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The role of local and regional environmental factors for *Calanus finmarchicus* and *C. hyperboreus* abundances in the Nordic Seas

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Abstract In the advective realm of the seas, it is challenging to disentangle the role of regional and local processes on zooplankton populations. However, comparative studies of spatially separated zooplankton populations can provide valuable insights into this issue. We studied interannual abundance variation of the key zooplankton species *Calanus finmarchicus* and *C. hyperboreus* in three near-shore locations of the Nordic Seas: off northern Norway, Svalbard, and northern Iceland. Average abundances of both species were similar among locations, while in each location the abundance of *C. finmarchicus* was about an order of magnitude higher than the abundance of *C. hyperboreus*. The abundance of both species decreased in northern Norway, while *C. finmarchicus* abundance increased in northern Iceland. *C. finmarchicus* abundance in northern Norway covaried with regional climate, while the Svalbard *Calanus* populations were related to local environment (hydrography, phytoplankton). In northern Iceland, *C. finmarchicus* abundance covaried with local environmental factors, while *C. hyperboreus* abundance covaried with climate variability. Top-down forcing could not be investigated. The results indicate that the mechanisms relating regional climate variability (North Atlantic and Arctic oscillations) to *Calanus* abundance are mediated through advection of water masses, while more local environmental variability involved bottom-up processes or advection.

Keywords Abundance variation · *Calanus* · Climate variability · Spatial ecology · Sub-Arctic Atlantic

Introduction

Environmental variability is an important driver of abundance in marine zooplankton, but the relationships between zooplankton dynamics and local as well as regional environmental factors are often poorly understood (Beaugrand [2012]). The analyses of abundance patterns over time can provide insight into the underlying mechanisms that determine abundance fluctuations in zooplankton at large geographical scales (Perry et al. [2004]; Mackas and Beaugrand [2010]) and at local scales (Eloire et al. [2010]). Such analyses are, however, rare, especially for populations in remote and inaccessible regions.

In the Nordic Seas, the genus *Calanus* is one of the most ecologically important zooplankton taxa (Melle et al. [2004]; Wassmann et al. [2006]). The congeneric species *Calanus finmarchicus*, *C. glacialis*, and *C. hyperboreus* represent a main food source for many planktivores, including economically important species such as capelin (Falk-Petersen et al. [1986]), cod (Ellertsen et al. [1987]), and herring (Dalpadado et al. [2000]; Varpe et al. [2005]). *Calanus* spp. have different reproductive strategies and generation times. *C finmarchicus* usually has a one-year generation time and reproduces in surface waters when sufficient food is

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present, often in spring (Melle and Skjoldal 1998; Niehoff et al. 2000). *Calanus glacialis* has a life cycle of 1–3 years and is capable of boosting reproduction from lipid reserves before the start of the bloom, but sometimes starts reproduction in the presence of other food sources (Falk-Petersen et al. 2009; Daase et al. 2013). In contrast, the generation time of *C. hyperboreus* is 2–5 years, and eggs are produced deep in the water column, based on reserves in the absence of food (Hirche and Niehoff 1996; Halvorsen 2015). Although the ecology of the *Calanus* spp., and *C. finmarchicus* in particular, is fairly well described (Tande and Miller 2000), better understanding of their long-term abundance fluctuations is needed for any predictions of marine ecosystem change in the northernmost areas of the North Atlantic (Villarino et al. 2015).

Large-scale changes in the distribution of these *Calanus* spp. occurred in response to climate change, as evident from the shifts of their distributions (Beaugrand et al. 2002; Chust et al. 2013). The hydroclimatic regime of the northern hemisphere is influenced by changes in the atmospheric climate, characterized by the North Atlantic Oscillation index (NAO) and the Arctic Oscillation index (AO). These climatic oscillations have been shown to covary with zooplankton abundances in the North Atlantic via their effect on advection (Greene and Pershing 2000), primary production (Skreslet et al. 2015), or an interaction of physical and biological factors (Fromentin and Planque 1996; Planque and Taylor 1998). If such regional and more local environmental factors exhibit similar patterns across large distances, the Moran effect can be observed (Koenig et al. 2002), when environmental factors provide similar effects on the distinct zooplankton populations and thus cause synchrony in the zooplankton population dynamics (Lodi et al.; Batchelder et al. 2012).

For example, the increase in sea surface temperature in the Barents Sea (Wassmann et al. 2011), the Norwegian Sea (Walczowski et al. 2012), and in the Arctic Ocean (Steele et al. 2008) may shift the North Atlantic *Calanus* community to a state characterized by more boreal and fewer arctic species (Carstensen et al. 2012; Kjellerup et al. 2012). As the smaller, boreal *C. finmarchicus* provides less nutritional value per individual than its Arctic congeners *C. glacialis* and *C. hyperboreus*, such shifts may reduce energy flows to higher trophic level organisms in the Arctic (Falk-Petersen et al. 2007; Karnovsky et al. 2010). Alternatively, the responses of *Calanus* abundance to regional forcing may not be uniform across the North Atlantic, if the local manifestations of the hydroclimatic variations differ between locations (Planque et al. 1997; Drinkwater et al. 2013), e.g. in terms of advection of water masses (Sundby 2000; Hansen et al. 2012), changes in temperature, or the timing of the spring bloom (Fromentin and Planque 1996). In parts of the western North Atlantic, *C. finmarchicus* abundance is positively related to NAO (Greene et al.

2003), while the correlation is negative in the eastern North Atlantic (Planque and Taylor 1998). Also, congeneric populations and distinct life-cycle stages of *Calanus* may vary in their responses to climate variability (Turner et al. 2006) and water temperature (Persson et al. 2012).

Here, we study abundance variation of *C. finmarchicus* and *C. hyperboreu*s, by utilizing long-term data series from three locations of the Nordic Seas: northern Norway, Svalbard, and northern Iceland. We aim to identify and discern (1) long-term abundance trends, (2) common regional drivers affecting populations across the basin, and (3) specific local conditions driving *Calanus* populations in these locations.

Materials and methods

Study areas

We focus on the Nordic Seas region of the North Atlantic Ocean (Fig. 1). The oceanic circulation in the Nordic Seas is influenced by the inflow of Atlantic water (Hansen and Østerhus 2000). A main source of Atlantic water is the Norwegian Atlantic Current (NAC, Fig. 1). The NAC flows along the shelf break off western and northern Norway and bifurcates with one branch entering the Barents Sea and the other flowing northwards along the western coast of Svalbard as the West Spitsbergen Current (WSC, Fig. 1) (Sætre et al. 2004; Blindheim and Østerhus 2005). Northwest of Svalbard the WSC splits, and one branch enters the Arctic Ocean, while the other branch is deflected southwards along the east coast of Greenland and enters the Iceland Sea parallel to the East Greenland Current (EGC, Fig. 1) (Blindheim and Østerhus 2005). The EGC transports cold and Arctic water masses to the Iceland Sea, while the North Icelandic Irminger Current (NIIC, Fig. 1) supplies warmer Atlantic waters to the area north of Iceland. The East Icelandic Current (EIC) brings Arctic water masses eastwards along the North Icelandic continental slope (Valdimarsson and Malmberg 2003). Together with the EGC, the EIC forms a strong temperature gradient where it meets the warm Atlantic waters of the NIIC (Valdimarsson and Malmberg 1999). The Faroe current (FC; Fig. 1) enters the Nordic Seas between Iceland and the Faroe Islands and supplies Atlantic Water to the southwest part of the Norwegian Sea. The whole circulation cycle in the Nordic Seas is suggested to take around 15 years (Aksnes and Blindheim 1996; Blindheim and Østerhus 2005).

