Figure 7b). The station nearest to the coast (Station 1) and the one farthest from shore (Station 8) thus exhibited very different long-term variability, with numbers being generally high at Station 1 when they were low at Station 8 and *vice versa* (see also Figure 7).

For the southern area (Selvogsbanki), the RDA showed a significant difference in stage composition of *C. finmarchicus* among years ($p = 0.001$), with 54.9% of the total variance being explained by the explanatory variable year, and 1.8% by the covariable stations. However, from the random arrangement of the years on the

ordination plot no unidirectional temporal trend was evident (Figure 8a). The youngest copepodite stages (C1–4) were mainly associated with the first canonical axis of the RDA (high abundance on the left side on Figure 8), whereas the adults were mainly associated with the second canonical axis (high abundance on top).

For the northern area (Siglunes), variability between years in stage composition was also relatively high (53.1%) and significant ($p = 0.001$), and the variability explained by the covariables (stations) low in comparison (1.9%). As in the south, no unidirectional trend in stage structure was evident (Figure 8b). The first canonical axes describe a gradient from low abundance of all stages at the negative end to high abundance at the positive end.

The RDAs designed to test statistically for if there were temporal trends (unidirectional change) in the data and were unable to detect any temporal trend in stage composition of *C. finmarchicus* in either region ($p > 0.2$).

RDA performed to examine which factors were causing the year-to-year variability in stage structure of *C. finmarchicus* in the southern region (Selvogsbanki) failed to find a relationship between any of the explanatory variables tested (temperature, salinity, chlorophyll *a*, NAO, used N, and freshwater index) and stage structure of *C. finmarchicus* ($p > 0.05$) (Figure 9a). For the northern area (Siglunes), on the other hand, temperature and
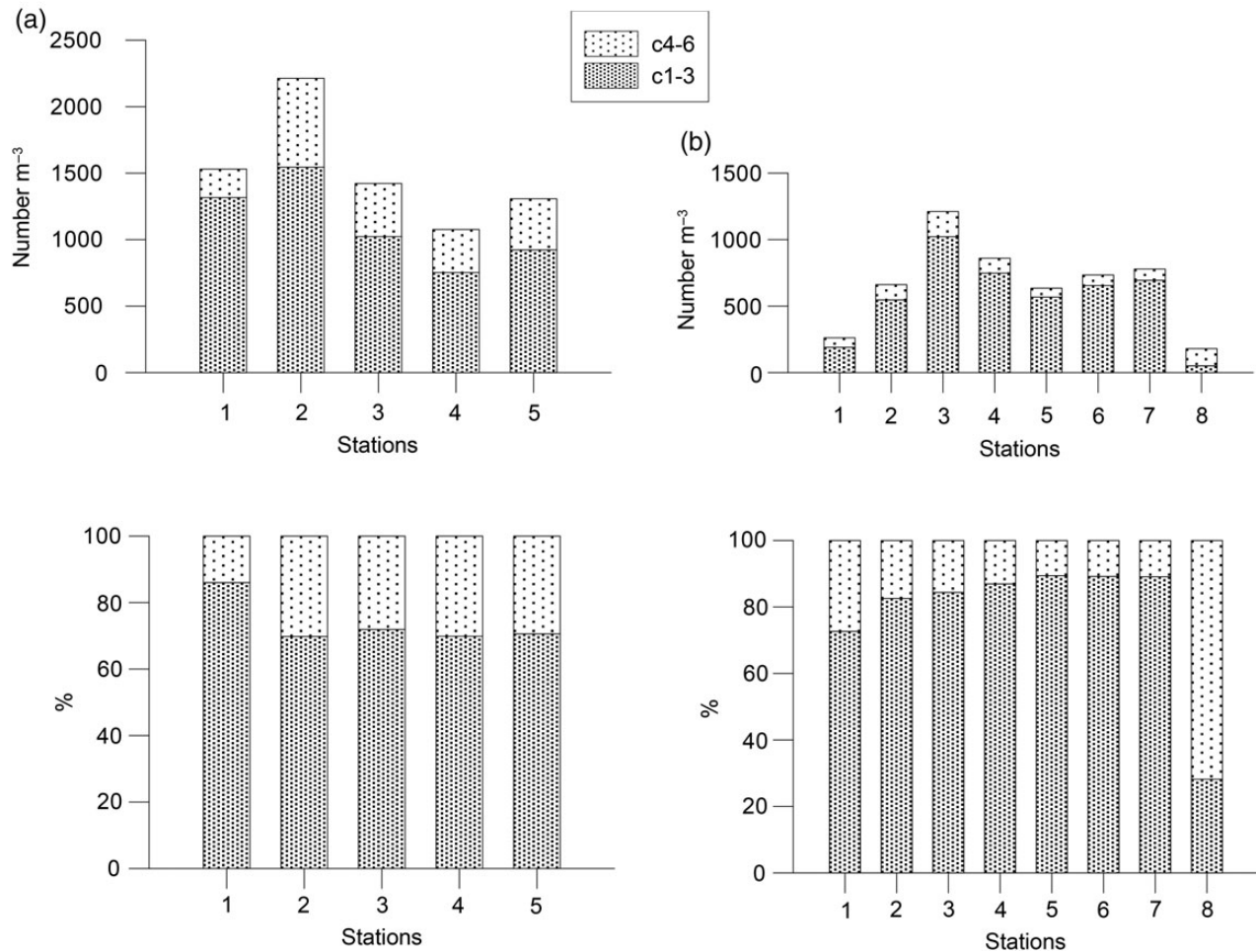
Figure 4. Average abundance (numbers per m^3) and percentage stage composition of *C. finmarchicus* along the Selvogsbanki (a) and Siglunes (b) transects in spring. The stations are counted from land.

