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The influence of advection on *Calanus* near Svalbard: statistical relations between salinity, temperature and copepod abundance

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We quantify statistical relationships between hydrography and abundance of Calanus spp. in the Arctic–Atlantic transition zone around Svalbard (78–82°N) during early autumn. The Atlantic species C. finmarchicus was more abundant in warmer and more saline waters, as expected from its distributional core area. Conversely, the Arctic species C. hyperboreus was more abundant in colder and fresher waters. However, the Arctic species C. glacialis showed opposing relationships with hydrography in shallow compared with deep regions. In shallow waters, the numbers of C. glacialis decreased with temperature and salinity as expected, while somewhat surprisingly the opposite trend was found in deep locations. Sub-surface hydrography between 50–150 m was in most cases a better predictor for Calanus spp. abundance than near-surface conditions, the former generally explaining up to ∼50% of the variability in abundance of each species. Despite finding significant relationships between hydrographic properties and the abundance of each of the three Calanus species, we did not detect significant relationships between the total Calanus biomass and temperature.

INTRODUCTION

Recent ocean warming (Levitus *et al.*, 2000) has extended the geographical range of many temperate marine species, although many cold-adapted species have declined (Barry *et al.*, 1995; Holbrook *et al.*, 1997; Beaugrand *et al.*, 2002). There are indications that the Arctic is warming faster than the global mean trend (Manabe *et al.*, 1992; ACIA, 2004). This is partly due to the elevated inflow of relatively warm and saline Atlantic water masses into the Arctic over the last decades (Morison *et al.*, 2000; Hansen *et al.*, 2004). It is, however, not clear how an increase in temperature and salinity (Morison *et al.*, 2000; Schauer *et al.*, 2004) will affect Arctic marine ecosystems.

Pelagic ecosystems, and zooplankton in particular, are likely to be strongly affected by hydrographic changes and variations in water mass distribution and advection (Ottersen and Stenseth, 2001; Hays *et al.*, 2005). This may have ecological and economic repercussions since zooplankton links primary production to higher trophic levels.

Zooplankton production depends strongly on local primary productivity (Irigoien *et al.*, 2004; Richardson and Schoeman, 2004), but there can also be substantial advective transport of organisms between areas and populations (Aksnes and Blindheim, 1996; Heath *et al.*, 1999; Torgersen and Huse, 2005).

Where Arctic and Atlantic water masses meet, the boreal copepod *Calanus finmarchicus*, the Arctic

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shelf-associated *C. glacialis* and the Arctic *C. hyperboreus* co-occur (Conover, 1988; Hirche and Mumm, 1992). Together, these copepods dominate the mesozooplankton biomass in the North Atlantic and Arctic Ocean (Conover, 1988; Hirche, 1991; Mumm *et al.*, 1998; Melle *et al.*, 2004). Their production supports nearly all higher trophic levels (Bradstreet and Cross, 1982), and they are important for the biological pump of biogenic carbon into the deep ocean (Pasternak *et al.*, 2002).

Here, we assess the links between physical properties in the water column and the abundance of the three *Calanus* species in a border area between Arctic and Atlantic water masses, as found in the northern Fram Strait and in waters around Svalbard. The inflow of relatively warm and saline Atlantic waters to the Arctic varies strongly between years (Aagaard and Carmack, 1989; Swift *et al.*, 1997; Grotefendt *et al.*, 1998; Saloranta and Haugan, 2001), and a main driver for ocean climate variability in this area is the variable strength of the North Atlantic Current and its northernmost extension, the West Spitsbergen Current (Aagaard *et al.*, 1987). The presence of water masses with differing physical and biological characteristics makes this region well suited for analysing the links between pelagic community structure and physical properties of the water.

Although the biogeography of the *Calanus* species is well known (e.g. Grainger, 1961, 1963; Jaschnov, 1970; Conover, 1988), this study attempts to quantify the relationships between hydrography and *Calanus* abundance by using simple statistical models. The objective is to gain new insights regarding the importance of physical variability in governing this important component of the mesozooplankton community.

METHOD

Hydrographic profiles and *Calanus* spp. were sampled on eight separate surveys during 2000–2004. The dataset was restricted to a period from 23 August–26 September so as to reduce variability caused by seasonal changes in reproduction and population development. The dataset comprised 86 samples collected at 52 locations west and north of Svalbard (latitude 78°54′–82°30′N, longitude 1°12′–22°22′E; Fig. 1).