Calanus finmarchicus and *C. hyperboreus* abundance data

Three areas of the Nordic Seas are considered in the study: northern Norway in the east, western Svalbard shelf in the
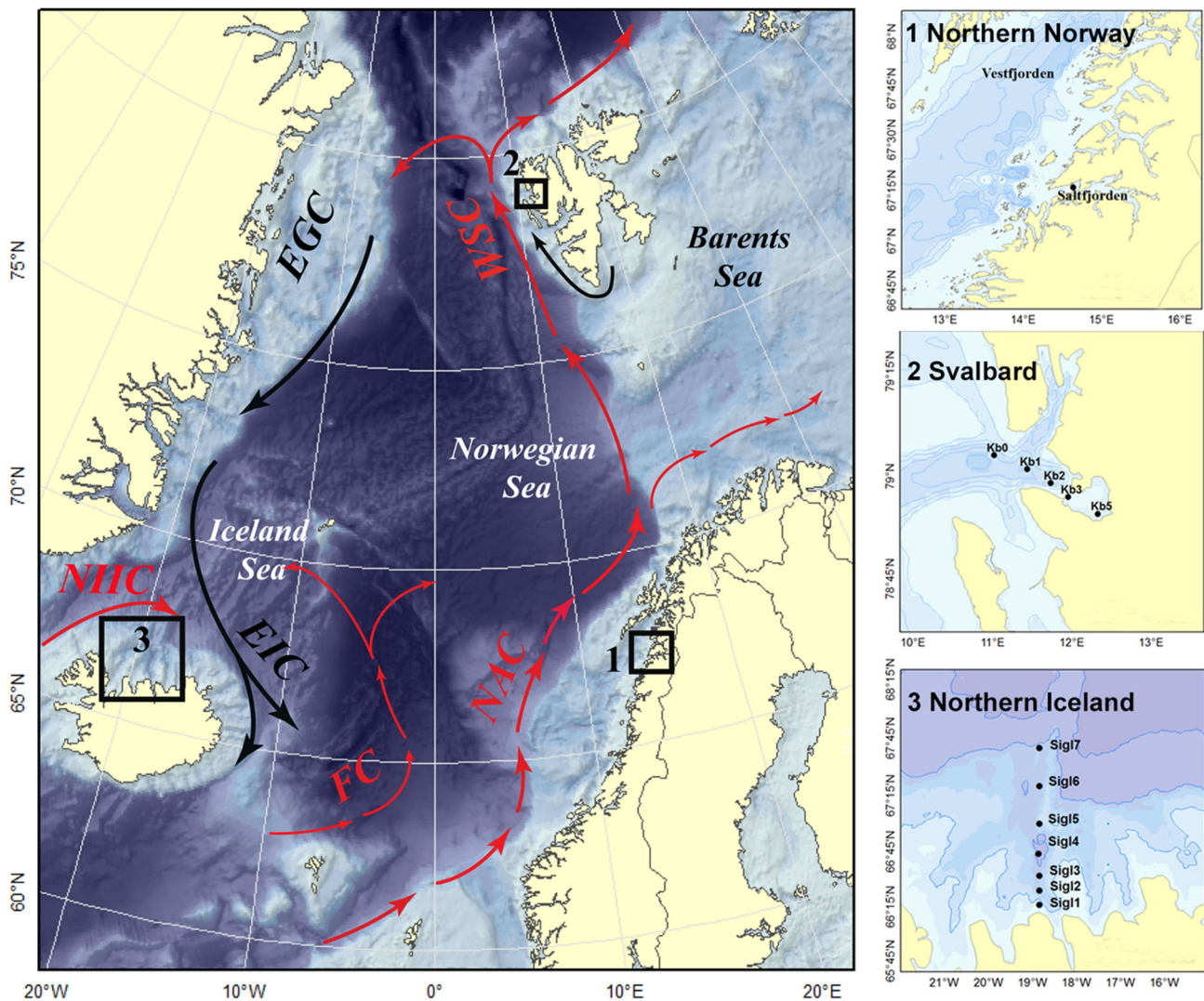
Fig. 1 Map of the study area with sampling locations and main oceanic circulation, based on Loeng and Drinkwater (2007) and Drinkwater et al. (2013). *1* a fjord station in northern Norway; *2* a transect on the west coast of Svalbard; *3* a transect in the northern Icelandic waters. The codes for indicated currents are *FC* Faroe current, *NIIC* North Icelandic Irminger current, *NAC* Norwegian Atlantic current, *WSC* West Spitsbergen current, *EGC* East Greenland current, and *EIC* East Icelandic current. *Red and black arrows* denote warm and cold water currents, respectively

north, and the northern Icelandic shelf in the west (Fig. 1). This allows large spatial coverage from three similar but well-separated near-shore locations. Importantly, however, the sampling at the three locations took place at different times of a year (October, July, and May, respectively), and the sampling design (sampling depth and equipment) differed slightly between the locations. These differences could lead to variation in the abundance and composition of the developmental stages between the locations. However, to the best of our ability, we take these differences into account when comparing the variation of the species abundances between the locations. We focus on identifying the specific responses of *Calanus* in relation to the location and time of sampling, and when interpreting these

responses, we seek to describe location-specific mechanisms. Thus, although different times of sampling complicate some of the interpretations, the cost of losing information due to different sampling times in return improves spatial coverage of the study and allows for between-location comparisons.

In northern Norway, zooplankton was sampled at a fixed station in Saltfjorden (67.15°N, 14.38°E; Fig. 1) in October from 1983 to 2010 (except in 1985) (Table 1). Five replicate hauls were taken with a Juday net (0.1 m^2 aperture and 180 μm mesh size) from near the seabed at 370 m depth to the surface.

Kongsfjorden (79°N, 12°E; Fig. 1) is a glacial fjord located on the west coast of the Svalbard archipelago.

Table 1 Overview of the data series from northern Norway, Svalbard, and northern Iceland, used in this study

Location and stations	Sampling gear	Sampling depth (m)	Year and season	Total number of samples
Northern Norway, Saltfjorden	Juday net (180 μm)	0–370	October, 1983–2010	133
Svalbard				
KB0	Multinet (180 μm)	315–200–100–50–20–0	July, 1996–2010	63
KB1		352–200–100–50–20–0		
KB2		330–200–100–50–20–0		
KB3		329–200–100–50–20–0		
KB5		96–50–20–0		
Northern Iceland, Siglunes (Sigl) 1–7	WP2 net (200 μm)	0–50	May, 1990–2011	152

Zooplankton samples were collected in July at five stations from 1996 to 2010, but not 1998 and 2005 (Table 1; Fig. 1), by vertical hauls of a Multinet (Hydrobios ltd.; 0.25 m² aperture and 180 μm mesh size). Station KB0 was not sampled in 1996 and station KB5 was not sampled in 2007. Samples were collected from near the seabed at maximal 352 m depth to the surface in five depth bins.

Data from northern Iceland were collected along a transect of seven stations extending from the coast to the Iceland Sea (67°N, 18°50'; Fig. 1) in May from 1990 to 2011 (Gislason et al. 2014). Station Sigl 1 was not sampled in 2000 and station Sigl 6 was not sampled in 2007 (Fig. 1; Table 1). In 1990 and 1991, a Hensen plankton net (0.42 m² mouth area and 200 μm mesh size) was used. All subsequent sampling was conducted with a WP2 net (0.25 m² aperture and 200 μm mesh size). Both Hensen and WP2 nets were towed from 50 m to the surface. The sampling depth in northern Iceland was much shallower than in northern Norway and Svalbard. However, most of *Calanus* individuals at this time of a year (May) in northern Iceland reside in surface areas for spawning and feeding (Gislason and Silva 2012), and thus, the potential underestimation was likely minor.

Sample treatment and abundance calculations were equivalent in all regions. The zooplankton samples were preserved in a 4% formaldehyde–seawater solution until enumeration in the lab. *C finmarchicus* was staged (copepodite developmental stages CI–CVI) in all samples, while only total abundance of *C. hyperboreus* was counted for northern Norway. Species separation of *Calanus* was done from randomly selected subsamples based on prosome length distributions (Unstad and Tande 1991; Hirche et al. 1994). Abundance estimates (ind m⁻²) were calculated assuming 100% filtering efficiency of the net, except for WP2 nets in northern Iceland, where filtered water volume was measured with a flowmeter (Hidrobios ltd.) fitted in the mouth of the net.