freshwater index contributed significantly to the year-to-year variation in stage structure of *C. finmarchicus*, temperature explaining 21.5% ($p = 0.0004$), and freshwater 6.7% ($p = 0.0108$) of variation (Figure 9b), with high abundance of young copepodite stages at relatively high-temperature values and high abundance of copepodite stages C4−6 at relatively high freshwater index values. Although the stations are inserted on the plot as supplementary, thus not affecting the ordination, the plot nevertheless clearly indicates the different nature of Station 8, being characterized by low abundance of *C. finmarchicus* and low-temperature values (Figure 9b).

The first PRC 1 shows that the stage structure varies greatly between years (Figure 10). In most years, abundance of *C. finmarchicus* was lower in the northern region (Siglunes). In general, abundance of female *C. finmarchicus* was higher in north, whereas abundance of all other stages was higher in the south (Selvogsbanki) (Figure 10).

Discussion

The long-term mean total abundance of *C. finmarchicus* was more than twofold higher in the south than the north of Iceland (Figures 3 and 4). In line with this, the PCA plot for all stations shows increasing abundance of all stages of *C. finmarchicus* from north to south (Figure 5). This accords with previous findings as both biomass and secondary production is generally found to be much higher in the warm Atlantic waters to the south and west of

Iceland than in the colder waters off the north and east coasts (Gislason, 2005). It is reasonable to assume that the regional variability in biomass and secondary productivity of *C. finmarchicus* around Iceland is related to differences in primary productivity around the island. Long-term investigations around Iceland have shown that the average annual primary production is relatively high south and west of Iceland, and considerably lower north and east of the island (Thórdardóttir, 1994). This supports the suggestion of a bottom-up control of the productivity of *C. finmarchicus* in Icelandic waters, with primary production acting as an important factor influencing the productivity of the species.

