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# Fine-scale zooplankton vertical distribution in relation to hydrographic and optical characteristics of the surface waters on the Arctic shelf

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One of the main challenges in contemporary biological oceanography is to understand the factors that drive the spatial heterogeneity of pelagic organisms. Our study was performed at 10-m depth intervals within the upper 50 m of the ocean, at two different localities on the West Spitsbergen Shelf in the summers of 2009 and 2010. The fine-scale patterns in vertical zooplankton distribution were studied concurrently with measurements of hydrographic and optical properties of the water. We adopted a novel approach to the acquisition of information on light, phytoplankton and particle distributions by *in situ* measurements with optical sensors. Based on our data, we distinguished specific zooplankton vertical distribution patterns such as the aggregation of *Calanus finmarchicus* and small copepods toward the surface and the relatively high contribution of *C. glacialis* to subsurface layers. A vertical separation of *Calanus* sp. developmental stages was observed, and zones of rather even zooplankton distributions were also found. The variability in zooplankton distribution and community structure was closely related to the hydrographic and optical characteristics of the water; therefore, we hypothesize that these patterns could be the result of fine-scale microhabitat selection by different zooplankton species and life stages.

**KEYWORDS:** zooplankton vertical distribution; *Calanus*; optical water properties; arctic

## INTRODUCTION

“Fine-scale” zooplankton distribution refers to a scale of meters (Haury *et al.*, 1978; Prairie *et al.*, 2012). Typically, vertical sampling of zooplankton is performed by towing a net through tens to hundreds of meters, which results in integration across broad sampling distances in the water column. Previous studies have shown that during the Arctic summer, the majority of zooplankton biomass was concentrated in the upper 50 m (Sameoto, 1984; Kosobokova and Hirche, 2000, 2009; Auel and Hagen, 2002; Blachowiak-Samolyk *et al.*, 2007; Hirche and Kosobokova, 2007), but detailed knowledge on the distribution of species and their life stages within this layer is still very sparse, because the sampling has often been conducted with coarse vertical resolution, e.g. 50-0 m (e.g. Auel and Hagen, 2002; Ashjian *et al.*, 2003; Daase *et al.*, 2008; Kwasniewski *et al.*, 2010), 50-25-0 m (e.g. Kosobokova and Hirche, 2009; Kosobokova and Hopcroft, 2010) or 50-20-0 m (e.g. Blachowiak-Samolyk *et al.*, 2007, 2008; Falk-Petersen *et al.*, 2008; Lane *et al.*, 2008; Søreide *et al.*, 2008). Because the surface layer is the most productive and dynamic zone of the ocean, sampling resolution needs to be refined if we are to advance our understanding of the fine-scale distribution of zooplankton and how it is affected by environmental factors. Such an approach is particularly important in areas with high biological productivity and impacts of climate warming, such as the West Spitsbergen Shelf (WSS; e.g. Stempniewicz *et al.*, 2007; Kwasniewski *et al.*, 2010).

Zooplankton have limited ability to control their horizontal position, but they can, to a large extent, regulate their vertical distribution by their own mobility (Price, 1989; Pearre, 2003; Hirche *et al.*, 2006). Hence, zooplankton can be expected to select a habitat (water layer) that optimizes feeding conditions and minimizes their perceived predation risks (Fiksen and Giske, 1995; Aksnes *et al.*, 2004; Basedow *et al.*, 2010), which usually entails diel vertical migration. Generally, however, Arctic zooplankton do not perform synchronized vertical migrations under midnight sun conditions (Kosobokova, 1978; Fortier *et al.*, 2001; Blachowiak-Samolyk *et al.*, 2006; Cottier *et al.*, 2006; Falk-Petersen *et al.*, 2008).