Morphological criteria are not always a reliable taxonomical tool and may lead to misidentification between *C.* *finmarchicus* and *C. glacialis,* as shown by molecular identification methods (Lindeque et al. 2006; Gabrielsen et al. 2012). According to Skreslet et al. (2015), the number of *C. glacialis* misidentified as *C. finmarchicus* in northern Norway was about 5%, and in Svalbard, misidentification could be up to 20% (Gabrielsen et al. 2012), while such estimates are not available for northern Iceland.

Environmental variables

We distinguish between local and regional environmental variables. We consider those environmental variables that vary on the spatial scale of sampling (such as hydrographic variables) as primarily local variables, while those varying on a regional (e.g. North Atlantic) scale, such as climate indices, as large-scale environmental variables. Local-scale environmental variables are temperature, salinity, and chlorophyll *a* (Chl *a*), and were measured as follows: before 1991, water temperature in Northern Norway was measured with calibrated reversing thermometers fitted to Nansen bottles, and salinity was measured in the lab from water samples with a salinometer. From 1991 onwards, salinity and temperature were measured with a conductivity, density, and temperature (CTD) profiler (either Sea-Bird Electronics or Sensordata). In Svalbard and northern Iceland, a CTD cast (Sea-Bird Electronics) at each sampling station obtained salinity and temperature profiles. In situ Chl *a* concentrations are available for northern Iceland only and were estimated by filtering 1 or 2 L water samples collected at 10 and 30 m depth onto GF/C glass fibre filters that were subsequently analysed by a spectrophotometer as described in UNESCO/SCOR (1996). For all locations, depth-averaged (0–50 m) hydrographic data were used for analyses.

The degree of overlap between timing of the phytoplankton spring bloom and the occurrence of early developmental stages can be an important factor for copepod recruitment (Diel and Tande 1992; Melle and Skjoldal 1998; Søreide et al. 2010). To study relationships between

Calanus abundance and year-to-year variability in the timing of the spring bloom, we estimated the start date of the yearly spring blooms based on remote sensing data on changes in Chl *a* concentration in the vicinity of our study locations. We used data collected by NASA (SeaWifs and Aqua-MODIS) and ESA (MERIS) available from the Hermes portal of the European Service of Ocean Colour (http://hermes.acri.fr/index.php?class=archive). The downloaded Chl *a* levels are measurements from 8-day intervals from site-specific areas of approximately 4.63 × 4.63 km merged by a Garver, Siegel, and Maritorena model (GSM) (Maritorena and Siegel 2005; Maritorena et al. 2010). To avoid distortion caused by terrestrial interference for the locations in northern Norway and Svalbard, measurements were taken from rectangular areas outside the fjords (from 67°10′N to 67°37′N and 12°30′W to 14°15′W; and 78°45′N to 79°14′N and 9°30′ to 11°, respectively). For northern Iceland, remote Chl *a* measurements were extracted from a rectangular area enclosing the transect (from 66°30′N to 67°45′N and from 17°30′W to 19°15′W). The satellite Chl *a* levels were extracted and processed in R (R Core Team 2016). A linear interpolation with respect to day numbers between recorded concentrations of Chl *a* from the selected areas was performed for the years 1998–2010 (until 2011 for northern Iceland). The spring bloom start was estimated as the day number when Chl *a* concentration exceeded 5% above the median Chl *a* concentration for that year and location (Siegel et al. 2002; Henson et al. 2009).

As proxies for the regional climate variability, we used the North Atlantic Oscillation index (NAO; http://www.climate dataguide.ucar.edu) and the Arctic Oscillation index (AO; http://www.cpc.noaa.gov/) (Hurrell 1995; Cohen and Barlow 2005). NAO describes the difference in normalized atmospheric pressure between the Azores and Iceland. This is seen as the main mode of interannual variability of atmospheric circulation in the North Atlantic (Hurrell 1995; Hurrell et al. 2001) and affects marine ecosystems through the regulation of wind regime, storminess, and gyre circulation (Hurrell and Deser 2009). AO is a pressure seesaw that has the centre of action in the Arctic and regulates the climate and weather processes at high north latitudes. To assess the effect of large-scale climate on the interannual variation of *Calanus* abundances, we applied average annual indices of NAO and AO.

Data analysis

For each location and year, we calculated average total abundances of *Calanus* and relative composition (%) of copepodite stages of both species over stations in Svalbard and northern Iceland, and for replicates in northern Norway. The data sets of both abundances and environmental factors generally contained outliers and deviated significantly from normality (Shapiro–Wilks normality test);

thus, we used a non-parametric, Kendall's rank correlation (Kendall and Gibbons 1990) to test for covariation between environmental variables, between abundances of both *Calanus* spp., and each of the environmental variable, and to detect temporal change (trends) in *Calanus* abundances. All correlation tests were done in R (R Core Team 2016).

Abundance anomalies for overlapping years (1996–2010) for both *Calanus* species were calculated as $\hat{x} = (x - \mu) \times \sigma^{-1}$, where μ is the mean value of x (yearly average abundance) over the selected time window and σ is the corresponding standard deviation.

To describe the relationships between environmental variables and different developmental stages of *Calanus* and to identify environmental variables that significantly explained the interannual variation in stage-specific abundances, we applied a constrained ordination method—Redundancy Analysis (RDA) in Canoco v. 5.0 (ter Braak and Smilauer 2012). This is a linear model and it was preferred to the alternative unimodal model (Canonical Correspondence Analysis, CCA) based on the Detrended Correspondence Analysis (DCA). The DCA showed that the gradient length of the first axis was less than 4 standard deviations, indicating linear responses of both *Calanus* spp. to environmental variability (ter Braak and Smilauer 2012). For the RDA, the abundance data were ln $(x + 1)$ transformed to homogenize variance of the abundances. Temperature, salinity, Chl *a* concentration (for Icelandic data), and annual NAO and AO indices were included in the RDA as explanatory variables. The spring bloom start was not included in the RDA due to limited number of years (14) with data. To account for autocorrelation between stations in the data from Svalbard and northern Iceland, Monte-Carlo permutations (499) were restricted to a split-plot design. Permutations were not performed for the whole-plot factor (stations), but permutations for time-series data dependent across whole-plots were applied for split-plots (years) (ter Braak and Smilauer 2012). As the split-plot design required an equal number of samples each year, we interpolated the values for the missing samples in Svalbard and northern Iceland, using random imputation in R. In analysing data from northern Norway, permutations for time-series data were used in the Monte-Carlo test, as the data were collected annually from one station.

Results

Environmental variability

Average temperatures in the surface layer (0–50 m) were generally higher in northern Norway in autumn than in summer in Svalbard and in spring in northern Iceland (Table 2; Fig. 2). Temperature varied less in northern

Table 2 *Calanus finmarchicus* and *C. hyperboreus* average abundances (ind m^{-2}) and environmental variables in northern Norway in October (1983–2010), in Svalbard in July (1996–2010), and in northern Iceland in May (1990–2011)

Variable (mean)	Northern Norway	Svalbard	Northern Iceland
C. finmarchicus abundance, ind m^{-2} (SD)	44914.2 (27880.2)	50022.9 (37151.9)	37431.1 (54239.1)
C. hyperboreus abundance, ind m^{-2} (SD)	1476.8 (2350.7)	3108.9 (2360.9)	1080.1 (2247.6)
Temperature, °C (SD)	8.99 (0.64)	3.57 (1.25)	3.63 (1.20)
Salinity, psu (SD)	32.17 (0.74)	33.60 (1.10)	34.75 (0.23)
Chl *a* concentration, µg L^{-1} (SD)	NA	NA	5.58 (3.75)
The spring bloom start, day of a year (SD)	121 (4.82)	147 (14.00)	154 (11.92)

Temperature, salinity, and Chl *a* are averages from 0 to 50 m. The spring bloom start is derived from satellite data

SD standard deviation, *NA* data not available

Fig. 2 Averaged temperature (°C, *black circles*) and salinity (*open circles*) in 0–50 m over all stations, and the start day of the spring bloom (day of year; *diamonds*) from northern Norway (**a**, **d**), Svalbard (**b**, **e**), and northern Iceland (**c**, **f**). The start day of the spring bloom was calculated from the remote sensor data on Chl *a* concentration (see text for details)

Norway, whereas in Svalbard and northern Iceland it varied at about the same amplitude. Northern Iceland had the highest average salinities, while in Svalbard waters salinity was intermediate and more variable, and the lowest average salinity was observed in northern Norway (Table 2; Fig. 2).

