Effects of environmental conditions on the biomass of *Calanus* spp. in the Nordic Seas

JACOB CARSTENSEN[1]*, AGATA WEYDMANN[2], ANNA OLSZEWSKA[2] AND SŁAWOMIR KWAŚNIEWSKI[2]

[1]DEPARTMENT OF BIOSCIENCE, ARCTIC RESEARCH CENTRE, AARHUS UNIVERSITY, FREDERIKSBORGVEJ 399, DK-4000 ROSKILDE, DENMARK AND
[2]INSTITUTE OF OCEANOLOGY, POLISH ACADEMY OF SCIENCES, POWSTAŃCÓW WARSZAWY 55, 81-712 SOPOT, POLAND

*CORRESPONDING AUTHOR: jac@dmu.dk

The biomass of *Calanus* spp. in the Norwegian Atlantic Current and the West Spitsbergen Current (2001–2009) was statistically related to a combination of salinity, temperature, water depth and sea ice concentration. The aim of this study was to identify the significance of these environmental factors for controlling the species-specific biomass distribution and the nature of such relationships. *Calanus finmarchicus* dominated the entire area and its biomass was mainly related to salinity. *Calanus glacialis* was mainly found along the northwest shelf of the Barents Sea, but its biomass was also related to the sea ice concentration and temperature with a critical threshold ∼6°C, above which the presence and biomass of *C. glacialis* decreased. The *Calanus hyperboreus* biomass was related to all environmental factors, which characterized by a confined spatial distribution to water associated with the Greenland Sea Gyre. We conclude that *C. hyperboreus* is an expatriate to the study area. The *Calanus* biomass distribution will not change greatly in the study area with an expected increase of water temperature by 2°C, whereas the critical temperature threshold for *C. glacialis* will be exceeded with temperature increases of ∼4°C with a likely disappearance of this cold water species from the north-west shelf of the Barents Sea.

KEYWORDS: generalized additive model; geographical distribution; life strategy; northeast Atlantic; tipping point

INTRODUCTION

The global sea surface temperature (SST) has increased by 0.135°C per decade from 1979 to 2005 (HadSST2), but temperature trends in many areas of the Arctic have been three to four times greater (ACIA, 2004; Steele *et al.*, 2008). These trends are partly associated with increasing temperature and salinity in the inflowing Atlantic water masses (Morison *et al.*, 2000; Hansen *et al.*, 2004; Walczowski and Piechura, 2007). The temperature increase has led to a rapid decline in the sea ice cover in the Arctic (Stroeve *et al.*, 2007; Comiso *et al.*, 2008). Such changes in the physical setting of the Arctic Ocean may precipitate changes in the food-web structure through changed light conditions and mixing processes, and consequently primary production (Gradinger, 1995; Arrigo *et al.*, 2008). Warming can also affect the plankton community structure through temperature-dependent physiological constraints (Roleda *et al.*, 2008), alteration of ecological niches and seasonality (Helaouët and Beaugrand, 2007) and invasion of

lower-latitude species into the Arctic (Carmack and Wassmann, 2006).

In the Arctic, copepods are important grazers of the primary production (Nielsen and Hansen, 1995), constitute an important food source for numerous fish, bird and whale populations (Gislason and Astthorsson, 2002; Heide-Jørgensen and Acquarone, 2002; Karnovsky et al., 2003) and enhance the biological pump of biogenic carbon into the deep ocean (Pasternak et al., 2002). Moreover, copepods enhance the vertical flux of organic matter to the benthic community by producing fast-sinking faecal pellets (Pedersen et al., 2006). Three copepods of the genus *Calanus* dominate the mesozooplankton biomass in the North Atlantic–Arctic Ocean area (Conover, 1988; Falk-Petersen et al., 2007). *Calanus finmarchicus* is a subarctic species associated with Atlantic water. *Calanus glacialis* is a cold-adapted (Arctic) species associated with the productive shelf waters of the Arctic seas. *Calanus hyperboreus* is a cold water (Arctic) species too, but with centres of distribution associated predominantly with deeper waters of the Greenland Sea and the Arctic Ocean. Both larger Arctic species have a higher total lipid content allowing for longer diapause and multiyear life cycles at high latitudes, whereas the smaller *C. finmarchicus* has a lower lipid content and typically a one-year life cycle, although multi-generation cycles within 1 year are observed in warmer waters (Conover, 1988; Lee et al., 2006; Falk-Petersen et al., 2009). The largest of the North Atlantic–Arctic Ocean species, *C. hyperboreus*, because of its size and higher energy reserves may live longer periods with limited food supplies; thus it can better survive long distance advection and become expatriated (Conover, 1988).

These species-specific differences in sizes, lipid content and life strategies are believed to be mainly controlled by seasonal variation in primary production, as well as differences in the habitats that the *Calanus* species occupy (Falk-Petersen et al., 2009). All three *Calanus* species time their ascent from diapause to the occurrence of the spring primary production bloom, although recent studies suggest that *C. glacialis* may time its seasonal migration with the ice algae spring development that precedes the pelagic bloom (Leu et al., 2011). The pelagic primary production in the Arctic has increased in the recent decade, with an earlier onset of the pelagic bloom and an extended growing season (Arrigo et al., 2008). However, due to the earlier melting of the sea ice, the growth season and production of ice algae has reduced (Søreide et al., 2010). Hence, temperature increases and the melting of the sea ice are likely to shift the food availability from ice algae more towards phytoplankton, and this may lead to shifts in

optimal conditions for the *Calanus* species with different life strategies (Søreide et al., 2010).

Temperature increases may also cause shifts between *Calanus* species, because of differences in their temperature-dependent physiology. In addition to food availability, *Calanus* ingestion rates are also temperature dependent with optimum rates $\sim 11-12°C$ for *C. finmarchicus* and *C. hyperboreus* and somewhat lower ($\sim 9°C$) for *C. glacialis* (Møller et al., unpublished results). In a laboratory experiment from Western Greenland, the early spawning *C. glacialis* had a higher specific egg production at lower temperatures than *C. finmarchicus*, whereas the specific egg production of *C. finmarchicus* increased greatly and exceeded that of *C. glacialis* for temperatures above 5°C (Kjellerup et al., 2012). For *C. hyperboreus*, laboratory experiments did not show a temperature effect ($0-10°C$) either on egg production or faecal pellet production (Henriksen et al., 2012). Based on the results from laboratory experiments, it is likely that warming of the Arctic will competitively benefit *C. finmarchicus* more than *C. glacialis* in a situation without food limitation during the onset of the pelagic primary production, because of higher ingestion and egg production rates, whereas *C. hyperboreus* might be unaffected by increasing temperatures.

The objective of the present study was to investigate if temperature, in addition to other environmental factors, could explain the biomass distribution of the three *Calanus* species in the Nordic Seas region, where Atlantic and Arctic water masses mix and all three species are present. Secondly, we wanted to examine the nature of such a temperature relationship for potential tipping points that may drastically alter the zooplankton community and assess potential consequences thereof in a warming North Atlantic region.

METHOD

The Norwegian Atlantic Current (NAC) and its continuation, the West Spitsbergen Current (WSC), constitute the main conduit of Atlantic water into the Arctic Ocean (Rudels et al., 2004; Walczowski et al., 2012) and provide the dominant oceanic heat source for the Arctic (Schauer et al., 2004). The northward flow of the Atlantic water along the Nordic Seas (the spatial distinction including the Icelandic, Norwegian, Greenland and Barents Seas) is channelled also by hydrological fronts, separating cold waters of the Greenland Sea and the Barents Sea; therefore the region of the WSC is a mixing zone between the warm saline Atlantic water and cold-less saline Arctic waters. This forms a confluence

zone where the three dominant *Calanus* species may co-occur (Hirche *et al.*, 1991).

Data

In the study area, hydrographic profiles and zooplankton have been collected at 52 stations along longitudinal transects from south to north (Fig. 1) over a 9-year period (2001–2009). Transects covered the depth gradient from the deep parts of the Greenland and Norwegian Seas to the shallower shelf areas of the Barents Sea and Svalbard. Depths at the stations ranged from 51 m to almost 5000 m with an average of 1543 m. Eleven of the 52 stations were located on the shelf (<500 m, Daase *et al.*, 2007). The monitoring cruises were conducted with the Institute of Oceanology Polish Academy of Sciences (IO PAS) SY Oceania, every year during a 3-week period from late June to mid-July, and the timing of the cruises only changed by a few days between years. Between 18 and 37 stations were sampled each year, totalling 237 profiles of the hydrographic conditions and zooplankton distribution.

Temperature and salinity were sampled with a SeaBird SBE 49 FastCAT temperature, conductivity, depth (CTD) probe, or its equivalent, and zooplankton was collected with a WP-2 mesozooplankton net (mouth opening 0.25 m^2, 180 μm mesh, Tranter and Fraser, 1968). Depth-stratified hauls were taken from a depth of 200 m to the surface, typically from three or two layers indicated by the temperature–salinity distribution profile to represent the different types of waters.