Both south and north of Iceland, the large proportion of juvenile stages C1−3 in May (60−90%) indicate populations in vigorous growth during this time (Figures 3 and 4). In the north (Siglunes), the proportion of youngest stages was higher (∼80−90%) than in south (Selvogsbanki, ∼60−70%, Figures 3 and 4). Assuming that the reproduction of *C. finmarchicus* generally takes place at similar time in both regions (April and May) as suggested by previous seasonal studies (Gislason and Astthorsson, 1998; Gislason *et al.*, 2000; Gislason, 2005), this finding, of a lower proportion having developed to the more advanced stages, may indicate a slower development of the populations in the colder waters north of Iceland. The fact that the numbers of females were generally higher north of Iceland (Figure 10) may also indicate slower development in the

northern region. The fact that the sampling at Siglunes took place on average ∼8 days earlier than at Selvogsbanki may enhance the apparent difference in phenology north and south of Iceland. Low abundance and small proportion of juvenile stages observed at the outermost station of the Siglunes transect (N8, Figures 4 and 5) indicate low spawning activity of *C. finmarchicus* concurrent with the

Arctic influence. Noteworthy, is the very low percentage of young stages in 1995 (Figure 3), a year when temperatures were record low (Figure 2b), which may suggest low spawning activity in the cold water.

For the southern region (Selvogsbanki), the first principal component of the PCA, explaining almost two-thirds of the total long-term variability, identified a dominant pattern in long-term variability in abundance of *C. finmarchicus* that is more or less common for all stations along the transect (Figure 6). For the northern transect (Siglunes), the PCA isolated a dominant pattern of abundance variations common to all but two stations, ∼44% explainable by the first principal component (Figure 7). The two outlier stations in the north (Stations 1 and 8, Figure 1) may be assumed to be atypical for the shelve areas north of Iceland in general due to their location in either the most coastal (Station 1) or Arctic (Station 8) affected environments. For both the south and the north study areas, the long-term variability is characterized by lows and highs; however, the temporal sequencing of minima and maxima is not in tune in south and north (Figures 6 and 7a), suggesting that local factors rather than large-scale climatic ones are influencing the variability.

Although the stage structure of *C. finmarchicus* varied significantly from 1 year to another (Figure 10), no unidirectional trend could be detected for neither transect (Figures 6, 7, 8 and 10). This is somewhat surprising, at least for the southern area, where temperatures showed an increasing trend during the period of study (Figure 2). In the north, the warming is not as evident as in the south (Figure 2), although data from larger area north of Iceland show increasing temperatures from the mid-1990s there also (Valdimarsson *et al.*, 2012). As both egg production and feeding rates of *C. finmarchicus* are temperature dependent—with egg production of well-fed animals increasing at least until $10°C$ (Pasternak *et al.*, 2013) and feeding rates being at optimum at $11-12°C$ (Møller et al., 2012) so well within the temperature ranges observed here—one might expect that the temperature increase would affect abundance and development of *C. finmarchicus*. Both transects are, however, located at open shelf sites, where the
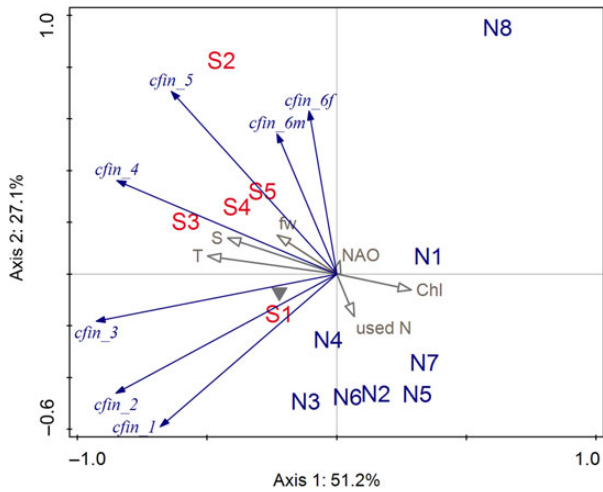