Temperature (°C) and salinity profiles were measured *in situ* by shipboard conductivity, temperature and density (CTD) profilers. Zooplankton was collected by vertical net hauls [either a WP2 net: mesh size 180 μm, mouth opening 0.255 m^2 or a Multinet (Hydrobios Kiel): mesh size 180 μm, mouth opening 0.25 m^2]. Hauls taken with the WP2 net were not depth-stratified; abundance data from depth-stratified hauls obtained with the Multinet were averaged over the entire sampling depth. Half of the stations were located over deep waters (520–3800 m), but for logistical reasons, only the upper 300–400 m were sampled. Depth-stratified hauls from deep stations showed that peak abundances of all three species occurred in the uppermost 100 m, and the population here consisted of younger stages than deeper in the water column. At shallow locations, practically the entire water column was sampled and depth-resolved hauls showed that the populations were more equally distributed throughout the water column. However, peak abundances were observed deeper in the water column where older stages prevailed. Thus, it seems that during the sampling period (late August–late September), the older stages in the *Calanus* populations had already started the seasonal descent to over-wintering depths (Conover and Huntley, 1991; Hirche *et al.*, 2006). Depth resolved abundance estimates did not reveal clear patterns, possibly because of the reduced sample size (only Mulinet hauls) or the vertical behaviour of *Calanus*. Thus we present our analysis based on depth averaged abundance data. This should not affect our results for the shallow locations, but for the deeper stations, it may imply a sampling bias against the older developmental stages which would partly be located in their over-wintering habitats

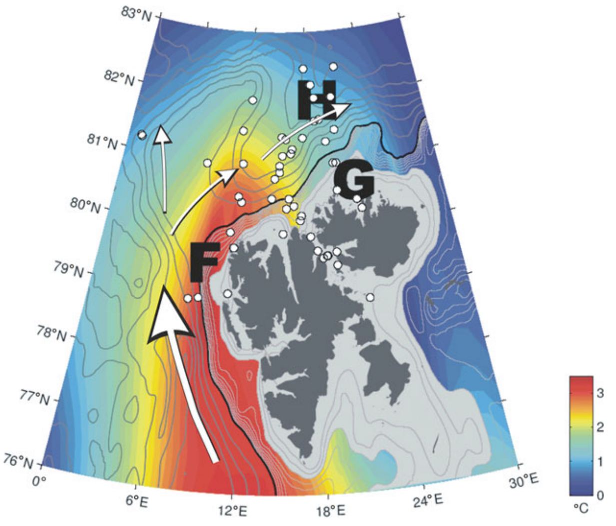

Fig. 1. Map of study area with sampling sites (circles). F, G and H indicate the core ranges of *C. finmarchicus*, *C. glacialis* and *C. hyperboreus*. Colours show average water temperature at 150 m depth [annual mean of 2001 (NOAA Atlas NESDIS 45 World Ocean Database 2001. National Virtual Ocean Data System (NVDOS), http://ferret.pmel.noaa.gov/NVODS/servlets/dataset)]. Arrows indicate the West Spitsbergen Current of inflowing Atlantic water. Depth contours are in 50-m intervals down to the shelf break at 500 m (heavy black line), then 500-m intervals to 4000 m.

below our sampling strata (Conover, 1988; Kaartvedt, 1996). The consequence of this is that our results from the deep locations represent the active parts of the populations in upper waters, and may not be valid outside the sampling period.

Samples were fixed in a 4% formaldehyde-in-seawater solution, brought to the lab and split into random sub-samples (>150 copepodites of *Calanus* spp.) from which copepodite stages were counted. We distinguished between copepodite stages of *C. finmarchicus* and *C. glacialis* as well as young stages of *C. hyperboreus* from measurements of the prosome length (Daase and Eiane, 2007). *Calanus* densities (ind m^{-3}) are based on filtered volumes either calculated from flow meters attached to the Multinet or by multiplying mouth opening area of the WP2 net with vertical hauling distance assuming 100% filtration efficiency. *Calanus* species composition and abundances at the different locations are described in detail elsewhere (Daase and Eiane, 2007).