Averaged Chl *a* concentration recorded in northern Iceland in May was 5.6 µg L^{-1} (Table 2). The average day of the spring bloom start during the investigated period (1998–2010 in northern Norway and Svalbard, and 1998–2011 in northern Iceland) occurred in late April in northern Norway, in late May in Svalbard, and in the beginning of June in northern Iceland (Table 2). We did not detect trends in any of the environmental variables studied.

Both NAO and AO indices were low at the beginning (1985, 1987) and at the end of the study period (2010), and relatively high values occurred in 1986, 1990, and 2011 for NAO, and in 1989 and 1990 for AO (Fig. 3). Low values of NAO and AO coincided with relatively low temperature and salinity values in Svalbard in 2010 (Figs. 2, 3), and positive correlations were found between NAO, AO, and salinity and temperature in Svalbard (Table 4). AO correlated positively with the spring bloom start in northern Iceland (Table 4) and negatively in Svalbard (Table 4).
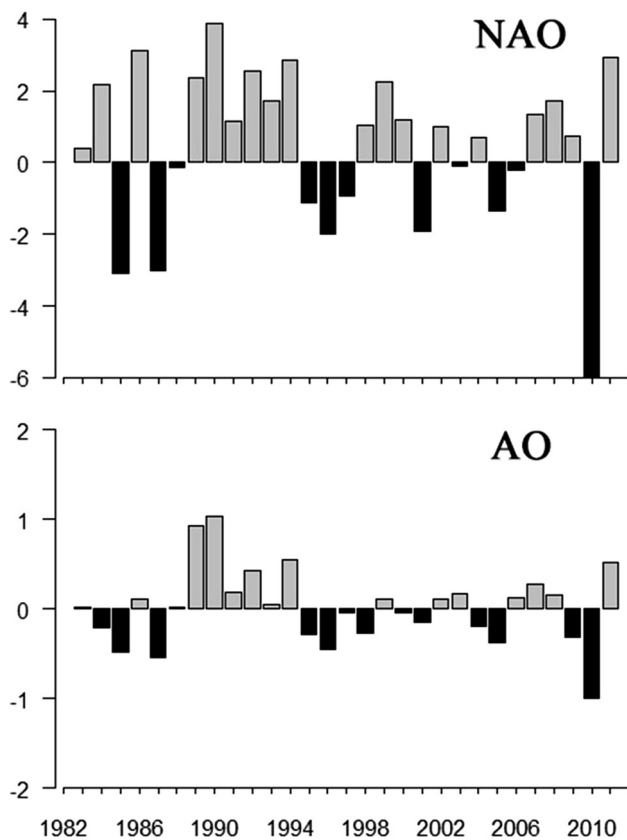
Fig. 3 Annual mean NAO and AO during 1983–2011

Variations of *Calanus* spp. abundances between locations

The average abundances of *C. finmarchicus* in the study locations were fairly similar (Table 2; Fig. 4). *Calanus hyperboreus* abundances were substantially lower than those of *C. finmarchicus* in all three locations (Table 2; Fig. 4). For both *C. finmarchicus* and *C. hyperboreus*, the abundance variability was higher in northern Iceland than in northern Norway and Svalbard (Table 2). The population of *C. finmarchicus* consisted almost exclusively of late copepodite stages IV and V in northern Norway in October (Fig. 5). In contrast, samples in Svalbard and northern Iceland were taken relatively soon after spawning of *C. finmarchicus*, and the stage structure in both locations was more variable, with stages CI–III being abundant (typically accounting for 50–90% of the population). The population of *C. hyperboreus* in Svalbard consisted mainly (ca. 90%) of copepodites stages IV and V, while in northern Iceland young copepodites (CI–CIII) accounted for ca. 66% of total counts (Fig. 5). We have no information on the stage structure of *C. hyperboreus* in northern Norway.

In northern Norway, abundances of *C finmarchicus* and *C. hyperboreus* decreased during the study period, while in northern Iceland, *C. finmarchicus* abundance increased

(Table 3). We did not observe temporal change in the abundance of *C. hyperboreus* in northern Iceland and in either species in Svalbard.
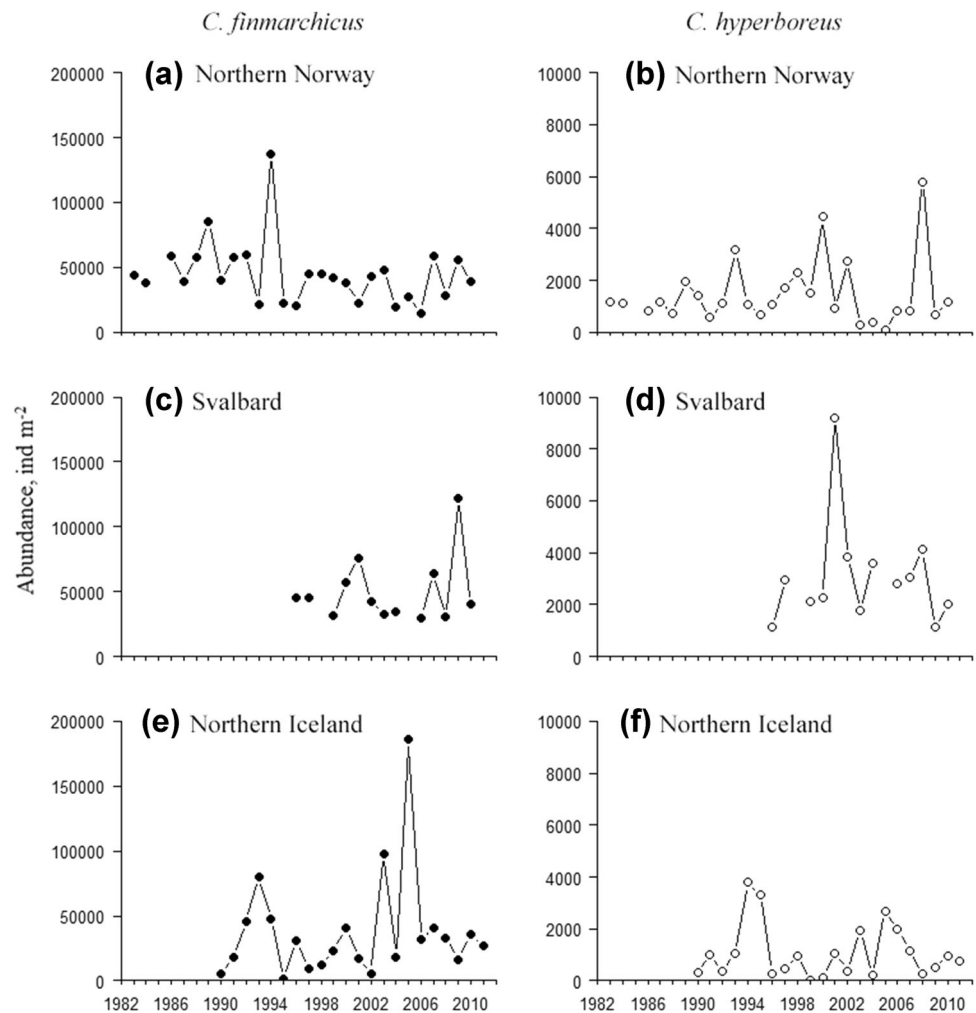
For 1996–2010, where we have data for all three study locations, positive and negative abundance anomalies for *C. finmarchicus* were relatively evenly distributed in northern Norway (Fig. 6). In the other populations, however, most years were characterized by negative abundance anomalies. While negative anomalies were largely <1 SD (in absolute values), the relatively few years with positive abundance anomalies were sometimes 2–3 SD above the period mean (Fig. 6). Interestingly, the highest positive anomalies of *C. finmarchicus* and *C. hyperboreus* abundances in northern Iceland in 2005 coincided with the earliest spring bloom start (early May). However, neither species in northern Iceland correlated significantly with the spring bloom start. In Svalbard, the high positive anomalies of *C. finmarchicus* in 2009 and of *C. hyperboreus* in 2001 coincided with delayed spring bloom start (beginning of June), and *C. finmarchicus* abundance correlated positively with the spring bloom start in Svalbard (Table 5).