Figure 5. Selvogsbanki and Siglunes transects combined. PCA biplots of data on abundance of *C. finmarchicus* (numbers per m³) collected in May−June 1990−2013. PCA Selvogsbanki and Siglunes combined. *Calanus* stages are response variables. Supplementary variables: stations are categorical (Selvogsbanki 'S', Siglunes 'N', the stations are counted from land), and salinity (S), temperature (T), chlorophyll (Chl), NAO, used N and freshwater index (fw) are continuous. The arrows point in the direction of the steepest increase of the respective variable, and the length of the arrows shows the strength of the gradient. The angle between the arrows reflects their correlations. The first two axes of the PCA plot account for 78.3% of total variation in abundance of *C. finmarchicus*. For PCA model design, refer to main text.
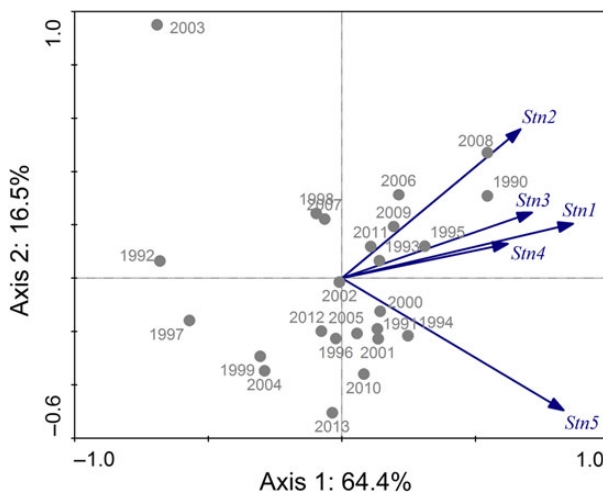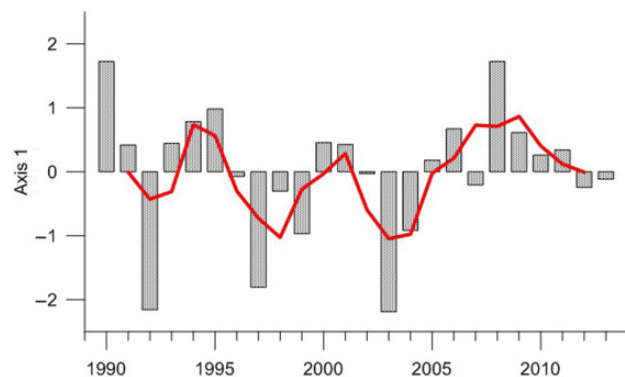