As a measure for food availability for predators on *Calanus*, we used estimates of biomass concentration (mg dry weight m^{-3}). For *C. finmarchicus* and *C. glacialis*, biomass was calculated from taxon- and stage-specific dry weights (DWs) (Richter, 1994; Hirche *et al.*, 2001) and from weight−length relationships (Hirche, 1991; Mumm, 1991). Average prosome length for each stage was used to convert weight−length relationships into DW estimates. Weight−length relationships given by Mumm (Mumm, 1991) resulted in ash free DWs (AFDW). Those were converted into DWs assuming a ratio of AFDW:DW = 0.9 (Richter, 1994). Species and stage-specific estimates of DWs obtained from these four references were averaged and used to convert abundance of *C. finmarchicus* and *C. glacialis* into biomass (DW). DW for copepodite stages CI and CII of *C. hyperboreus* were obtained in a similar way but in addition values given by Hirche (Hirche, 1997) were included. DW estimates for *C. hyperboreus* CIII−CVI were taken only from Hirche (Hirche, 1997), since these were season-specific and higher than those given by the other studies.

Measures of local production were unfortunately not available for the season leading up to the copepod sampling. *Calanus* abundance showed no relation to fluorescence (indicating algal biomass) at the time of copepod sampling (results not shown).

Statistical analysis

Calanus abundance was log-transformed to stabilize the variance. Then, separate linear regressions were made for each species against each hydrographic variable (temperature and salinity) in interaction with a categorical variable indicating whether bottom depth was less or >500 m. Figure 2 demonstrates the approximate homoskedasticity, normality of residuals and linearity of log (abundance) versus the hydrographic predictors. Zero-values were omitted for convenience in the log-transformation; this was a conservative action because all zero-values occurred where the model results predicted low abundance. In addition, we omitted one station from the analysis of *C. glacialis* because this clear outlier was situated in the extreme southwest of the dataset, far outside the normal range of this species.

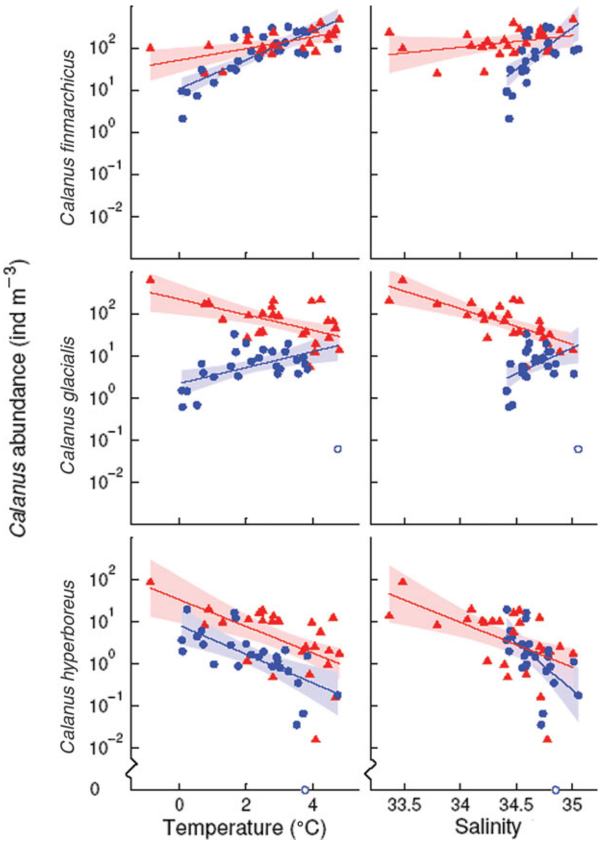

Fig. 2. Relationships between *Calanus* spp. abundance and hydrographic variables. There are species- and bottom-depth-specific differences in the co-variation between the abundance of each *Calanus* species and hydrographic variables. Depth categories were "deep" (>500 m, blue) and "shallow" (≤500 m, red). Abundance and hydrographic covariates were averaged from the surface down to 300 m or bottom depth, whichever was less. Regression lines and 95% confidence bands are given for a model allowing mean and intercept to differ between deep and shelf locations, but assuming equal residual variance. Open symbols denote observations omitted from regression: For *C. glacialis*, the southwestern most station was omitted because it is outside the normal geographical range of this species. For *C. hyperboreus*, zero-observations were omitted for convenience in log-transformation.