Correlations between total abundances and environmental factors

In northern Norway, *Calanus* abundances covaried with climate indices only. Abundance of *C. finmarchicus* correlated positively with the yearly mean AO and the yearly mean NAO (Table 5). In Svalbard waters, *C. finmarchicus* correlated positively with both average temperature and salinity in 0–50 m, and the spring bloom start, whereas *C. hyperboreus* correlated positively with temperature. However, temperature and salinity in Svalbard covaried (Table 4). In northern Iceland, *C. finmarchicus* correlated positively with temperature and salinity, but correlated inversely with Chl *a* concentration, while *C. hyperboreus* inversely correlated with NAO. Average temperature and salinity in the upper 50 m were also correlated in northern Iceland (Table 4).

The relationships between stage-specific abundances of *Calanus* and environmental variables (temperature, salinity, annual NAO and AO, and for northern Iceland, Chl *a*; Fig. 7) showed that in Svalbard annual AO contributed significantly ($P = 0.036$) to explaining the interannual variation of the stage-specific abundances of *C. finmarchicus* and *C. hyperboreus*, and accounted for 8.2% of the variation in the abundances of the copepodite stages of the two *Calanus* spp. In northern Iceland, temperature contributed significantly ($P = 0.04$) to explaining the variation of *Calanus* stages' abundances and accounted for 8% of the total variation in the copepodite stages' abundances (Fig. 7). Copepodite stages II and III of *C. hyperboreus* in Svalbard were inversely related to AO anomalies, while other copepodite stages of *C. hyperboreus* and

Fig. 4 Average abundance (ind m^{-2}) of *Calanus finmarchicus* (*black circles*) and *C. hyperboreus* (*open circles*) from northern Norway (**a**, **b**), Svalbard (**c**, **d**), and northern Iceland (**e**, **f**)

copepodite stages of *C. finmarchicus* were not related to AO. Early copepodites (CI to CIII) of *C. finmarchicus* showed an association with higher temperatures, while CI of *C. hyperboreus* were found in higher abundances at lower temperatures (Fig. 7). None of the environmental variables contributed significantly to the variation in *Calanus* copepodite abundances in northern Norway.

Discussion

Our results suggest that the dynamics of the studied *Calanus* populations were related to environmental variability driven by both local and regional processes, and these relationships were species—and location—specific.

Effects of regional and local environment on *Calanus*

The abundances of *C. finmarchicus* in northern Norway correlated positively and *C. hyperboreus* in northern Iceland correlated negatively with climate variability (NAO or AO). Skreslet and Borja (2003) and Skreslet et al. (2015) attribute the relationship between NAO and *C. finmarchicus* in northern Norway to high freshwater discharge to coastal waters during periods of high NAO (Hurrell and Deser 2009). Higher freshwater inflow, they hypothesize, tends to increase primary productivity and, as an effect of increased food availability, may elevate the abundance of *C. finmarchicus*.

Positive NAO and AO anomalies are associated with strong westerly winds in the North East Atlantic and thus with an intensified inflow of Atlantic water masses to subpolar regions (Kerr 1999; Dickson et al. 2000; Ottersen et al. 2001). This inflow is associated with advection of Atlantic zooplankton (of which *C. finmarchicus* is a dominant species) onto the northern Norwegian shelf (Helle and Pennington, 1999). Thus, strong westerly winds are positively related to *C. finmarchicus* abundance on the shelf (Samuelsen et al. 2009). The relationship between *C. finmarchicus* abundance and climate variability in northern Norwegian
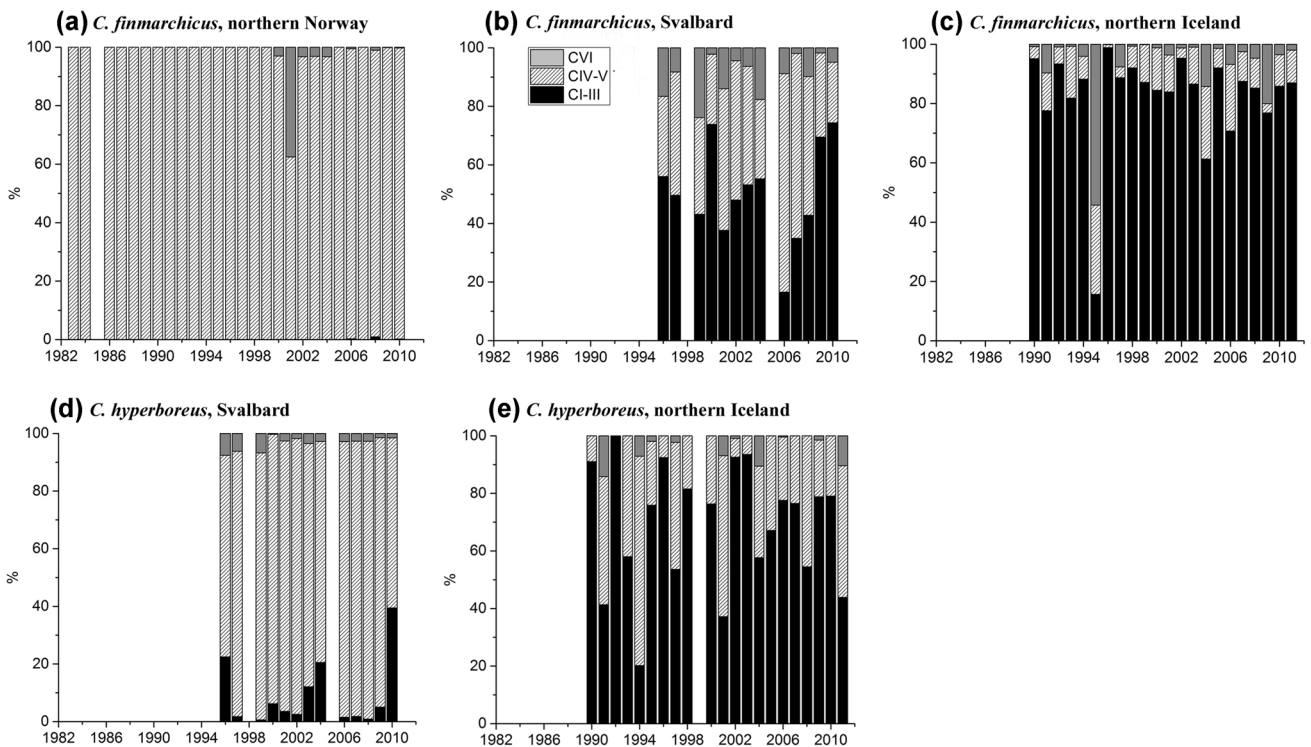
Fig. 5 Stage composition based on averaged abundance (ind m^{-2}) of *Calanus finmarchicus* in northern Norway in October (**a**) and of *C. finmarchicus* and *C. hyperboreus* in Svalbard in July (**b**, **d**) and in northern Iceland in May (**c**, **e**). CI–CIII, CIV–CV, and CVI, denote the combined relative abundance (%) of copepodite stages I through III, IV, and V, and of adult females and males, respectively

Table 3 Temporal change in total abundances (ind m^{-2}) of *Calanus finmarchicus* and *C. hyperboreus* in northern Norway (1983–2010) and northern Iceland (1990–2011) as indicated by Kendall's rank correlation between abundance and year

Species	Location	τ	P	df
C. finmarchicus	Northern Norway	−0.179	0.003	131
C. hyperboreus		−0.123	0.04	131
C. finmarchicus	Northern Iceland	0.133	0.02	150