Figure 6. Selvogsbanki transect. PCA biplot of data on total abundance of *C. finmarchicus* (numbers per m³) collected in May−June 1990−2013 (left) and the year-to-year variability of the first principal components (right). The curved thick line shows 3 year running mean. The direction pointed by the arrows shows the direction of increasing abundance at the respective stations, and the length of the arrows shows the strength of the gradient. The angles between the arrows reflect their correlations. The first two axes of the PCA account for 80.9% of total long-term variation in total abundance of *C. finmarchicus*. For PCA model design, refer to main text.
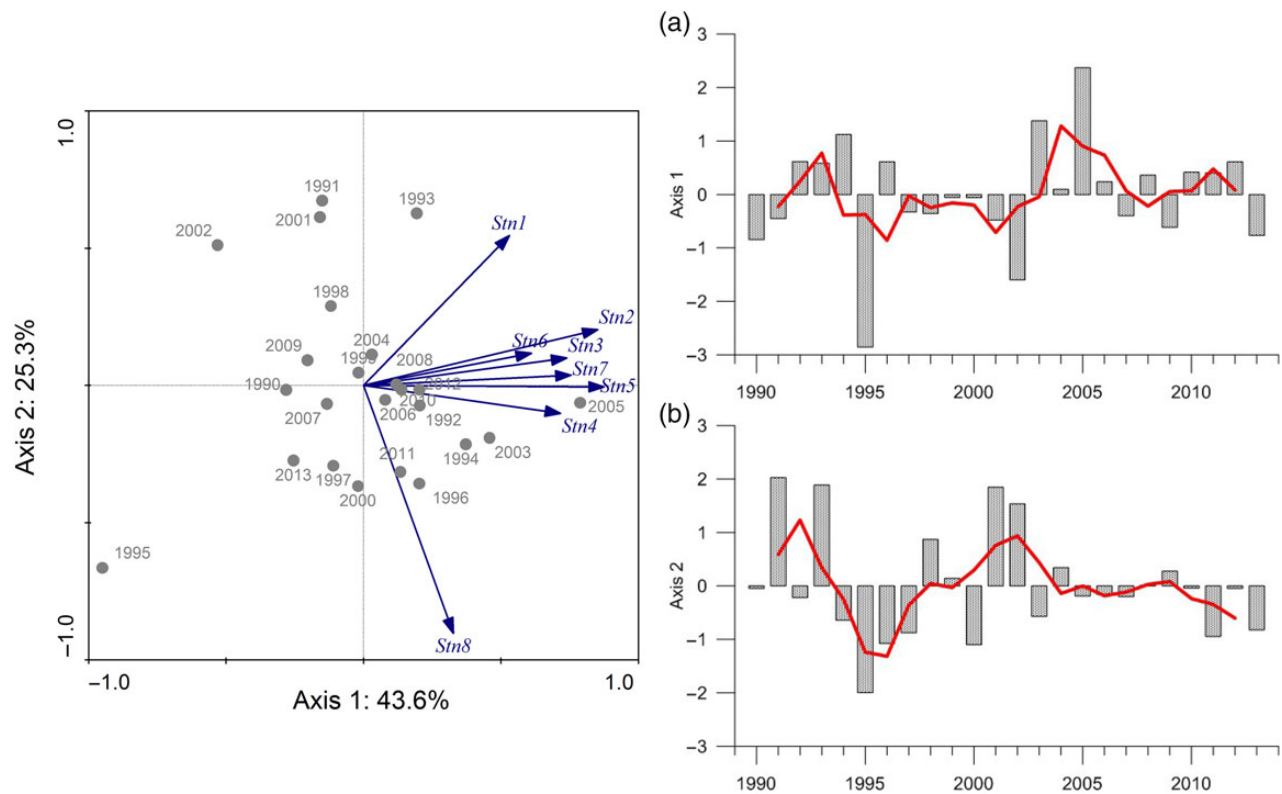
Figure 7. Siglunes transect. PCA biplot of data on total abundance of *C. finmarchicus* (numbers per m^3) collected in May – June 1990 – 2013 (left) and the year-to-year variability of the first (a) and second (b) principal components (right). The curved thick lines show 3 year running means. The direction pointed by the arrows shows the direction of increasing abundance at the respective stations, and the length of the arrows shows the strength of the gradient. The angles between the arrows reflect their correlations. The first two axes of the PCA account for 68.9% of total long-term variation in total abundance of *C. finmarchicus*. For PCA model design, refer to main text.

demography of *C. finmarchicus* is likely to be heavily influenced by advective processes. Under such circumstances, interpretation of data such as presented here may be difficult. It may also be of significance here, that due to the location of Iceland in the middle of the North Atlantic, between the main distribution centres of *C. finmarchicus* (Conover, 1988; Aksnes and Blindheim, 1996; Bucklin *et al.*, 2000; Sundby, 2000), the populations around Iceland may be influenced by influx of animals from them both. Future research should address the effects of advection on the growth and development of *C. finmarchicus* around Iceland

According to the RDA results from the southern area (Figure 9a), none of the explanatory variables tested could explain the observed year-to-year variation in abundance and stage structure of *C.finmarchicus*. Evidently, some other factors than tested here are more important in influencing abundance and distribution of *C. finmarchicus* in the Selvogsbanki region. One such factor might be predation. The Selvogsbanki transect is near the main spawning grounds of most of the commercially important Icelandic fish stocks. Eggs and juveniles of *C. finmarchicus* are known to be important food for the larvae and juveniles of fish as they are growing up (Thorisson, 1989) so predation from fish may well be contributing to the observed variability. Another factor could be onshore advection of animals from the south which is difficult to estimate with the environmental variables we have.