Abundance data for stations sampled with multiple hauls were pooled to avoid pseudoreplication. Such pooling sacrifices statistical power because it "throws away" some of the data. We therefore also fitted mixed-effect models with a random intercept for each station, and also for each station within each survey. However, the effect estimates were almost identical to those from the pooled-data analyses and we therefore focus only on the simpler model. In addition, we estimated biomass from the pooled abundance data. Log *Calanus* biomass correlated with log abundance (*r* was between 0.61 and 0.93 for all species), and hence biomass correlated with temperature and salinity in much the same way as abundance. We therefore limited our analysis to total *Calanus* biomass in this paper.

The predictors used in the regression analyses (temperature and salinity) were vertically averaged from the surface down to 300 m or the bottom depth, whichever was less. This approach means that the relative influence of the upper waters on hydrographic averages will vary between some data points in the "shallow" category. The depth at which conditions correlated best with vertically-averaged *Calanus* abundance was identified by regressing abundance on salinity and/or temperature calculated for depths of 0–200 m in 10 m intervals, at 250 m and 300 m.

We also regressed the abundance of individual developmental stages of each species against temperature and salinity and generally found similar trends across stages within each species. For simplicity, we limit our presentation to the pooled abundances for each species.

RESULTS

The relationship between abundance and hydrography differed between the species and depended on bottom depth (Fig. 2, Table I). *Calanus finmarchicus* correlated positively with vertically averaged temperature and salinity in both deep and shallow locations, whereas the opposite was observed for *C. hyperboreus* (Fig. 2). The abundance of *C. glacialis* declined with salinity and temperature in samples from shallow areas, but showed the opposite pattern in northern and deep waters (Fig. 2, Table I).

Table I gives regression analysis (slope and intercept) for "deep" and "shallow" stations, respectively, and the difference in slope and intercept between bottom-depth categories. As an example of interpreting the coefficient estimates, *C. finmarchicus* in shallow areas increases in abundance by about $[\exp(0.32) - 1] = 38\%$ per °C increase in average temperature. In deep areas, the increase is ~120%. In contrast, *C. glacialis* abundance decreases by ~34% per °C increase in temperature in shallow areas, whereas in deep areas, it increases by ~53% per °C increase. The interpretation of regressions of total *Calanus* biomass against hydrography is analogous and all effects on abundance and total biomass are summarised in Table II.

Model fits of vertically averaged *Calanus* abundance against depth-resolved temperature and salinity were generally as good, or better, at intermediate depths as

Table I: Regression analyses of log-transformed Calanus abundance (as ind m^{-3} for each species, as well as total DW as mg m^{-3} for all species) against the Boolean predictor "shallow" (whether bottom depth $<$ 500 m) and two hydrological measures (each species–predictor pair analysed separately; six regressions in total)

	Slope			Intercept				
	Deep	Shallow	Difference	Deep	Shallow	Difference	R^2	*n*
Temperature (°C)								
Abundance (ind m^{-3})								
Calanus finmarchicus	0.79 (0.11)*	0.32 (0.10)**	0.47 (0.15)*	2.38 (0.28)*	3.95 (0.34)*	−1.57 (0.44)*	0.62	52
Calanus glacialis	0.43 (0.14)**	−0.42 (0.12)**	0.86 (0.19)***	0.80 (0.35)***	5.40 (0.42)*	−4.60 (0.54)*	0.71	51
Calanus hyperboreus	−0.79 (0.20)*	−0.73 (0.19)*	−0.06 (0.28)*	2.10 (0.51)*	3.51 (0.62)*	−1.40 (0.81)****	0.44	51
Biomass (mg DW m^{-3})								
Total *Calanus*	0.11 (0.09)	−0.09 (0.08)	0.20 (0.12)****	1.94 (0.22)*	3.99 (0.27)*	−2.05 (0.35)*	0.67	52
Salinity (*S*-34.75)								
Abundance (ind m^{-3})								
Calanus finmarchicus	4.55 (1.06)*	0.64 (0.46)	3.91 (1.16)**	4.58 (0.20)*	5.14 (0.24)*	−0.56 (0.32)****	0.38	52
Calanus glacialis	2.81 (1.10)***	−1.94 (0.42)*	4.75 (1.18)*	2.04 (0.20)*	3.44 (0.22)*	−1.40 (0.30)*	0.74	51
Calanus hyperboreus	−5.12 (1.68)**	−2.46 (0.70)**	−2.67 (1.82)	−0.14 (0.32)	0.42 (0.37)	−0.57 (0.50)	0.37	51
Biomass (mg DW m^{-3})								
Total *Calanus*	0.59 (0.63)	−0.70 (0.27)***	1.30 (0.69)****	2.25 (0.12)*	3.46 (0.15)*	−1.21 (0.19)*	0.69	52