Fine-scale zooplankton distribution is determined by the interactions between biological and physical processes, but most studies on Arctic zooplankton have focused on the importance of hydrography (e.g. Daase *et al.*, 2007; Blachowiak-Samolyk *et al.*, 2008; Kwasniewski *et al.*, 2010) and there has been little study of the effects of other environmental characteristics on zooplankton distribution patterns. We investigated the fine-scale vertical distribution patterns of zooplankton within the upper 50 m in relation to additional environmental characteristics, which can be

described by optical indices. As the light penetrates the water column, its intensity is reduced and the colour balance is changed by selective absorption, by both the water and its organic constituents, and the light is scattered by the phytoplankton and other suspended particles (Jerlov, 1976). Therefore, the optical properties of the water not only characterize the light conditions for primary production, but also may provide information on various other characteristics such as water transparency and underwater visibility or the amount and composition of suspended particles.

The effects of light intensity and other optical water properties on phytoplankton are already well understood, but relatively little is known about the effects of light on zooplankton; this subject definitely deserves more attention, particularly in the Arctic (Fortier *et al.*, 2001; Cottier *et al.*, 2006; Båtnes *et al.*, 2013). For example, Daase *et al.* (Daase *et al.*, 2008) pointed to the importance of light and optical water properties for the behaviours, distributions and life histories of the dominant Arctic copepods (*Calanus* spp. and *Metridia longa*) at the end of the productive season. However, these authors did not conduct any direct measurements of light attenuation, and could only estimate it from salinity and fluorescence profiles.

To assess the potential use of, and the ecological significance of, various optical water properties, we analysed a set of optical water indices, including the most important ones, such as the levels of photosynthetically active radiation (PAR) and the light attenuation coefficient. Measurements of PAR provided basic data on the light available for photosynthesis, whereas light attenuation determined water transparency and hence exposure of zooplankton to visual predators (Zaneveld and Pegau, 2003; Stempniewicz *et al.*, 2013). It is also possible to distinguish between non-absorbing small (mostly mineral) and larger (algal and non-algal) particles by analysing the combination of spectral light absorption and scattering coefficients. To this end, we used the ratio of absorption in the second chlorophyll *a* peak to attenuation coefficients of bulk particulate matter as well as the ratio of light scattering coefficients of the shortest and longest wavebands. Measurements of upwelling and downwelling spectral light distribution were used to calculate remotely sensed reflectance, commonly referred to as ocean colour. The measurements of ocean colour provide synthetic information about the relationships between the absorption and the backscattering properties of the water and its constituents. This can be used as a proxy for assessing many biological and physical features, such as particle content, water transparency, phytoplankton functional types and pigment concentrations (Nair *et al.*, 2008).