North of Iceland, the interannual variability in abundance and stage structure of *C. finmarchicus* was positively related to freshwater thickness west of Iceland, a measure of the strength of the coastal current (Olafsson, 1985) and temperature (Figure 9b). Consequently, this result suggests that advection of animals with warm currents from the south and west of Iceland may be important for the abundance of *C. finmarchicus* north of Iceland. But the positive link between temperature and the abundance of the youngest copepodite stages (Figure 9b) may also signify a more direct or local, correlation of temperature and conditions for phytoplankton growth, i.e. higher surface waters temperature being indicator of the surface water stabilization and conditions favourable for bloom of phytoplankton, and thus food for growth of *C. finmarchicus*.

We found no significant effect of the climatic index NAO on interannual variations in abundance of *C. finmarchicus* off Iceland. Similarly, Gislason *et al.* (2009) did not find a relationship between NAO and community structure of zooplankton in the region. As discussed by these authors, the lack of a relationship may be related to the fact that Iceland is at one end of the dipole across which the NAO index is calculated.

The ecology and biology of *C. finmarchicus* are very well studied. Recent studies on the long-term changes of *C. finmarchicus* report a decline coupled with northward shifts in distribution of the species since the 1960s in the North Sea, The Norwegian Sea and the Northeastern Atlantic (e.g. Beaugrand *et al.*, 2002; Reid *et al.*, 2003; Hátún *et al.*, 2009; Heath *et al.*, 2009; Cust et al., 2014). The present data demonstrate no consistent and persistent temporal decline as reported in the above studies, thus further supporting the interpretation mentioned above, that local conditions are important to the long-term variations observed.