No temporal change of abundance was detected in Svalbard

τ Tau Kendall's rank correlation coefficient, *P* significance level of the rank correlation test, *df* degrees of freedom
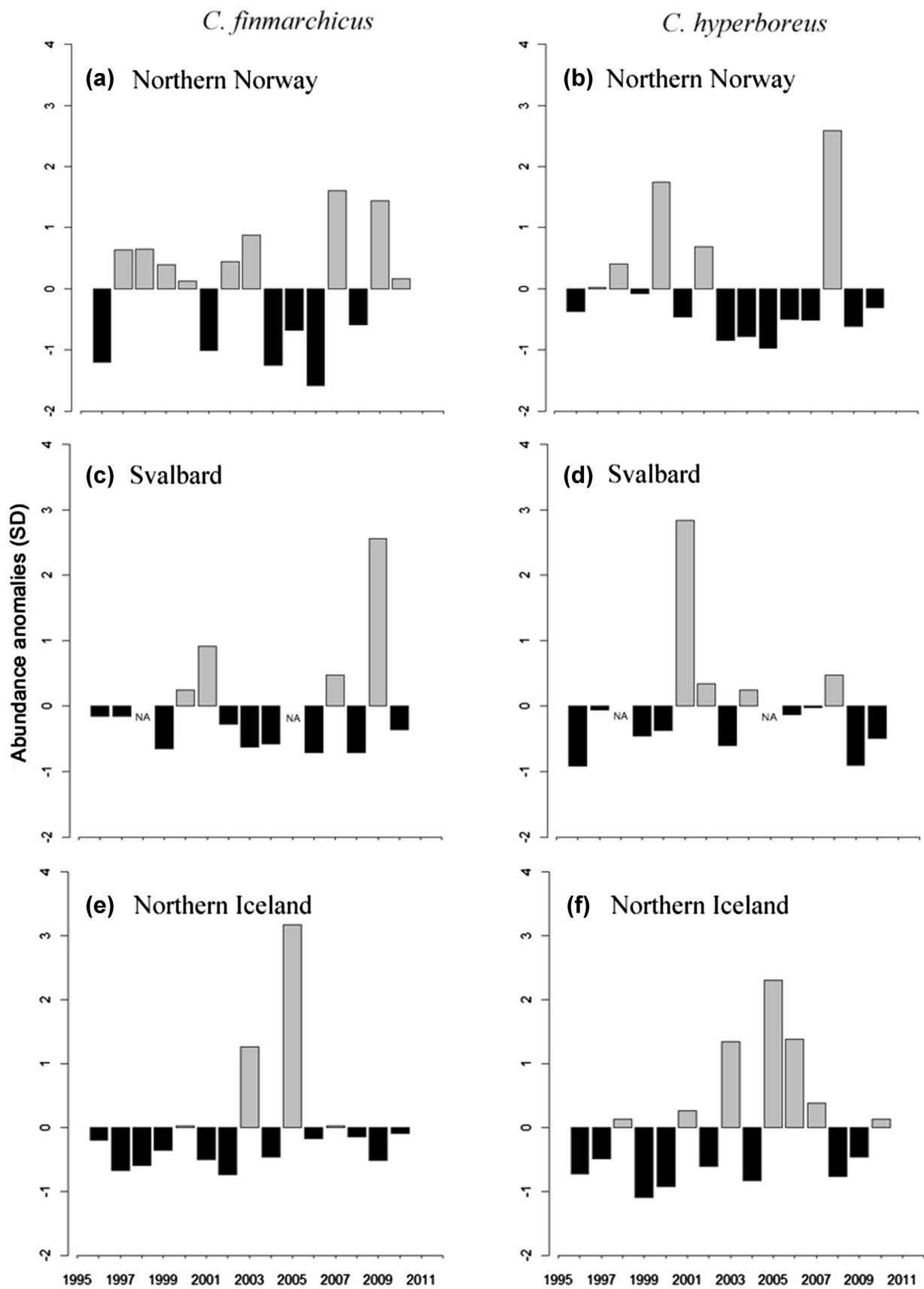
waters, therefore, may reflect changing fjord productivity and advection levels. Thus, a decreasing trend of both species in northern Norway (Table 3) may be a result of the years with low NAO between 1994 and 2010 (Fig. 3) as was earlier suggested by Skreslet et al. (2015).

Earlier observations in other Norwegian fjords suggest that predation by mesopelagic fish and large copepods can lead to a substantial loss in the abundances of *C. finmarchicus* (Bagøien et al. 2001; Eiane et al. 2002). Thus, although sufficient data on predator abundances in the location in northern Norway are absent, the negative trend in overwintering stocks of *C. finmarchicus* and *C. hyperboreus* may have been caused by predation pressure by

fish. In addition, an underlying effect of predation during overwintering months may alter the relationship between abundances and local environmental factors, contributing to the lack of direct relationship between *Calanus* abundances in northern Norway and hydrography or start date of the spring bloom.

The positive relationships between salinity and temperature and the abundance of *Calanus* in Svalbard waters likely reflect variability in the inflow of Atlantic waters originating from the relatively warm and saline WSC (Fig. 1). Such episodes of Atlantic inflow to the western Svalbard shelf are associated with advection of *C. finmarchicus* (Daase and Eiane 2007; Karnovsky et al. 2010) as well as some *C. hyperboreus* (Smith et al. 1985; Hirche 1991). WSC inflow intensifies in summer (Cottier et al. 2005) when our samples were taken, which may have strengthened the *Calanus*–hydrography signal in our data.

An underlying covariation between climate indices and *Calanus* abundance on the western Svalbard shelf may have been masked by time lags (Kwasniewski et al. 2012), caused by the time required for the intensified Atlantic inflow during positive NAO phases to propagate to Arctic latitudes and affect Svalbard shelf waters (Saloranta and Haugan 2001; Visbeck et al. 2013). These climate–zooplankton time lags may exceed several years in Svalbard waters (Kwasniewski et al. 2012). As our data series are

◄**Fig. 6** Normalized abundance anomalies (in units of standard deviation, SD) of *Calanus finmarchicus* (*left panels*) and *C. hyperboreus* (*right panels*) during 1996–2010 in northern Norway in October (**a**, **b**), Svalbard in July (**c**, **d**), and northern Iceland in May (**e**, **f**)

too short (15 years) to allow for effective testing of time-lagged effects (Legendre and Legendre 1998), we cannot rule out lagged climate responses in Svalbard *Calanus* populations.

By resolving stage structure, we found that the younger copepodite stages of *C. hyperboreus* responded inversely to AO variability in Svalbard (Fig. 7). Probably, such responses are more apparent in the young stages because of the noise inherent in total abundance estimates at a time when several generations of the long-lived *C. hyperboreus* overlap (Conover 1988). Such noise may weaken signals of interannual climate variability in data sets taken during the productive season.

High AO is associated with warmer winters in the Arctic (Kerr 1999). Increased temperature in surface waters accelerates the development of *C. hyperboreus* nauplii (McLaren and Corkett 1981) and increases food requirement sufficiently to reduce nauplii survival (Jung-Madsen et al. 2013). For the nauplii reaching surface waters in winter, this may result in a temporal mismatch with the food and, subsequently, in low numbers of young copepodites in the following summer (Plourde et al. 2003).

Similar to the situation in Svalbard, we assume that the positive correlation between *C. finmarchicus* and temperature and salinity off northern Iceland (Table 5) was related to the inflow of relatively warm and saline Atlantic water masses of the NIIC (Fig. 1). The NIIC is associated with the advection of *C. finmarchicus* to northern Icelandic waters (Gislason et al. 2009, 2014). In addition, the Atlantic influence increases primary productivity in this area (Astthorsson et al. 1983; Thórdardóttir 1984), hence further strengthening *Calanus* populations through improved feeding conditions. The NIIC inflow has intensified since the mid 1990s (Valdimarsson and Malmberg 2003; Valdimarsson et al. 2012), and we hypothesize that this may have contributed to the increase in *C.*

finmarchicus abundance detected in northern Iceland (Table 3). The collinearity between temperature and salinity, both in waters north of northern Iceland and in western Svalbard, strengthens the view that part of the *Calanus* abundance variation may reflect shifting distribution of water masses with a corresponding change in the abundances of the associated fauna (Astthorsson et al. 1983; Daase et al. 2007).