Zooplankton samples were preserved in 4% solution of buffered formaldehyde in seawater, immediately after sampling, and counted later in a laboratory. *Calanus* species and their copepodid stages were identified from measured prosome lengths following the procedures in Kwaśniewski *et al.* (Kwaśniewski *et al.*, 2003) and Weydmann and Kwaśniewski (Weydmann and Kwaśniewski, 2008). The *Calanus* biomass was calculated from abundance data and taxon- and stage-specific dry mass values according to Bachowiak-Samoyk *et al.* (Bachowiak-Samoyk *et al.*, 2008). The majority of the *Calanus* community was found in the uppermost 100 m, and therefore only the surface and middle layer samples, representing the seasonal upper mixed and pycnocline
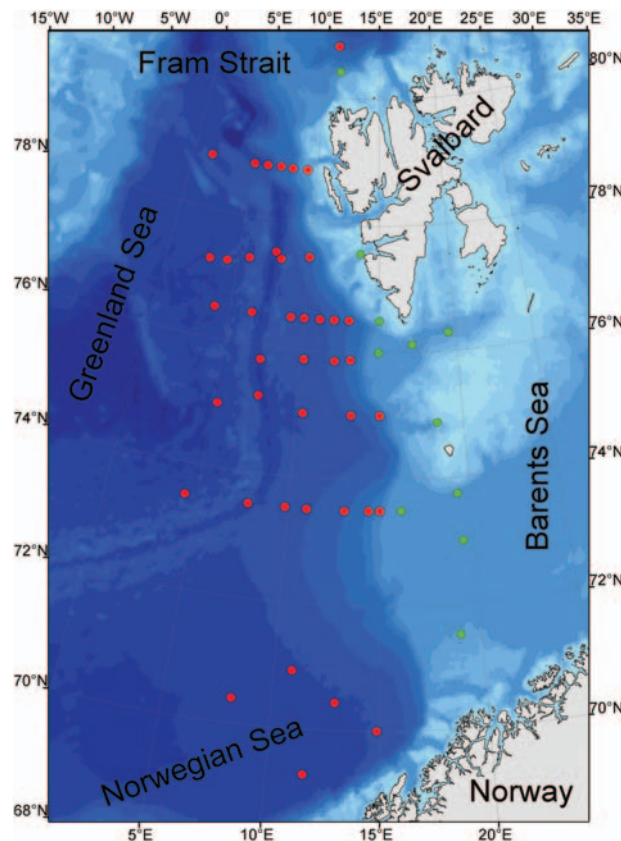

Fig. 1. Location of zooplankton sampling stations (green = shelf; red = oceanic) in the Northeast Atlantic (2001–2009). Bathymetry is the ETOPO2 from the NOAA National Geophysical Data Center (www.ngdc.noaa.org).

layers, were taken into consideration. For the purpose of the study, the abundance and biomass data were aggregated and expressed as abundance and biomass in cubic meter of the water column ($\sim$100–0 m).

Temperature and salinity were calculated as average values for the upper and middle layers, and combined in the database with the zooplankton data. Additionally, the average sea ice concentration, a measure of the ice coverage between 0 and 100%, for the first 6 months of the year was obtained from satellite imagery (www.nsidc.org) by identifying the nearest grid cell to the sampling stations. This measure gives an estimate of the length of the ice-covered period prior to the zooplankton sampling.

Statistical analyses

Prior to the statistical analyses, various transformations were employed to stabilize the variance, reduce the influence of observations in the tails of the empirical distributions and to produce a more even spread of the observations (Supplementary data, Fig. S1 and S2). The *Calanus* biomass was strongly right-skewed suggesting that the observations should be log-transformed. *Calanus finmarchicus* was found in all samples and the ordinary log-transformation applied, whereas *C. hyperboreus* was found in 221 out of 237 samples ($\sim$93%) and therefore the log-transformation [$\log(X + 0.01)$] was applied to account for the presence of zero observations, where the value 0.01 was chosen as slightly smaller than the lowest observed biomass. This transformation was justified given the relatively few samples without *C. hyperboreus*. However, *C. glacialis* was found in only 180 out of 237 samples ($\sim$76%), which would make most statistical analyses more sensitive to the choice of a small added value in the log-transformation. Therefore, *C. glacialis* was analysed as a compound distribution using a binomial distribution to describe the presence/absence and a lognormal distribution to describe the biomass, when present (180 samples). The water depth was log-transformed and temperature was not transformed. Salinities, corresponding to zooplankton samples, ranged from 33.7 to 35.2 with a tendency to concentrate at the upper limit. Therefore, the following transformation, $\log(35.3 - X)$, was applied to give more even spread of salinity and reduce the potential influence of observations with lower salinity. Finally, sea ice concentrations were log-transformed using $\log(X + 1)$ to account for zero observations. Estimates from the statistical analyses were back-transformed using the inverse transformation representing median values. All statistics were carried out using SAS version 9.3.

Temporal trends of the physical characteristics and the biomass of the *Calanus* species were investigated using the generalized mixed model presented below, on the transformed variables, assuming these to be normally distributed, except for the presence/absence of *C. glacialis* that was binomially distributed and linked to the predictors using the logistic transformation. Thus, Υ denotes any of the physical or *Calanus* transformed variables modelled as

$$\Upsilon = year + area + year \times area + station(area) + year \\ \times station(area) + e, \tag{1}$$

where *year* describes the variation between years (df $= 8$), *area* describes the difference between oceanic and shelf stations (df $= 1$) and *year* $\times$ *area* is a factor indicating if the trends differed from oceanic to shelf stations (df $= 8$). The random factors (each having 1 df) are the variation among stations within area (*station(area)*), the variation in trends among stations (*year* $\times$ *station(area)*) and the residual variation *e*. Annual means for the 9 years were calculated as marginal means from equation (1), unbiased by differences in the stations sampled across years, and back-transformed to represent a median statistic in the annual distributions.

The biomass of the different *Calanus* species, as well as the presence/absence of *C. glacialis*, was analysed in relation to salinity, temperature, sea ice concentration and water depth with the transformations described above. It was assumed that salinity and temperature characterize the different water masses, whereas water depth, sea ice concentration and temperature might explain differences in inter-species competition and life strategies. The four explanatory variables would constitute the most important predictors for the *Calanus* species, although the nature of these relationships was not known. Therefore, a non-parametric modelling approach, generalized additive models (GAM, Hastie and Tibshirani, 1990), was employed using splines to describe relationships between the physical variables and the *Calanus* biomass as well as the presence/absence of *C. glacialis*. The degrees of freedom for the splines, a proxy measure of its curvature, were selected by general cross-validation, however, with a maximum of 3 degrees of freedom imposed to reduce the potential deformation of the fitted curve. The least significant explanatory factor was removed until all remaining effects were significant in the manner by which non-significant splines were reduced to linear functions and non-significant linear functions were removed. By this backward-elimination process, only those explanatory variables capable of explaining a significant portion of the

variation in the *Calanus* biomass and its presence/absence were retained.

The spatial distribution of the *Calanus* species over the study area ($\sim$425 000 km^2) was predicted from the estimated GAMs using spatial information on salinity, temperature, sea ice concentrations and bathymetry. The spatial distribution of salinity and temperature was found by spatial interpolation (ordinary kriging, Cressie, 1993) of station means obtained from equation (1), and sea ice concentrations (January–June) were averaged over the 9-year period. The resulting *Calanus* biomass distributions only described the large-scale spatial variations of the study area.

The potential effect of seawater temperature increase on the *Calanus* species was assessed by predicting the spatial distribution of the biomass of the three species from the GAMs using the present spatial temperature distribution and adding an expected temperature increase of 2°C at the end of the century as estimated for the neighbouring Barents Sea by Slagstad *et al.* (Slagstad *et al.*, 2011), and consistent with the zooplankton

scenarios in Ji *et al.* (Ji *et al.*, 2012). Slagstad *et al.* (Slagstad *et al.*, 2011) also predicted minor changes in salinity and almost complete disappearance of sea ice in the Barents Sea by the end of the century, and therefore, the salinity remained unchanged in the scenario and it was assumed that sea ice will have disappeared from the study area.

RESULTS

Temporal trends

The summer mean temperatures in the study area varied from 3.4°C in 2001 to 5.8°C in 2006 at the shelf stations and from 4.7°C in 2001 to 6.5°C in 2006 at the oceanic stations (Fig. 2A). The inter-annual variations in temperature were rather synchronous for shelf and oceanic stations as confirmed by the non-significant interaction *year* × *area* for temperature (Table 1). Mean salinities were significantly lower at the shelf stations and varied between 34.6 in 2001 and 35.0 in 2007,
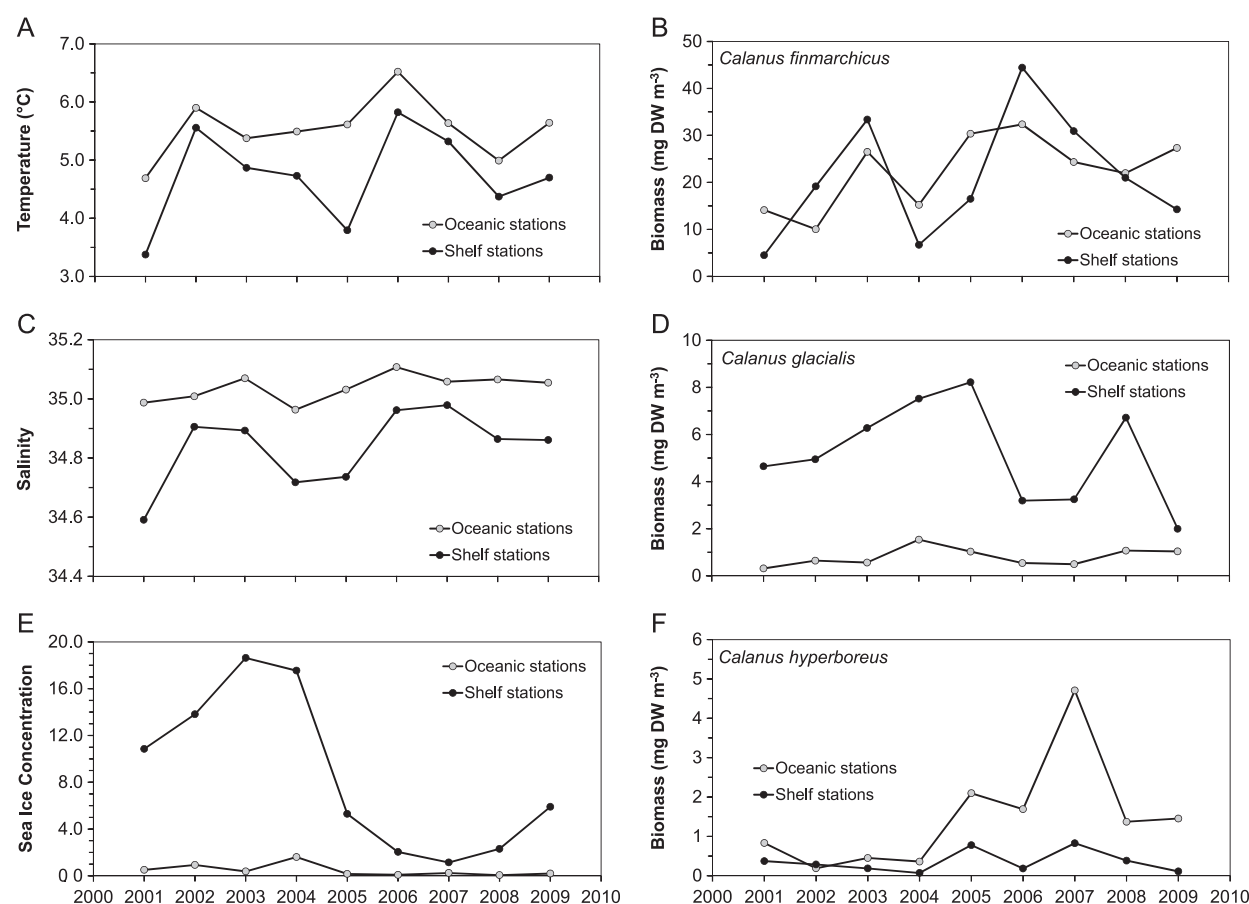