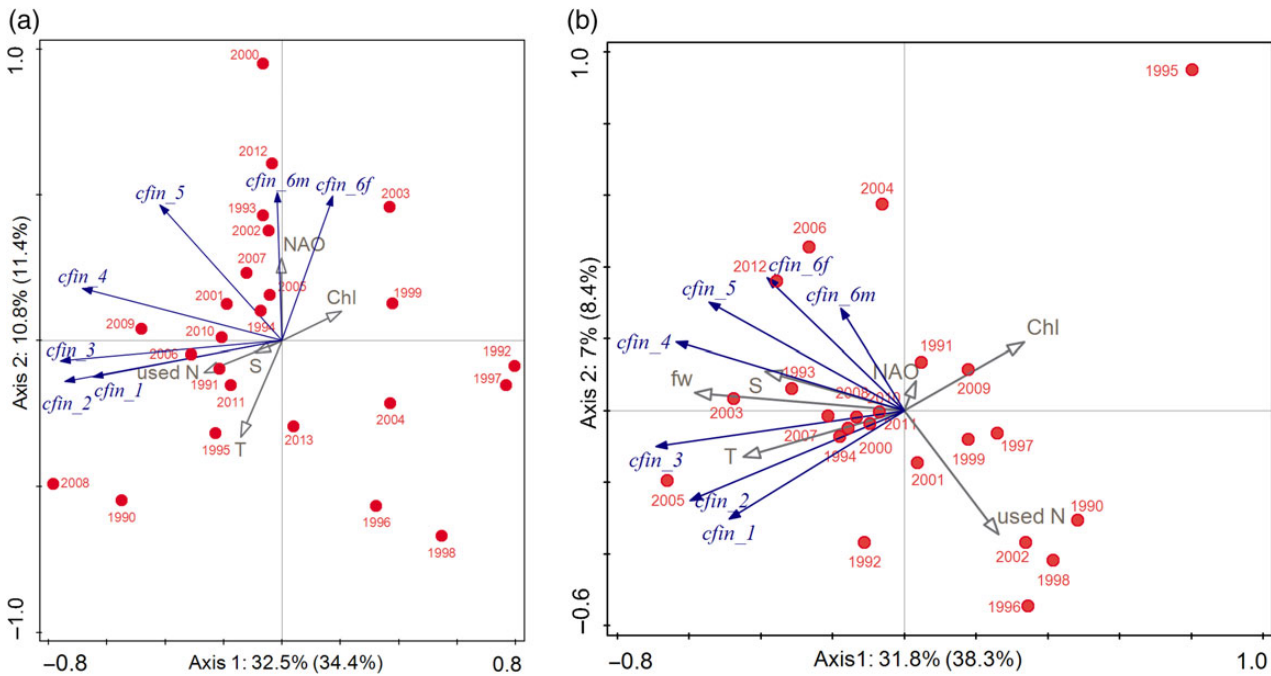
Figure 8. RDA biplots of data on abundance of *C. finmarchicus* by stages (thin blue arrows) and the nominal environmental variable year (red circles), grey arrows are supplementary variables, for Selvogsbanki transect (a) and Siglunes (b) transects. In both panels, the arrows point in the direction of steepest increase of the respective variable and the length of the arrows shows the strength of the gradient. The angles between the arrows reflect their correlations. For Selvogsbanki (a) and Siglunes (b) transects, the plots explain, respectively, 45.8 and 46.7% of the constrained variation in the abundance data. For RDA model design, refer to main text.
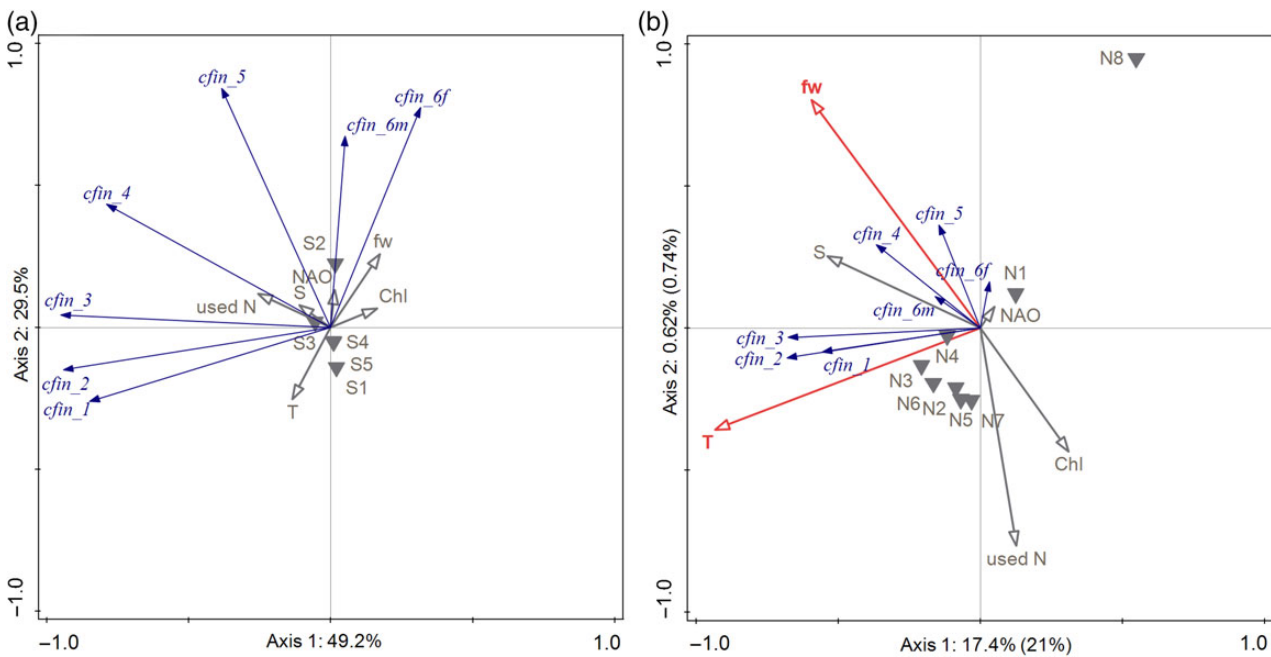
Figure 9. Multivariate biplots of data on abundance of *C. finmarchicus* by stages (thin blue arrows) and environmental variables (red arrows for significant and grey for insignificant passively put on the graph), PCA for Selvogsbanki transect as no environmental variable tested significant (a) and RDA for Siglunes (b) transect. Environmental variables are Chla, chlorophyll *a*; used N, reduction in nitrate concentrations relative to average winter values; NAO, North Atlantic Oscillation Index; S, salinity; T, temperature; fw, freshwater thickness. In both panels, the arrows point in the direction of steepest increase of the respective variable and the length of the arrows shows the strength of the gradient. The angles between the arrows reflect their correlations. For Siglunes transect (b), the first two canonical (constrained) axes explain 21.7% of the constrained variation in the abundance data. For model design, refer to main text.