Data are from 52 stations (latitude >78°54′N, longitude <22°22′E, Julian day 237–269). Repeated samples were pooled within each station before this analysis. Entries in the table body give estimates, standard errors in parentheses and statistical significance level (indicated as $*0 < P < 0.001$; $**0.001 < P < 0.01$; $***0.01 < P < 0.05$; $****0.05 < P < 0.1$) for the slope and intercept for "deep" and "shallow" stations, as well as for the difference between them.

Table II: Summary of effects (as %change) on the abundance and total biomass of Calanus spp. caused by a one unit increase in temperature or salinity as predicted from regression analyses in Table I

	Temperature (°c)		Salinity	
	Deep	Shallow	Deep	Shallow
Abundance (ind m^{-3})				
Calanus finmarchicus	**120**	**38**	**9363**	90
Calanus glacialis	**54**	**−34**	**1561**	**−86**
Calanus hyperboreus	**−55**	**−52**	**−99**	**−91**
Biomass (mg DW m^{-3})				
Total *Calanus*	12	−9	80	**−50**

Statistically significant effects (at 95% level) are reported in bold font type.

compared with near-surface waters (Fig. 3). *Calanus finmarchicus* correlated poorly with salinity but very well with temperature at depths of 0–50 m in shallow parts of our study. In the open sea, the relationship with salinity was as strong as with temperature and best fits were observed with salinity and temperature between 90–180 m.

At shallow locations *C. glacialis*, and to a lesser extent *C. hyperboreus*, were better predicted by salinity than by temperature and the relationships with hydrography were best with measurements taken between 50 and 120 m (50–200 m for *C. hyperboreus*). At deep locations, *C. glacialis* was more strongly related to sub-surface (100–170 m) than near-surface conditions, and the relationship with salinity was as strong as with temperature (Fig. 3). For *C. hyperboreus*, temperature had more predictive power than salinity at deep locations and the strongest relationships were observed with hydrographic conditions near the surface (20–80 m). Combining temperature and salinity in the regression models did not improve the regression fits for any of the species compared with the best one-parameter models.

DISCUSSION

The positive correlation of the Atlantic species *C. finmarchicus* with vertically averaged temperature and salinity and the negative correlation of the Arctic species *C. hyperboreus* are as expected considering the core distribution areas of these two species and the anticipated effect of mixing water masses (i.e. van Aken *et al.*, 1991; Ashjian *et al.*, 1995; Melle *et al.*, 2004).

For *C. glacialis*, however, the positive correlation with temperature and salinity in deep locations is somewhat surprising. We find it unlikely that this is an artefact caused by a sampling bias against deep dwelling animals (see Method) as the expected earlier migration to over-wintering depth due to rapid growth in warmer waters (Fiksen and Carlotti, 1998) should counteract the observed relationship. Although *C. glacialis* is associated with Arctic shelf seas (Grainger, 1963; Conover, 1988), and the central Arctic Ocean, the deeper regions north of Svalbard are outside its main range (Mumm *et al.*, 1998). Thus occurrence of *C. glacialis* in this area may be ascribed to individuals from core production areas on the shelf being displaced by modified Atlantic water masses (Manley, 1995). Hence, temperature and salinity in this region may act as indicators of advective transport and therefore result in positive relationships with *C. glacialis* abundance, explaining why *C. glacialis* is less common under salinity and temperature conditions where it should normally thrive (Grainger, 1963; Conover, 1988; Manley, 1995; Mumm *et al.*, 1998).