Fig. 2. Trends in the annual means of the physical variables (left panel) and the *Calanus* biomass (right panel) for oceanic and shelf stations (see Fig. 1). The significance of the variation across years and oceanic versus shelf stations is given in Table I.

whereas inter-annual variation was less at the oceanic stations ranging between 35.0 and 35.1 (Fig. 2B). However, salinity trends at the shelf stations did not significantly differ from those of the oceanic stations due to large random variation in the trends among stations within shelf and oceanic stations (Table I). Sea ice conditions at the shelf stations varied substantially across years, peaking in 2003 and with a minimum in 2007 (Fig. 2C), and this trend was significantly different from that observed at the oceanic stations with little sea ice recorded (Table I).

The biomass of *C. finmarchicus* was about one order of magnitude higher than those of *C. glacialis* and *C. hyperboreus* at both shelf and oceanic stations (Fig. 2D–F). The *Calanus glacialis* biomass did not exhibit any significant systematic variation across the 9 years, neither at the shelf stations nor in general, whereas both *C. finmarchicus* and *C. hyperboreus* showed significant inter-annual variations in biomass, which were similar at both the shelf and oceanic stations (Table I). *Calanus glacialis* biomass was significantly higher at the shelf stations (median of 5.4 versus 0.88 mg DW m^{-3} at the oceanic stations), whereas the opposite was observed for *C. hyperboreus* (medians of 1.00 and 0.28 mg DW m^{-3} at the oceanic and shelf stations, respectively), and the biomass of *C. finmarchicus* was more similar across both

shelf and oceanic stations (median of 19.0 mg DW m^{-3}, Table I). Trends of the *C. finmarchicus* biomass significantly correlated with salinity trends for both oceanic and shelf stations, but also (and to a lesser degree) with sea ice concentrations for oceanic stations and to temperature for shelf stations (Table II). Trends in the biomass of *C. glacialis* and *C. hyperboreus* did not correlate with any of the trends in physical variables.

GAM relationships to physical properties

Separating the water depth into oceanic and shelf stations may seem somewhat arbitrary and therefore the water depth was included in the GAM approach, in addition to salinity, temperature and sea ice concentration, to better describe the continuum from a shallow to deep station. Following the approach of maintaining significant predictors only, variations in the *C. finmarchicus* biomass could be linked to salinity (transformed) in a linear manner and to the water depth in a non-linear manner (Fig. 3). The strong linear relationship with the transformed salinity variable ($P < 0.0001$) resulted in a curvilinear relationship suggesting that the biomass of *C. finmarchicus* increased by an order of magnitude going from salinities <34 to >35. The relationship to the water depth was less significant and indicated highest

Table I: A generalized mixed model [equation (1)] for describing transformed variables for the physical conditions and Calanus *species*

Variable	Transformation	# of obs.	P(year)	P(area)	P(year × area)
Temperature	—	237	**<0.0001**	0.1316	0.5421
Salinity	Log(35.3 − X)	237	**<0.0001**	**0.0004**	0.4492
Sea ice conc.	Log(X + 1)	237	**<0.0001**	**<0.0001**	**<0.0001**
C. finmarchicus	Log(X)	237	**0.0046**	0.3653	0.4068
C. glacialis (B)	Log(X)	180	0.6412	**0.0001**	0.8656
C. glacialis (I)[a]	Logistic	138	0.2241	0.8672	0.0847
C. hyperboreus	Log(X + 0.01)	237	**0.0002**	**0.0113**	0.4133

For *C. glacialis*, both biomass (B) and presence/absence (I) were modelled.
The three last columns list the significance of the three fixed factors in equation (1) with those significant at the $P < 0.05$ level emphasized in bold.
[a]Model run for those years only, when *C. glacialis* was found both present and absent in the samples (2001, 2004, 2006, 2007 and 2009).

Table II: Pearson's correlation coefficients and their probability of significance (in parentheses below) for trends in the Calanus *biomass versus trends in physical variables (SIC, sea ice concentration) stratified by oceanic and shelf stations (*n = 9 years)

Biomass	Oceanic stations			Shelf stations		
	Salinity	Temp.	SIC	Salinity	Temp.	SIC
C. finmarchicus	**0.78 (0.0125)**	0.42 (0.2600)	**−0.71 (0.0307)**	**0.83 (0.0057)**	**0.71 (0.0334)**	−0.35 (0.3600)
C. glacialis	−0.34 (0.3753)	−0.02 (0.9669)	0.44 (0.2390)	−0.44 (0.2312)	−0.44 (0.2409)	0.40 (0.2922)
C. hyperboreus	0.39 (0.3005)	0.16 (0.6788)	−0.49 (0.1799)	0.05 (0.9040)	−0.23 (0.5437)	−0.53 (0.1457)

Correlations significant at the $P < 0.05$ level are emphasized in bold.

biomass concentrations at depths ranging from 100 to 1000 m, i.e. corresponding to the shelf break between the Norwegian/Greenland Sea and the Barents Sea/Bear Island and Spitsbergen shelf/slope area. The model predicted a halving in the biomass towards the deepest depths.

The biomass of *Calanus glacialis* was significantly related to several factors. The biomass decreased linearly with salinity (transformed), whereas the relationship to temperature was non-linear with a constant plateau for temperatures below ~6°C and decreasing biomass above this threshold (Fig. 4). The temperature effect on
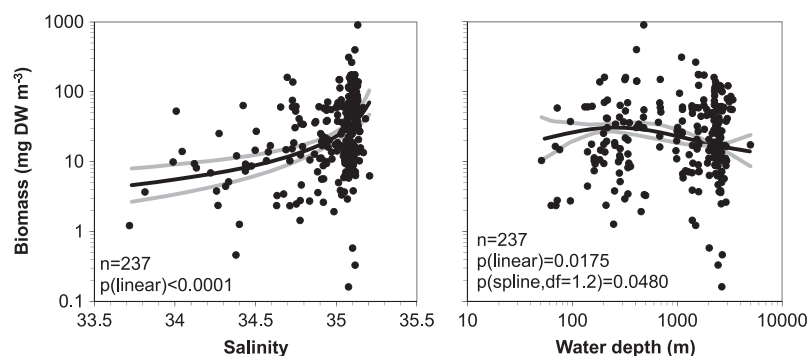

Fig. 3. The biomass of *Calanus finmarchicus* versus significant predictors and their estimated relationship from the GAM approach with 95% confidence interval marked by grey lines. Biomass, salinity and water depth have been transformed back to their original scale after estimating the relationships. The degrees of freedom (df) listed for the spline function is in addition to the linear function. Note the logarithmic scale for biomass and water depth. Spatial correlations of the residuals are shown in Supplementary data, Figure S3.
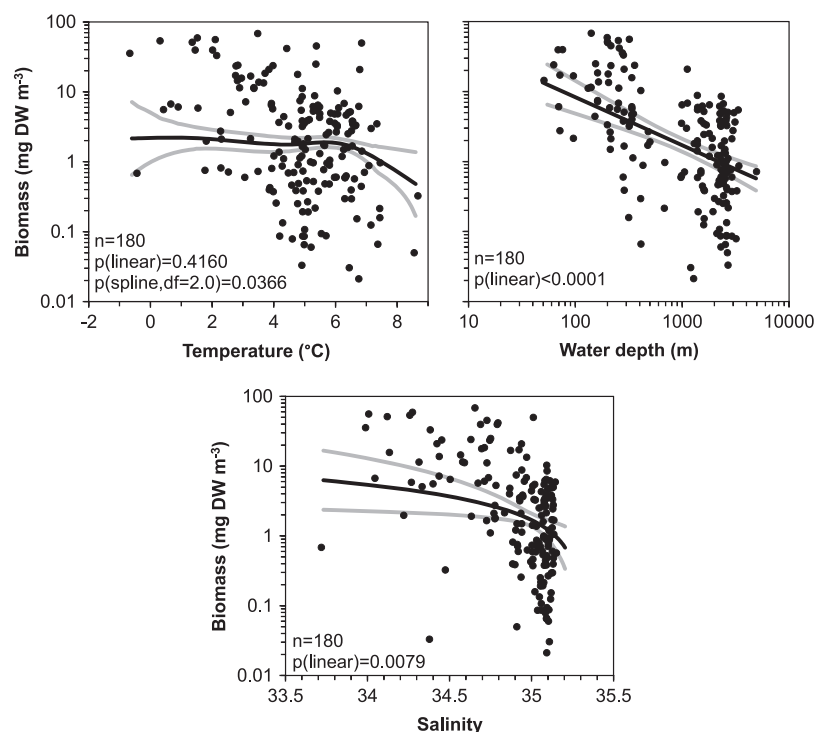