The positive relationship between temperature and the young copepodite stages (CI–CIII) of *C. finmarchicus* in northern Iceland (Fig. 7) also reflects an increase in the abundance of *C. finmarchicus* when warmer Atlantic water masses are dominating in the area (Gislason et al. 2009). Higher abundances of *C. hyperboreus* in northern Iceland tend to occur in years with relatively low Atlantic influence and a high inflow of colder waters of the EIC (Astthorsson et al. 1983) (Fig. 1), which likely explains the inverse relationship with temperature seen in the young copepodite (CI and CII) stages of this species.

We did not detect relationships between climate variability and *C. finmarchicus* in northern Iceland. This result corroborates earlier observations showing that climate variability as measured by NAO correlates neither with hydrography (Ólafsson 1999) nor with zooplankton (Gislason et al. 2009) in northern Iceland. The lack of correlation likely occurs because NIIC inflow in this area is mainly driven by variations in the local north and southerly wind patterns, which appear to vary independently from NAO (Ólafsson 1999). Thus, it may be that the relationship between climate and *C. finmarchicus* in this area are concealed in the data by more pronounced effects of variable NIIC inflow. In contrast, the indicated relationship between climate and *C. hyperboreus* (Table 5) may be linked to the intensified deep-water convection in the Greenland Sea during periods of low NAO (Dickson 1997; Hurrell and Deser 2009). Deep-water transport may enhance the advection of overwintering and ascending *C. hyperboreus* from the main distribution area in the Greenland Sea into the Iceland Sea (Richter 1994; Hirche and Kwasniewski 1997).

Our results indicated that *Calanus* populations in northern Norway responded differently to NAO variability

Table 4 Significant correlations between environmental variables within each location

Variable 1	Variable 2	Years	Kendall's tau	P	df
Temperature, Svalbard	AO	1996–2010	0.402	<0.001	61
Salinity, Svalbard	NAO	1996–2010	0.307	<0.001	61
Salinity, Svalbard	AO	1996–2010	0.324	<0.001	61
Bloom, Iceland	AO	1990–2011	0.157	0.035	94
Bloom, Svalbard	AO	1996–2010	−0.414	0.002	32

NAO North Atlantic oscillation, *AO* Arctic oscillation, *τ* Tau Kendall's rank correlation coefficient, *P* significance level of the rank correlation test, *df* degrees of freedom
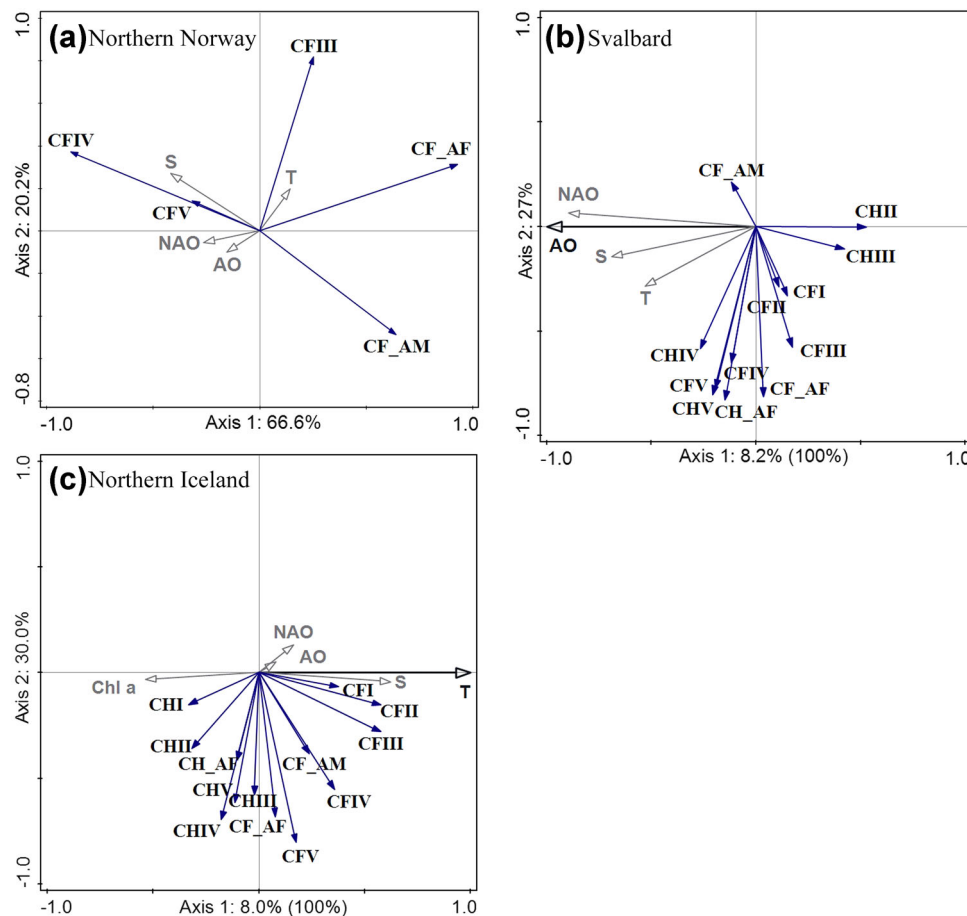
Fig. 7 Ordination plots of environmental data and *Calanus fin-marchicus* data from northern Norway (October, 1983–2010; **a**), and environmental data and *C. finmarchicus* and *C. hyperboreus* data from Svalbard (July, 1996–2010; **b**) and northern Iceland (May, 1990–2011; **c**). For northern Norway, environmental variables did not contribute significantly to explaining the variation in the species data, and thus the PCA plot is shown. For Svalbard and northern Iceland, RDA plots are shown. Developmental stages (CI—adults) and environmental variables are represented by *arrows*. Copepodite stage I of *C. hyperboreus* in Svalbard is not shown as this stage was

not found. Environmental variables shown as *black arrows* significantly explained the variation in *Calanus* stages' abundances. Environmental variables shown as *grey arrows* had no significant effect on *Calanus* abundances and did not influence RDA. *Arrows* point in the direction of the steepest increase of the respective variable. The angle between *arrows* reflects correlations between the variables. For Svalbard and northern Iceland, percentage values at the axes indicate total variation in data of both species explained by each axis and the amount of the species–environment relationship explained by the axes (*in parenthesis*)

than those in northern Iceland (Table 5). As NAO impacts are mediated through local environmental effects, such as temperature and circulation patterns, the ecological responses tend to differ spatially across the North Atlantic Ocean (Drinkwater et al. 2003). This may explain the lack of similarity in the climate responses of zooplankton in the different parts of the Nordic Seas. For example, high NAO induces winds and precipitation in northern Norway (Hurrell et al. 2001) with possible positive effects on primary production and likely enhances *C. finmarchicus* abundance. In the Labrador Sea, however, high NAO is associated with cooling of surface waters and increased Labrador current flow. This extends the distribution of *C. hyperboreus* onto the Labrador shelf. Concurrently, the Labrador Subarctic Slope Water, rich in *C. finmarchicus,* moves eastwards, decreasing abundance of this species on

the Labrador shelf (Greene and Pershing 2000; Johns et al. 2001). Thus, high NAO tends to increase abundances of *C. finmarchicus* in the North East Atlantic (northern Norway) and of *C. hyperboreus* in the North West Atlantic (Labrador shelf). Similarly, high NAO is associated with low *C. finmarchicus* abundance in the North Sea (Fromentin and Planque 1996), but high abundance of the species in the Gulf of Maine (Conversi et al. 2001), which demonstrates variable effects of NAO on *Calanus* in the different locations of the North Atlantic Basin.