Similar effects of advection on zooplankton abundance occur in the Barents Sea (Skjoldal *et al.*, 1992; Tande *et al.*, 2000; Dalpadado *et al.*, 2003; Edvardsen *et al.*, 2003a). For instance, an episode of strong inflow of Atlantic water during the winter of 1982/1983 displaced *C. finmarchicus* from the southwestern part of the Barents Sea (Skjoldal *et al.*, 1992). The species was scarce in the inflowing water because it spends the winter deep in the Norwegian Sea, below the depth at the entrance to the Barents Sea. Inflow during spring and summer would have the opposite effect.

In simulation studies, advection has been estimated to account for ~80% of the *C. finmarchicus* biomass in the southwestern Barents Sea in summer (Edvardsen *et al.*, 2003b). The importance of advection is supported by our observations of *Calanus* abundance generally being strongly related to hydrography at intermediate depths (Fig. 3). However, surface water conditions seemed more relevant for *C. finmarchicus* in shallow locations and *C. hyperboreus* in deep locations, suggesting that their abundance may be more affected by growth conditions and food availability near the surface. Further investigation would benefit from time-series of abundance, production and advection throughout the productive season.

It seems unlikely that *Calanus* abundance was limited by temperature or salinity *per se*, as all three species show similar tolerance to low temperature (Hirche, 1987) and because the modest variability in salinity encountered over our study (range: 33.5–35.5) would have negligible effect on plankton physiology (McLaren *et al.*, 1968; Kinne, 1971).

In contrast to our findings, Tande *et al.* (Tande *et al.*, 2000) found no clear relationship between interannual variability in copepod abundance (including