Fig. 4. The biomass of *Calanus glacialis* versus significant predictors and their estimated relationship from the GAM approach with 95% confidence interval marked by grey lines. Biomass, salinity and water depth have been transformed back to their original scale after estimating the relationships. The degrees of freedom (df) listed for the spline function is in addition to the linear function. Note the logarithmic scale for biomass and water depth. Spatial correlations of the residuals are shown in Supplementary data, Figure S4.

the biomass from 6 to 8°C was almost one order of magnitude, as was the effect of salinity changing from <34 to >35. Additionally, the biomass of *C. glacialis* decreased linearly with the log-transformed water depth (Fig. 4), confirming that this species is predominantly found on the shelf and in association with Arctic-type waters. The change from the shallowest to the deepest stations was more than one order of magnitude in biomass concentration.

The presence of *Calanus glacialis* was, as for the biomass, related to temperature in a non-linear manner with a high probability of the presence (90–95%) for the temperatures below ~6°C and then declining rapidly with <50% chance of presence for temperatures >7.4°C (Fig. 5). In fact, *C. glacialis* was observed in almost every sample with temperature <5°C, except for five samples from the northwest of the study area, likely influenced by water from the Greenland Sea Gyre. The probability of presence was also positively related to the sea ice concentration (Fig. 5), such that *C. glacialis* would typically be observed at stations that had sea ice during the 6 months before sampling. Only three samples with a reasonable sea ice cover did not have any *C. glacialis*, although these samples were from stations where *C. glacialis* would normally be observed.

The biomass of *Calanus hyperboreus* was related to all physical variables in the GAM approach (Fig. 6). The model predicted a biomass increase with salinity (transformed) by almost one order of magnitude from salinities <34 to >35, although biomass observations at low salinities were higher than the modelled ones. On the other hand, these observations were explained by temperature that had a linear negative relationship to the biomass. Temperature actually described variations in the biomass across the entire range, corresponding to three orders of magnitude. The biomass of *C. hyperboreus*

was also related to sea ice concentrations with the highest values observed in ice-free waters, although changes in the biomass over the range of sea ice concentrations be less than one order of magnitude. Finally, the biomass increased with the water depth up to 200 m, remained at a constant level of ~0.3 mg DW m^{-3} up to 1000 m, and then increased with the water depth again.

The residuals from the GAMs were analysed for potential spatial correlation by examining the variograms of the residuals stratified by year (Supplementary data, Fig. S3–S5). Spatial correlation in the residual influences the significance of the identified explanatory factors (P-values increase) if present, but the residuals from the GAMs did not show any systematic tendency to be spatially correlated. The advantage of the GAM approach to correlating trends (Table II) was that it included several factors and their variations in time and space, whereas the correlation analysis considered one explanatory factor at a time for $n = 9$ years only. Therefore, the GAM approach was more powerful than the correlation analysis for discerning potential relationships, and, as a result, significant explanatory factors were found for *C. glacialis* and *C. hyperboreus* by the GAM approach, which were not identified by the correlation analysis.

Spatial distribution of *Calanus* spp.

Predicting the spatial distribution of the three dominating *Calanus* species from the GAMs required that the mean spatial distributions of salinity and temperature were computed first from station means using ordinary kriging. The mean salinity decreased gradually from over 35.1 in the southwest of the study area towards the Barents Sea and Fram Strait, reaching 34.6 in the northern corner of the study area (Fig. 7A). Mean
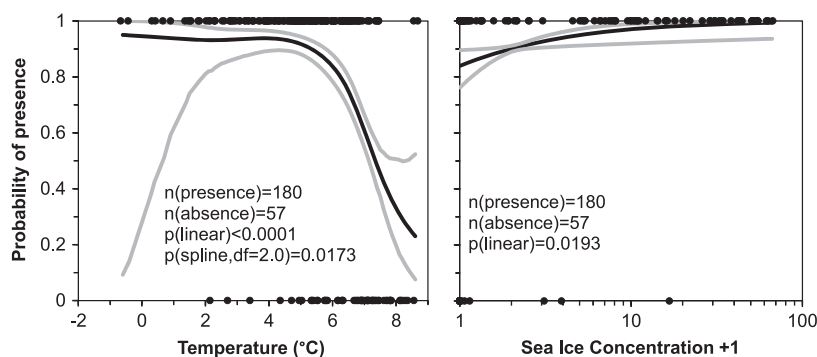

Fig. 5. The presence/absence of *Calanus glacialis* versus significant predictors and the estimated relationship for the probability of presence estimated from the GAM approach with 95% confidence interval marked by grey lines. Sea ice concentration has been transformed back to its original scale after estimating the relationship. The degrees of freedom (df) listed for the spline function is in addition to the linear function. Note the logarithmic scale for sea ice concentration.
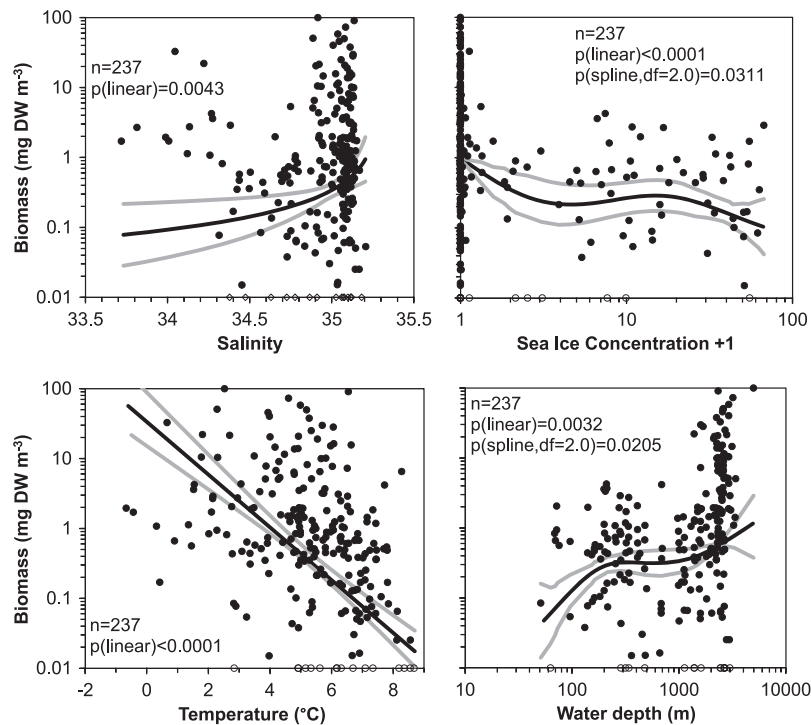
Fig. 6. The biomass of *Calanus hyperboreus* versus significant predictors and their estimated relationships from the GAM approach with 95% confidence interval marked by grey lines. Biomass, salinity, sea ice concentration and water depth have been transformed back to their original scale after estimating the relationships. The degrees of freedom (df) listed for the spline functions is in addition to the linear functions. Open symbols show observations without any *C. hyperboreus* counted, and which for the statistical analyses were substituted by a low biomass of 0.01 mg DW m^{-3}. Note the logarithmic scale for biomass, sea ice concentration and water depth. Spatial correlations of the residuals are shown in Supplementary data, Figure S5.

temperatures were relatively high along the tongue of water constituting the NAC and the WSC running along the shelf break until confronted with Arctic and Polar waters in the Fram Strait (Fig. 7B). Temperatures decreased towards the Barents Sea shelf and the Greenland Sea. The mean temperature ranged from 0.4°C in the north to 8.6°C in the south. Large parts of the study area were ice-free (77% had sea ice concentration <1) with sea ice found only around Svalbard and close to the Fram Strait (Fig. 7C).

The biomass of *C. finmarchicus* was strongly related to salinity yielding a spatial distribution similar to Figure 7A, although with decreases in biomass towards the deeper Greenland Sea (Fig. 8). The *C. finmarchicus* biomass was not related to temperature (only salinity and water depth were significant; see Fig. 3) and therefore the scenario analysis for temperature increase was not conducted. *Calanus glacialis* was mainly distributed on the shelf around Spitsbergen and towards Bear Island, south of Spitsbergen (Fig. 9A). This shallow area is influenced by sea ice and transport of Arctic waters from the east. A 2°C increase in the water temperature will have a minor effect on the biomass of *C. glacialis*

(Fig. 9B), because temperatures in this area are low (Fig. 7B) and will not exceed the potential critical threshold ~6°C (Fig. 4). However, this threshold will be exceeded with a temperature increase of 3–4°C, with predicted declines in the biomass of *C. glacialis* as a consequence. *Calanus hyperboreus* was entirely distributed in the deeper and colder waters in the western study area (Fig. 10A). Owing to the strong linear relationship with temperature found in our study (Fig. 6), the biomass of *C. hyperboreus* is predicted to be reduced by >80% from a 2°C increase in water temperature, suggesting that *C. hyperboreus* will disappear from the study area (Fig. 10B).