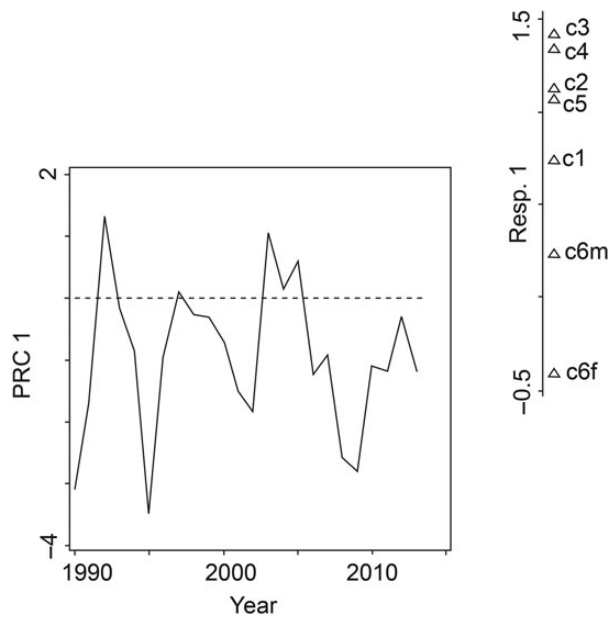
Figure 10. First PRC 1 diagram showing the long-term variability of *C. finmarchicus* stage structure for the combined Selvogsbanki and Siglunes dataset. In the diagram on the left, the first principal component of the variance explained by 'treatment' (sites, in the present study) is displayed on the *y*-axis (PRC1), whereas time (years) is shown on the *x*-axis. Species weights (*C. finmarchicus* stages, in the present study) are shown on the right to illustrate the affinity of the stages with the responses displayed in the PCR diagram. On the PCR diagram, the temporal variability on Selvogsbanki is constrained to a horizontal line (broken line) and the temporal response pattern at Siglunes (whole line) is expressed as deviations from that line.

In conclusion, the present analysis shows large fluctuations in abundance of *C. finmarchicus* from one year to another. The variations are not in tune in south and north, in line with the differences of these two marine systems. In south of Iceland, the long-term changes in abundance of *C. finmarchicus* could not be explained by any of the environmental variables tested, whereas north of Iceland advection to the region from the south appears important. No unidirectional long-term temporal trend was observed in abundance of *C. finmarchicus*, neither in the south nor the north. Based on comparisons with time series from nearby areas, and the lack of a relationship between the NAO and the abundance data presented here, it is hypothesized that the growth and development of *C. finmarchicus* in Icelandic waters is more affected by local conditions than large-scale climatic forcing.

Acknowledgements

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