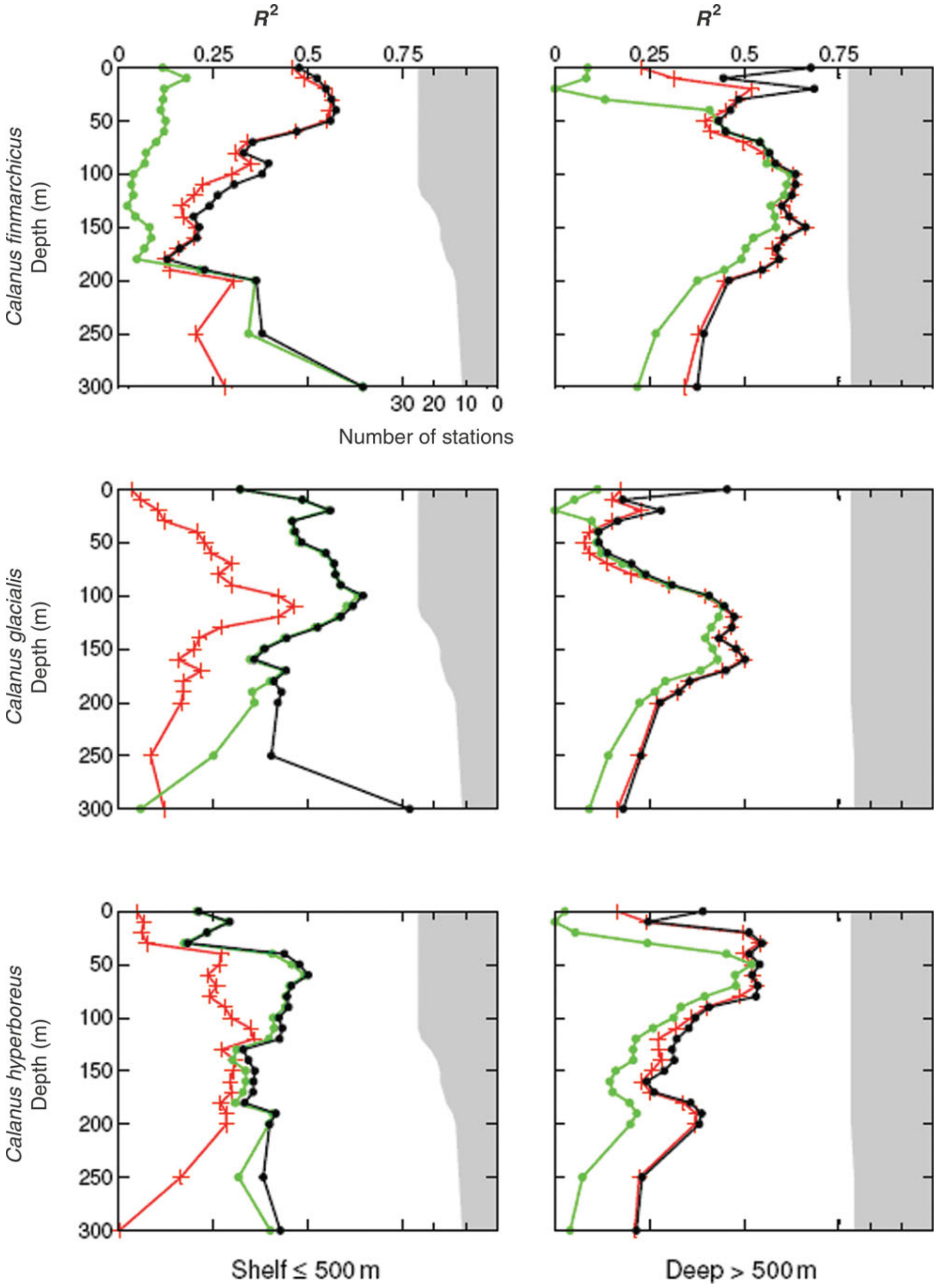

Fig. 3. R^2 values of regression analyses of *Calanus* spp. abundance against temperature and salinity calculated for depths of 0–200 m in 10 m intervals, at 250 m and 300 m. Lines show coefficient of determination (R^2) versus the depth from which temperature and/or salinity was taken, in regression models with temperature (red line with crosses), salinity (green) and both (black). Note that in the "shallow" category, locations are excluded from regressions with hydrography for depths below their bottom depth. If the excluded locations are outliers in the regression, this can be one reason why R^2 might improve with depth (grey shading shows statistical sample size at each depth; measurements at 250 and 300 m were missing for two deep locations).

C. finmarchicus) and water temperature during spring and early summer in the northeastern Norwegian Sea and Barents Sea. North Atlantic zooplankton distribution, on the other hand, is linked both to temperature and salinity as well as to large-scale circulation indices (Fromentin and Planque, 1996; Heath *et al.*, 1999; Beaugrand *et al.*, 2002) and advective transport (Heath *et al.*, 1999; Harms *et al.*, 2000; Speirs *et al.*, 2006).

Our results suggest that the biomass available for the next trophic level in the pelagic ecosystem is relatively robust to variability in the species composition of *Calanus*. *Calanus finmarchicus* dominates numerically when water temperature exceeds 2.2°C in our shallow locations, whereas in the upper layer of the deep locations, it remains the dominant species irrespective of variability in temperature and salinity (Fig. 2). The variability in temperature recorded in our study did not show significant relationships with total *Calanus* biomass, and salinity resulted in a significant negative relationship only in shallow locations (Tables I and II). However, as *C. finmarchicus* is smaller than *C. glacialis* and *C. hyperboreus* (Hirche, 1991, 1997; Mumm, 1991), an increase in temperature implies that the available energy would be shifted towards smaller individuals. Since prey size affects energy content (Scott *et al.*, 2000) as well as prey detection in fish (Aksnes and Utne, 1997) and birds (Weslawski *et al.*, 1994), the size shift suggested by our models might affect the energy flow in the food web.

The relationship between *Calanus* abundance and near-surface hydrography was weak in most cases in our study. This is in contrast to reports from lower latitudes, where correlations between zooplankton abundance and sea surface temperature (SST) are often strong (Rutherford *et al.*, 1999; Beaugrand *et al.*, 2002; Lindley and Reid, 2002). A likely reason for this difference is that high heat loss through the surface in the Arctic may alter SST on much shorter time-scales (hours to days) than the time-scales characteristic of population dynamics of these species (months to years).

We have attempted to quantify ecosystem impacts of hydrographic variability which have previously been treated mainly qualitatively and through simulations (Edvardsen *et al.*, 2003b). Our results confirm that advection affects zooplankton abundance, but the relative importance of local production remains to be quantified. Further progress could be made by a comprehensive study covering large areas throughout the productive season, including deep waters and several taxa. This would also provide valuable ground truthing for realistic ocean models coupling water column physics and biology (Wassmann *et al.*, 2006).

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