DISCUSSION

Correlation analyses are useful tools for understanding and predicting how biological components may respond to changes in environmental factors. Although empirical relationships, such as those reported here, do not necessarily imply causal relationships, they provide important support to experimental and theoretical studies. Particularly, statistical analyses based on *in situ* data can discriminate
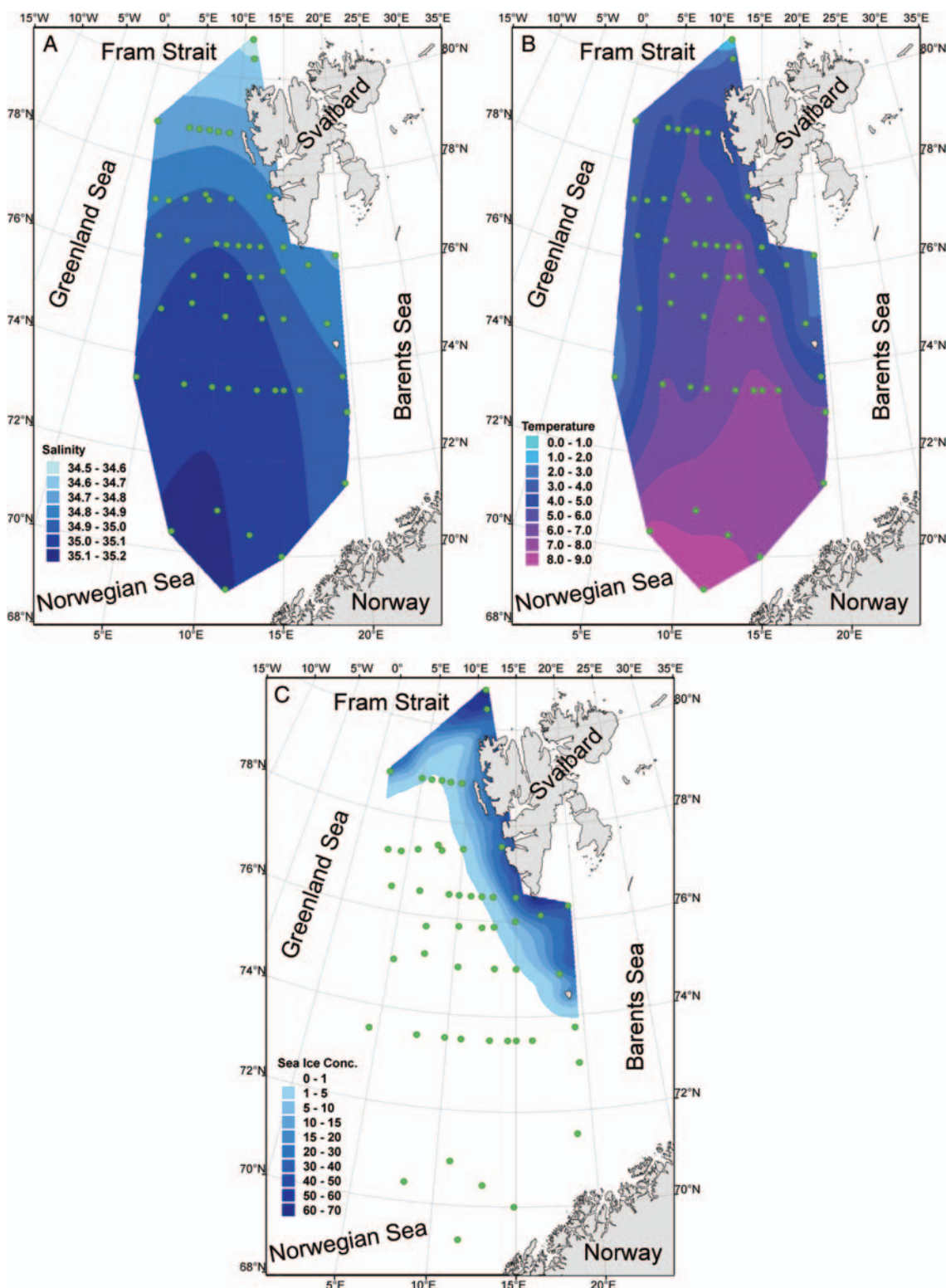
Fig. 7. The spatial distribution of salinity (**A**) and temperature (**B**) over the study area (beginning of July) calculated from station-specific means (2001–2009) interpolated using ordinary kriging. The average sea ice concentration in percent (**C**) for January–June (2001–2009) interpolated using ordinary kriging.
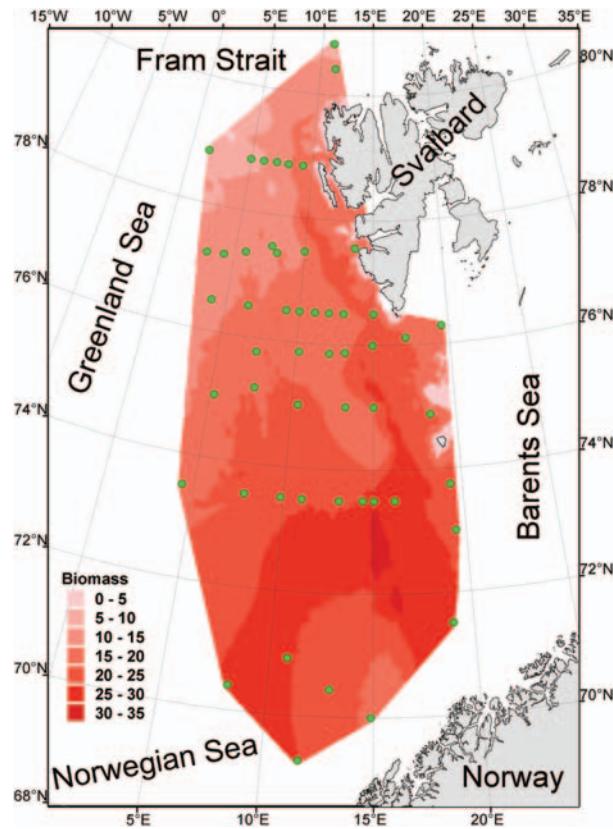
Fig. 8. The spatial distribution of the *Calanus finmarchicus* biomass (mg DW m^{-3}, beginning of July) predicted from the GAM approach [equation (1); Fig. 3]. The distribution was calculated within the spatial span of the sampling stations only.

between important and less important relationships reported in the literature. In this study, we have included four explanatory variables that directly or indirectly influence the presence and the population biomass of the three *Calanus* species present in the Nordic Seas. Differences in presence and biomass are due to species-specific life strategies, determining the species' core geographical distribution, and expatriation by ocean currents to regions that are not necessarily favourable to their life strategies (Conover, 1988). Temperature, and, particularly, salinity are indicators of the influence of water masses mixing in the study area, whereas water depth, sea ice concentrations and temperature may explain differences resulting from species-specific life strategies (Falk-Petersen *et al.*, 2009).

Most regional studies linking zooplankton communities to hydrology have investigated linear, or at least monotonic, relationships using various univariate or multivariate methods. Daase *et al.* (Daase *et al.*, 2007) used linear regressions, stratified between deep and shallow stations, to investigate relationships between *Calanus* abundances versus temperature and salinity from north of Svalbard. Dvoretsky and Dvoretsky (Dvoretsky

and Dvoretsky, 2011) also investigated linear relationships between copepod abundances in the northern Barents Sea and salinity and temperature. Kane (Kane, 2007) linked ordinations of the zooplankton community on Georges Bank with principal components of various environmental variables, including salinity, temperature, phytoplankton colour index from Continuous Plankton Recorders, North Atlantic Oscillation and total biomass of Atlantic herring and mackerel. Tande *et al.* (Tande *et al.*, 2000) used correspondence analysis to link the zooplankton community structure in the Norwegian and Barents Seas to the density, temperature, water depth, latitude, longitude and day of sampling. Finally, Reygondeau and Beaugrand (Reygondeau and Beaugrand, 2011) used salinity and temperature to estimate the probability of the presence of *C. finmarchicus* in the North Atlantic using a non-parametric approach. Thus, the four environmental variables we have chosen in our study seem common to most studies, but our approach is the first attempt to actually identify the nature of these relationships, going beyond the assumptions of linearity.