Species-specific variability

Calanus hyperboreus abundance was less closely related to environmental variables than the abundance of *C. finmarchicus* (Table 5). We assume that this is because the

Table 5 Significant covariation (Kendall's rank correlation) between environmental indices and total abundances (ind m^{-2}) of *Calanus finmarchicus* and *C. hyperboreus* in northern Norway (1983–2010), Svalbard (1996–2010), and northern Iceland (1990–2011)

Location	Species	Environmental variable	Environmental variable scale	Kendall's tau	P	df
Northern Norway	*C. finmarchicus*	NAO	Regional	0.386	0.004	26
Northern Norway	*C. finmarchicus*	AO	Regional	0.405	0.003	26
Svalbard	*C. finmarchicus*	Temperature	Local	0.186	0.031	61
Svalbard	*C. finmarchicus*	Salinity	Local	0.271	0.002	61
Svalbard	*C. finmarchicus*	Spring bloom start	Local	0.438	0.001	32
Svalbard	*C. hyperboreus*	Temperature	Local	0.177	0.040	61
Northern Iceland	*C. finmarchicus*	Temperature	Local	0.332	0.000	150
Northern Iceland	*C. finmarchicus*	Salinity	Local	0.234	0.000	150
Northern Iceland	*C. finmarchicus*	Chl *a* concentration	Local	−0.187	0.001	150
Northern Iceland	*C. hyperboreus*	NAO	Regional	−0.131	0.021	150

NAO North Atlantic oscillation, *AO* Arctic oscillation, *τ* Tau Kendall's rank correlation coefficient, *P* significance level of the rank correlation test, *df* degrees of freedom

Table 6 Hypothesized mechanisms accounting for the observed relationship between *Calanus finmarchicus* and *C. hyperboreus* populations in northern Norway, Svalbard, and northern Iceland, and environmental variability acting on local and regional spatial scales

Location	Spatial scale (environmental variable)	*C. finmarchicus*	*C. hyperboreus*
Northern Norway	Regional (climate)	High abundance at high NAO: increased fjord production and advective influx of individuals from oceanic population	
Svalbard	Local (hydrography)	High abundance when high advective influx from WSC waters	High abundance when high advective influx from WSC waters
	Local (phytoplankton)	High abundance when phytoplankton spring bloom is late: improved feeding conditions for early life stages	
Northern Iceland	Local (hydrography)	High abundance when high advective influx from NIIC	
	Local (phytoplankton)	High abundance at low Chl *a* concentration: high grazing pressure	
	Regional (climate)		High abundance at low NAO: increased deep-water transport of individuals from the Greenland Sea

relatively slow numerical response in the long-lived *C. hyperboreus* (Conover 1988; Hirche 1997) compared to that of *C. finmarchicus* (Østvedt 1955; Tande et al. 1985) weakens abundance responses to changes in the environment (May 1974) and render the link between *C. hyperboreus* dynamics and fluctuations in its local environment less strong than for *C. finmarchicus*. Moreover, *C. hyperboreus* is a capital breeder and, therefore, is capable of producing eggs at depth prior to the spring phytoplankton bloom (Varpe et al. 2009). This strategy likely reduces susceptibility to spring environment in contrast to that of the income breeding *C. finmarchicus*, which usually times egg reproduction to co-occur with the early phase of the spring phytoplankton bloom (Melle and Skjoldal 1998).

Calanus finmarchicus abundance was higher and varied less in all locations than that of *C. hyperboreus* (Table 2; Fig. 4). This difference between the two congeners can be attributed to the geographic location of our study sites, which were in the proximity of the centre of *C. finmarchicus* distribution, i.e. the Norwegian Sea Basin (Broms et al. 2009), or its extensions such as the WSC (Karnovsky et al. 2003). *Calanus hyperboreus*, on the other hand, is an Arctic oceanic species, with a centre of distribution in the Greenland Sea (Richter 1994; Hirche 1997). It is likely, therefore, that our study areas represented fringing or expatriated subpopulations of a much larger *C. hyperboreus* population located in the Greenland Sea proper. Such subpopulations are likely more susceptible to

stochastic processes (Hanski 1991), explaining high variability of *C. hyperboreus* in the study locations (Table 2).

Responses to productivity

Calanus finmarchicus abundance was high in years with delayed spring phytoplankton bloom (Table 5). We hypothesize that in such years, the species may have resorted to alternative, likely, microzooplankton food sources (Ohman and Runge 1994; Levinsen et al. 2000; Kwasniewski et al. 2013), which may have allowed for egg production in the absence of high phytoplankton concentrations. *Calanus finmarchicus* nauplii survive long periods of limited food availability (Hygum et al. 2000), and we speculate that years with delayed phytoplankton bloom may coincide with improved feeding conditions for intermediate developmental stages, and thus accelerated *Calanus* growth and development (Campbell et al. 2001; Cook et al. 2007). Such an effect likely enables an earlier descent to the overwintering habitat, thereby limiting exposure to the presumed seasonally increasing predation risk (Fiksen and Carlotti 1998; Pasternak et al. 2001; Varpe et al. 2007) and thus, increasing survival.

We believe that the negative relationship detected between Chl *a* and *C. finmarchicus* in northern Iceland occurred because the abundance of *C. finmarchicus* copepodites increased during the post-bloom phase, when Chl *a* concentration was decreasing (Heath et al. 2000; Head et al. 2013). Thus, rather than reflecting an abundance response to phytoplankton concentrations, this association likely reflected the recruitment of copepodite developmental stages into the population, which typically peaks after the spring Chl *a* maximum (Melle et al. 2014).

Implications for the Basin-scale variability in *Calanus* spp.

Our results suggest that several mechanisms, related to either food availability or advection, may explain the relationship between environmental variability and *Calanus* abundance in the Nordic Seas (Table 6). The environmental drivers involved could be characterized as acting primarily on local (hydrography, food) or regional scale (climate variability), yet the observed relationships largely seem to be brought about by variations in the influence of Atlantic water masses. This is in line with the view that advection-driven connectivity between populations in the subpolar Atlantic is a key to understand *Calanus* ecology (Speirs et al. 2006).

The differences in *Calanus* responses between locations observed in the present study likely reflected variable Atlantic influences on the study areas. In northern

Norwegian waters, for instance, the Atlantic influence largely reflects on-shore advection induced by climate-regulated wind stress (Helle and Pennington 1999; Ottersen et al. 2001). In western Svalbard waters, on the other hand, the Atlantic influence seems more controlled by climate-related variability in the WSC (Saloranta and Haugan 2001; Kwasniewski et al. 2012). In waters to the north of Iceland, the coupling between climate variability and Atlantic influence is less clear (Ólafsson 1999; Gislason et al. 2009).

Atlantic inflow to the Nordic Seas (red arrows in Fig. 1) varies with the interaction between the North Atlantic subpolar and subtropical gyres (Hátún et al. 2005), which tends to covary with NAO (Lohmann et al. 2008; Visbeck et al. 2013). Thus, we would expect a relationship between NAO and *Calanus* in all study locations. There are several reasons for why an underlying large-scale covariability may not produce detectable relationships with zooplankton abundances in studies like the present. Firstly, as discussed for Arctic waters above, there may be time lags between climate variability and biological responses (Heath et al. 1999; Blindheim et al. 2000), which makes detection of a climate signal difficult in the relatively short time-series available. Also, the recent warming of the North Atlantic has shifted the distribution of *Calanus* spp. (Chust et al. 2013), and in suboptimal habitats, climate responses may shift or weaken due to alterations in the thermal niche of the populations, as shown in the North Sea (Beaugrand 2012). Thus, it may be difficult to detect climate effects in data sets that include information from fringe populations. Thirdly, the total abundances composed of several cohorts of the multiannual species may not reveal significant covariation between individual developmental stages and climate indices.

Finally, most data sets, on which studies of zooplankton responses to climate are based, contain little information on top-down forcing, or how this may covary with climate. Predation is a significant mechanism regulating *Calanus* populations during both early (Plourde et al. 2009) and older developmental stages (Eiane et al. 2002). Thus, predation on *Calanus* may account for a considerable component of the interannual variability in *Calanus* populations (Ohman and Hirche 2001; Neuheimer et al. 2009). However, predator abundances are also significantly affected by climate variability (Orlova et al. 2010; Valdimarsson et al. 2012; Carscadden et al. 2013) in ways that may alter zooplankton abundances or life history strategies. This knowledge gap may bias our understanding of climate effects on zooplankton. Hence, we suggest that future research on *Calanus* abundance variations should consider both top-down and bottom-up mechanisms in addition to the effects of climate.

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