The sampling strategy moving from south to north during 1 month from late June to mid-July allowed the
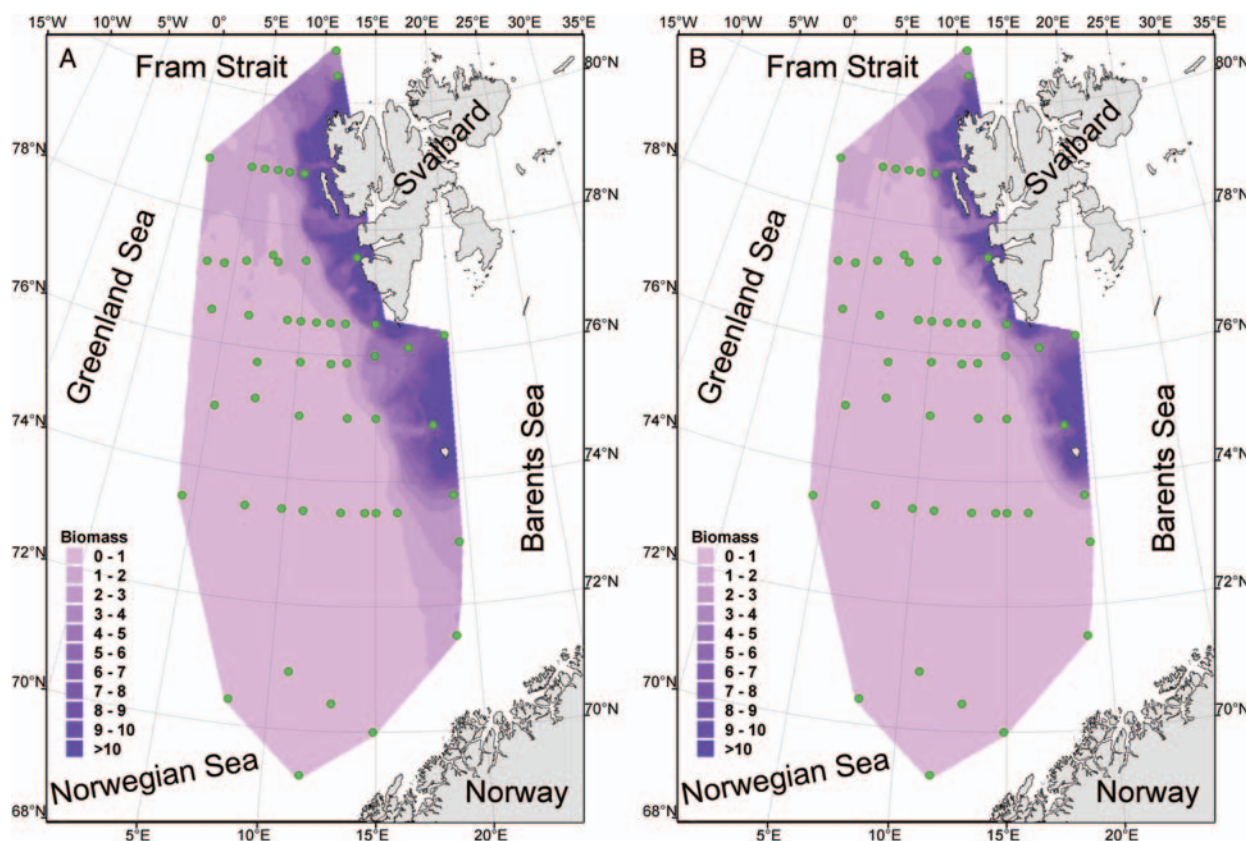
Fig. 9. The spatial distribution of *Calanus glacialis* biomass (mg DW m^{-3}, beginning of July) predicted from the GAM approach [equation (1); Figs 4 and 5] under present conditions (**A**) and from a 2°C temperature increase (**B**). The distribution was calculated within the spatial span of the sampling stations only.

expected pelagic bloom and ascendance of the *Calanus* to be followed. The fact that most of the biomass for all three *Calanus* species was found above the seasonal pycnocline confirms that sampling was not carried out in advance of their ascendance. For comparison, to the south of our study area, in the centre of the Norwegian Sea Østvedt (Østvedt, 1955) observed the beginning of the seasonal reappearance of *C. finmarchicus* at depths 600–100 m after mid-June, and Halvorsen and Tande (Halvorsen and Tande, 1999) reported that, at Northwestbanken, the largest part of the population of this species was found in the upper 50 m from April to September. Daase *et al.* (Daase *et al.*, 2007) sampled northeast of the present study area from mid-August to mid-September and found, similar to our results, that most of the *Calanus* biomass was present in the uppermost 100 m. However, they also observed that older stages of the *Calanus* populations were found in deeper waters, as they already started the seasonal descent. The chosen sampling strategy and the period therefore seem appropriate for characterizing the *Calanus* populations during and shortly after the peak of pelagic production,

consistent with the latitudinal differences outlined in Leu *et al.* (Leu *et al.*, 2011) and Speirs *et al.* (Speirs *et al.*, 2006).

Factors governing *Calanus* distribution

The biomass of *C. finmarchicus* was related primarily to salinity, consistent with the results in Daase *et al.* (Daase *et al.*, 2007) who also reported a one order of magnitude change in abundance within a similar salinity range at deeper stations (>500 m). This suggests that transport and mixing of water masses is an important mechanism regulating the abundance of this subarctic species in the study area. Since the study area constitutes the northern range of the geographical distribution, this is consistent with Speirs *et al.* (Speirs *et al.*, 2006) who found that transport has a limited impact on the distribution of *C. finmarchicus*, except for shelf areas and at the edges of the distribution. The higher biomass along the shelf break (intermediate water depth in Fig. 3) further shows that the flow of the NAC and the WSC is an important pathway of this boreal species into the Arctic (Halvorsen
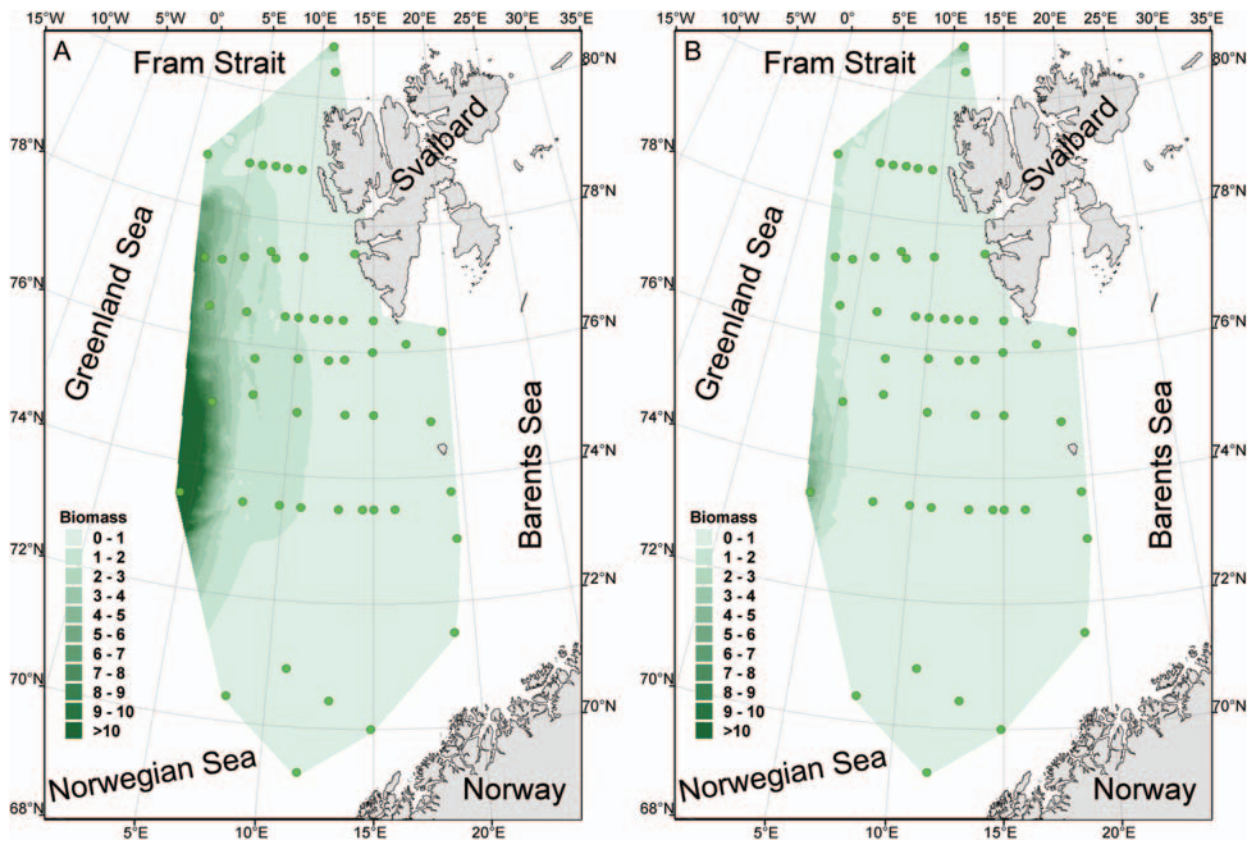
Fig. 10. The spatial distribution of the *Calanus hyperboreus* biomass (mg DW m^{-3}, beginning of July) predicted from the GAM approach [equation (1); Fig. 6] under present conditions (**A**) and from a 2°C temperature increase (**B**). The distribution was calculated within the spatial span of the sampling stations only.

et al., 2003; Hirche and Kosobokova, 2007). Does this mean that *C. finmarchicus* is only an expatriate and does not reproduce across the study area? Overwintering *C. finmarchicus* have been observed in the southern part of the study area (Halvorsen *et al.*, 2003; Gaardsted *et al.*, 2010), and reported summer currents in the area typically range between 1 and 4 cm s^{-1} (Walczowski and Piechura, 2007), giving a transportation time from south to north exceeding 1 year. Since *C. finmarchicus* migrates to the surface layer in spring and descends again at the end of the summer bloom (Gislason and Astthorsson, 2002; Falk-Petersen *et al.*, 2009), it is unlikely that it could have spread from a southern location to the entire study area. In a modelling study, Ji *et al.* (Ji *et al.*, 2012) also showed that *C. finmarchicus* successfully reaches diapause across the entire study area. Thus, *C. finmarchicus* must be considered endemic to the study area with a possibility of the positive relationship to salinity indicating that the species has several overwintering centres in the eddies along the flow of the NAC and the WSC. The higher abundance along the slope and shelf may result from the influence of the frontal system

providing conditions for enhanced and prolonged primary production during the summer, as suggested by Halvorsen and Tande (Halvorsen and Tande, 1999).

Calanus glacialis typically has a 2-year life cycle and diapauses at depths between 200 and 300 m (Falk-Petersen *et al.*, 2009) with the shelf around Spitsbergen forming the boundary of successful overwintering (Ji *et al.*, 2012). The association to the shelf was also apparent in the biomass relationship with the water depth that, despite a linear relationship, displayed a rather abrupt change in the biomass at water depths ∼200–300 m (Fig. 4). However, *C. glacialis* was not found on the shelf in the southern Barents Sea, because this area is occupied by the Atlantic waters of the North Cape Current, with a relatively higher salinity (cf. Fig. 7A) and this Arctic species is absent (Orvik and Skagseth, 2005). Thus, the combination of water depth and salinity (Fig. 4) could explain the restricted presence of *C. glacialis* outside the shelf areas around Spitsbergen. This could also indicate that the *C. glacialis* found at more oceanic stations were expatriated. Ice algae are important for the successful spawning of *C. glacialis* (Falk-Petersen *et al.*, 2009; Søreide

et al., 2010; Leu et al., 2011) and our results confirm an increasing probability of the presence of C. glacialis with sea ice concentration (Fig. 5). Calanus glacialis has higher egg production rates than its competitor C. finmarchicus at lower temperatures and vice versa at higher temperatures (Hirche and Kosobokova, 2007; Kjellerup et al., 2012), but C. glacialis egg production and metabolism do not cease abruptly at temperatures >6°C (Møller et al., unpublished results). However, the early spawning of C. glacialis and its potential reliance on ice algae combined with relatively lower egg production rates at higher temperatures in ice-free waters may actually prove to be a competitive disadvantage compared with C. finmarchicus that spawns during and after the bloom. Hence, the life strategy of C. finmarchicus is better adapted to a more variable pelagic bloom, whereas C. glacialis may totally miss the phytoplankton bloom due to its spawning strategy and the longer time required to develop to first feeding naupliar stages (Søreide et al., 2010).

Calanus hyperboreus is associated with the deep waters of the western Greenland Sea (Hirche, 1997; Mumm et al., 1998; Falk-Petersen et al., 2009) and would, according to Ji et al. (Ji et al., 2012), be considered an expatriate throughout our study area. Calanus hyperboreus has a multi-annual life cycle ranging from 2 to 5 years (Hirche, 1997; Scott et al., 2000) and uses its lipid reserves to spawn during winter in the deep waters, where the eggs ascend freely to the surface layer (Hirche and Niehoff, 1996). The life strategy of C. hyperboreus is adapted to a short productive period and it has the northern-most distribution of Calanus spp. in the Arctic Ocean (Ji et al., 2012). Our results confirm that C. hyperboreus is strongly related to the water depth (Fig. 6), although it is not abundant in all deep areas but mainly found in the western parts of the study area (Fig. 10A). It is likely that C. hyperboreus are expatriates from the Greenland Sea Gyre that have been captured with eddies forming along the Arctic Front, and eventually transported into the main path of the WSC along the western edge of the study area. Calanus hyperboreus were not abundant in the northern part of the study area, which is more dominated by the WSC. Thus, the combination of all four explanatory variables could explain the confined spatial distribution of C. hyperboreus declining to the north as a function of salinity and sea ice concentration, to the east as a function of the water depth and to the south as a function of temperature. In the latter case, if temperature was a proxy for mixing of water masses, then the relationship with temperature should only hold down to ~3°C, which is the temperature associated with the Greenland Sea Gyre water (Fig. 7B). Our empirical results cannot discriminate between a relationship between mixing water masses

with different temperatures and a potential temperature effect related to the life strategy of C. hyperboreus. Information on potential temperature effects on the functional biology of C. hyperboreus is still limited (Hirche, 1987; Plourde et al., 2003), although Henriksen et al. (Henriksen et al., 2012) did not find any temperature effect on either egg production or faecal pellet production. Given these considerations, it is most likely that the significant relationship with temperature, found in our study, is caused by the mixing of water masses.

Calanus distribution in a warmer climate

Warming of the surface water, melting of the sea ice and lengthening of the productive season are expected to change the trophodynamics in the Arctic and sub-Arctic regions, and marine plankton are considered sentinels of these changes (Hays et al., 2005). Our results show that in the study area and over the 2001–2009 period, the biomass of C. glacialis and C. hyperboreus was significantly related to temperature, whereas that of C. finmarchicus did not respond to temperature. Similarly, a non-uniform response to temperature was reported by Cook et al. (Cook et al., 2007), who found that temperature had a positive effect on the development of C. finmarchicus nauplii when fed, and a negative effect on survival rates when food limited. However, Reygondeau and Beaugrand (Reygondeau and Beaugrand, 2011) suggested that C. finmarchicus would increase their presence in the area.

Daase et al. (Daase et al., 2007) reported significant correlations with temperature for all three Calanus species at both deep and shallow stations, but their study did not distinguish between the effects of temperature versus salinity in a combined analysis as ours, and their results could therefore be affected by an apparent correlation between salinity and temperature. Moreover, for the reasons given above, the correlation between the biomass of C. hyperboreus and temperature is believed to be an expression of the mixing of water masses with the temperature used to characterize the cold and saline waters from the East Greenland Current, and consequently the +2°C scenario (Fig. 10B) is not realistic unless the abundance of C. hyperboreus in the East Greenland Current decreases significantly with temperature. However, the geographical distribution of C. hyperboreus in the East Greenland Current is not expected to change substantially from a 2°C temperature increase (Ji et al., 2012).

We conclude that C. glacialis is the only Calanus species in the study area that might be significantly affected by an increase in temperature and the melting of sea ice, but the predicted effect on C. glacialis of a

2°C temperature increase is relatively small (Fig. 10B), because the shelf area where *C. glacialis* resides has relatively low temperatures today (2−4°C) and temperatures will not exceed the critical threshold ∼6°C with the proposed scenario. However, *C. glacialis* may disappear from the shelf region of the study area if the temperature increases by ∼4°C and *C. finmarchicus* will become completely dominant as it presently is along the southern Barents Sea shelf.

SUPPLEMENTARY DATA

Supplementary data can be found online at http ://plankt.oxfordjournals.org.

ACKNOWLEDGEMENTS

FUNDING

REFERENCES

ACIA (2004) *Arctic Climate Impact Assessment. Impacts of a warming arctic: Arctic climate impact assessment.* Cambridge University Press, Cambridge, UK.

Arrigo, K. R., van Dijken, G. and Pabi, S. (2008) Impact of a shrinking Arctic ice cover on marine primary production. *Geophys. Res. Lett.*, **35**, L19603, doi:10.1029/2008GL035028.

Bachowiak-Samoyk, K., Søreide, J. E. and Kwaśniewski, S. et al. (2008) Hydrodynamic control of mesozooplankton abundance and biomass in northern Svalbard waters (79-81°N). *Deep-Sea Res. Pt. II*, **55**, 2210−2224.

Carmack, E. and Wassmann, P. (2006) Food webs and physical-biological coupling on pan-arctic shelves: comprehensive perspectives, unifying concepts and future research. *Prog. Oceanogr.*, **71**, 446−477.

Comiso, J. C., Parkinson, C. L. and Gersten, R. et al. (2008) Accelerated decline in the Arctic sea ice cover. *Geophys. Res. Lett.*, **35**, L01703, doi:10.1029/2007GL031972.

Conover, R. J. (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. *Hydrobiologia*, **167**, 127−142.

Cook, K. B., Bunker, A. and Hay, S. et al. (2007) Naupliar development times and survival of the copepods *Calanus helgolandicus* and *Calanus finmarchicus* in relation to food and temperature. *J. Plankton Res.*, **29**, 757−767.

Cressie, N. (1993) *Statistics for spatial data, revised edition.* Wiley-Interscience, New York.

Daase, M., Vik, J. O. and Bagøien, E. et al. (2007) The influence of advection on *Calanus* near Svalbard: statistical relations between salinity, temperature and copepod abundance. *J. Plankton Res.*, **29**, 903−911.

Dvoretsky, V. G. and Dvoretsky, A. G. (2011) Copepod communities off Franz Josef Land (northern Barents Sea) in late summer of 2006 and 2007. *Polar Biol.*, **34**, 1231−1238.

Falk-Petersen, S., Mayzaud, P. and Kattner, G. et al. (2009) Lipids and life strategy of Arctic *Calanus*. *Mar. Biol. Res.*, **5**, 18−39, doi:10.1080/17451000802512267.

Falk-Petersen, S., Pavlov, V. and Timofeev, S. et al. (2007) Climate variability and possible effects on arctic food chains: the role of Calanus. In Ørbæk, J. B., Kallenborn, R., Tombre, I., Hegseth, E. N., Falk-Petersen, S. and Hoel, A. H. (eds), *Arctic−Alpine Ecosystems and People in a Changing Environment*. Springer, Berlin/Heidelberg/New York, pp. 147−166.

Gaardsted, F., Zhou, M. and Pavlov, V. et al. (2010) Mesoscale distribution and advection of overwintering *Calanus finmarchicus* off the shelf of northern Norway. *Deep-Sea Res. Pt I*, **57**, 1465−1473.

Gislason, A. and Astthorsson, O. S. (2002) The food of Norwegian spring-spawning herring in the western Norwegian Sea in relation to the annual cycle of zooplankton. *Sarsia*, **87**, 236−247, doi:10.1080/00364820260294860.

Gradinger, R. (1995) Climate change and biological oceanography of the Arctic Ocean. *Philos. T. Roy. Soc. A*, **352**, 277−286.

Halvorsen, E. and Tande, K. S. (1999) Physical and biological factors influencing the seasonal variation in distribution of zooplankton across the shelf at Norvestbanken, northern Norway, 1994. *Sarsia*, **84**, 279−292.

Halvorsen, E., Tande, K. S. and Edvardsen, A. et al. (2003) Habitat selection of overwintering *Calanus finmarchicus* in the NE Norwegian Sea and shelf waters off Northern Norway in 2000−02. *Fish. Oceanogr.*, **12**, 339−351.

Hansen, B., Østerhus, S. and Quadfasel, D. et al. (2004) Already the day after tomorrow? *Science*, **305**, 953−954.

Hastie, T. J. and Tibshirani, R. J. (1990) *Generalized additive models*. Chapman & Hall, New York.

Hays, G. C., Richardson, A. J. and Robinson, C. (2005) Climate change and marine plankton. *Trends Ecol. Evol.*, **20**, 337−344.

Heide-Jørgensen, M. P. and Acquarone, M. (2002) Size and trends of the bowhead, beluga and narwhal stocks wintering off West Greenland. *Sci. N. Atl. Mar. Mamm. Comm.*, **4**, 191−210.

Helaouët, P. and Beaugrand, G. (2007) Macroecology of *Calanus finmarchicus* and *C. helgolandicus* in the North Atlantic Ocean and adjacent seas. *Mar. Ecol. Prog. Ser.*, **345**, 147−165.

Henriksen, M. V., Jung-Madsen, S. and Nielsen, T. G. et al. (2012) Effect of temperature and food availability on feeding and egg production of *Calanus hyperboreus* from Disko Bay, Western Greenland. *Mar. Ecol. Progr. Ser.*, **447**, 109−126.

Hirche, H.-J. (1987) Temperature and plankton. II Effect on respiration and swimming activity in copepods from the Greenland Sea. *Mar. Biol.*, **94**, 347−356.

Hirche, H.-J. (1997) Life cycle of the copepod *Calanus hyperboreus* in the Greenland Sea. *Mar. Biol.*, **128**, 607–618.

Hirche, H. J., Baumann, M. E. M. and Kattner, G. et al. (1991) Plankton distribution and the impact of copepod grazing on primary production in Fram Strait, Greenland Sea. *J. Mar. Sys*, **2**, 477–494.

Hirche, H.-J. and Kosobokova, K. (2007) Distribution of *Calanus finmarchicus* in the northern North Atlantic and Arctic Ocean— Expatriation and potential colonization. *Deep-Sea Res. Pt II*, **54**, 2729–2747.

Hirche, H.-J. and Niehoff, B. (1996) Reproduction of the Arctic copepod *Calanus hyperboreus* in the Greenland Sea—field and laboratory observations. *Polar Biol.*, **16**, 209–219.

Ji, R., Ashjian, C. J. and Campbell, R. G. et al. (2012) Life history and biogeography of *Calanus* copepods in the Arctic Ocean: an individual-based modelling study. *Prog Oceanogr.*, **96**, 40–56. doi:10.1016/j.pocean.2011.10.001.

Kane, J. (2007) Zooplankton abundance trends on Georges Bank, 1977–2004. *ICES J. Mar. Sci.*, **64**, 909–919, doi:10.1093/icesjms/fsm066.

Karnovsky, N., Kwasniewski, S. and Weslawski, J. M. et al. (2003) The foraging behaviour of little auks in a heterogeneous environment. *Mar. Ecol. Prog. Ser.*, **253**, 289–303.

Kjellerup, S., Dünweber, M. and Swalethorp, R. et al. (2012) The effects of a future warmer ocean on the coexisting copepods *Calanus finmarchicus* and *C. glacialis* in the Disko Bay Western Greenland. *Mar. Ecol. Prog. Ser.*, **447**, 87–108.

Kwaśniewski, S., Hop, H. and Falk-Petersen, S. et al. (2003) Distribution of *Calanus* species in Kongsfjorden, a glacial fjord in Svalbard. *J. Plankton Res.*, **25**, 1–20.

Lee, R. F., Hagen, W. and Kattner, G. (2006) Lipid storage in marine zooplankton. *Mar. Ecol. Prog. Ser.*, **307**, 273–306.

Leu, E., Søreide, J. E. and Hessen, D. O. et al. (2011) Consequences of changing sea-ice cover for primary and secondary producers in the European Arctic shelf seas: timing, quantity, and quality. *Prog Oceanogr.*, **90**, 18–32.

Morison, J., Aagaard, K. and Steele, M. (2000) Recent environmental changes in the Arctic: a review. *Arctic*, **53**, 359–371.

Mumm, N., Auel, H. and Hanssen, H. et al. (1998) Breaking the ice: large-scale distribution of mesozooplankton after a decade of Arctic and transpolar cruises. *Polar Biol.*, **20**, 189–197.

Nielsen, T. G. and Hansen, B. (1995) Plankton community structure and carbon cycling on the western coast of Greenland during and after the sedimentation of a diatom bloom. *Mar. Ecol. Prog. Ser.*, **125**, 239–257.

Orvik, K. A. and Skagseth, Ø. (2005) Heat flux variations in the eastern Norwegian Atlantic Current toward the Arctic from moored instruments, 1995–2005. *Geophys. Res. Lett.*, **32**, L14610, doi:10.1029/2005GL023487.

Østvedt, O. (1955) Zooplankton investigations from weather ship M in the Norwegian Sea, 1948–49. *Hvalråd. Skr.*, **40**, 1–93.

Pasternak, A., Riser, C. W. and Arashkevich, E. et al. (2002) *Calanus* spp grazing affects egg production and vertical carbon flux (the marginal ice zone and open Barents Sea). *J. Mar. Sys.*, 38, 147–164.

Pedersen, T. J., Nielsen, T. G., Michel, C. *et al.* (2006) Sedimentation following the spring bloom in Disko Bay, West Greenland, with special emphasis on the role of copepods. *Mar. Ecol. Prog. Ser.*, **314**, 239–255.

Plourde, S., Joly, P. and Runge, J. A. et al. (2003) Life cycle of *Calanus hyperboreus* in the lower St. Lawrence Estuary and its relationship to local environmental conditions. *Mar. Ecol. Prog. Ser.*, **255**, 219–233.

Reygondeau, G. and Beaugrand, G. (2011) Future climate-driven shifts in distribution of *Calanus finmarchicus*. *Global Change Biol.*, **17**, 756–766.

Roleda, M. Y., Hanelt, D. and Wiencke, C. (2008) Growth kinetics related to physiological parameters in young *Saccorhiza dermatodea* and *Alaria esculenta* sporophytes exposed to UV radiation. *Polar Biol.*, **28**, 539–549.

Rudels, B., Jones, E. and Schauer, U. et al. (2004) Atlantic sources of the Arctic Ocean surface and halocline waters. *Polar Res.*, **23**, 181–208.

Schauer, U., Fahrbach, E. and Osterhus, S. et al. (2004) Arctic warming through the Fram Strait: Oceanic heat transport from 3 years of measurements. *J. Geophys. Res.*, **109**, C06026, doi:10.1029/2003JC001823.

Scott, C. L., Kwasniewski, S. and Falk-Petersen, S. et al. (2000) Lipids and life strategies of *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* in late autumn, Kongsfjorden, Svalbard. *Polar Biol.*, **23**, 510–516.

Slagstad, D., Ellingsen, I. H. and Wassmann, P. (2011) Evaluating primary and secondary production in an Arctic Ocean void of summer sea ice: an experimental simulation approach. *Prog Oceanogr.*, **90**, 117–131.

Søreide, J. E., Leu, E. and Berge, J. et al. (2010) Timing of blooms, algal food quality and Calanus glacialis reproduction and growth in a changing Arctic. *Global Change Biol.*, **16**, 3154–3163, doi: 10.1111/j.1365–2486.2010.02175.x.

Speirs, D. C.,, Gurney, W. S. C. and Heath, M. R. et al. (2006) Ocean-scale modelling of the distribution, abundance, and seasonal dynamics of the copepod *Calanus finmarchicus*. *Mar. Ecol. Prog. Ser.*, **313**, 173–192.

Steele, M., Ermold, W. and Zhang, J. (2008) Arctic Ocean surface warming trends over the past 100 years. *Geophys. Res. Lett.*, **35**, L02614, doi:10.1029/2007GL031651.

Stroeve, J., Holland, M. and Meier, W. et al. (2007) Arctic sea ice decline: faster than forecast. *Geophys. Res. Lett.*, **34**, L09501, doi: 10.1029/2007GL029703.

Tande, K. S., Drobysheva, S. and Nesterova, V. et al. (2000) Patterns in the variations of copepod spring and summer abundance in the northeastern Norwegian Sea and the Barents Sea in cold and warm years during the 1980s and 1990s. *ICES J. Mar. Sci.*, **57**, 1581–1591.

Tranter, D. J. and Fraser, H. (1968) *Zooplankton sampling*. Monographs on Oceanographic Methodology 2. UNESCO, Paris.

Walczowski, W. and Piechura, J. (2007) Pathways of the Greenland Sea warming. *Geophys. Res. Lett.*, **34**, L10608, doi:10.1029/2007GL029974.

Walczowski, W., Piechura, J. and Goszczko, I. et al. (2012) Changes of the Atlantic Water properties: an important factor of the European Arctic marine climate. *ICES J. Mar. Sci.*, **69**, 864–869. doi:10.1093/icesjms/fss068.

Weydmann, A. and Kwaśniewski, S. (2008) Distribution of *Calanus* populations in a glaciated fjord in the Arctic (Hornsund, Spitsbergen) – an interplay between biological and physical factors. *Polar Biol.*, **31**, 1023–1035.