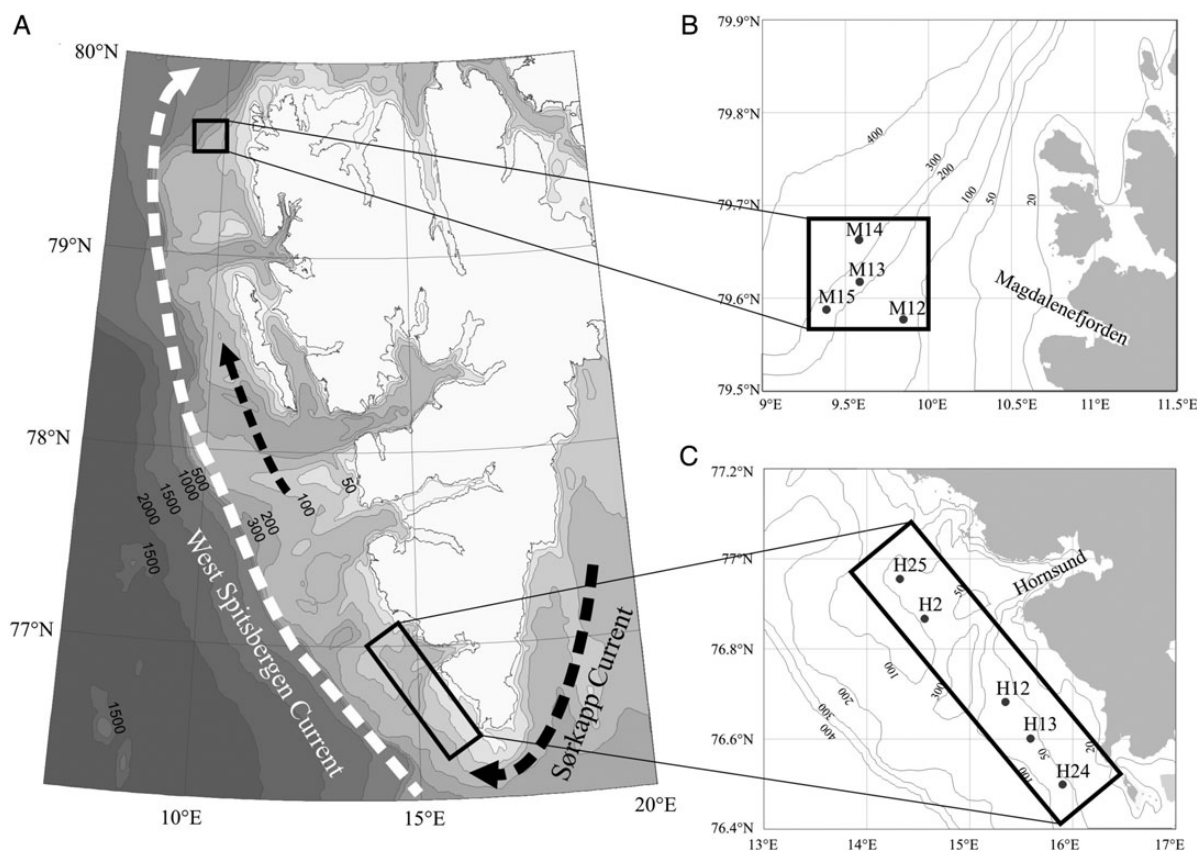
The goal of the present study was to examine fine-scale vertical distribution of zooplankton in relation to concurrently measured hydrographic and optical water characteristics in the surface waters of the WSS. We hypothesized that the vertical distribution of zooplankton will be complex, featuring individual patterns that would be the result of fine-scale micro-habitat selection by different species and life stages in response to water characteristics. Our specific objectives were: (i) to determine the fine-scale vertical zooplankton distributions in two different regions of the WSS, (ii) to describe the structure of the surface water habitats of the WSS, and (iii) to relate the zooplankton vertical distribution patterns to a range of water properties (temperature, salinity, %PAR, light attenuation, organic and inorganic particles contents and ocean colour).

## METHOD

The study was conducted at two sites on the WSS with different bottom topography and hydrography (Fig. 1).

The measurements and sampling were conducted from RV *Oceania* during two summer seasons, from 26 July to 1 August 2009 and from 28 July to 1 August 2010, at seven and six stations, respectively. Despite the study occurring during midnight sun conditions, the sampling and measurements were restricted to “night time” hours. One study site was situated near Magdalenefjorden (stations M12, M13, M14 and M15), in the northern sector of the WSS, which is a region under the influence of relatively warm and saline waters of Atlantic origin transported by the West Spitsbergen Current (Piechura *et al.*, 2001; Cottier *et al.*, 2005). The other study site was in the vicinity of Hornsund fjord (stations H12, H13 and H24 sampled in 2009 as well as H2 and H25 sampled in 2010), in the southern sector of the WSS, where colder and less saline Arctic-type waters are transported by the coastal Sørkapp Current (Saloranta and Svendsen, 2001).

By the end of June, the upper 50 m of the water column on the WSS is typically strongly stratified, with well mixed 10–20 m of fresher and warmer water above a transition layer with temperature and salinity gradients



**Fig. 1.** (A) Study area with ocean current patterns on the West Spitsbergen Shelf; the location of study sites marked with black rectangles, representing the close-ups of (B). Magdalenefjorden and (C) Hornsund regions, where the locations of zooplankton sampling stations are marked with dots.

of varying strength (Saloranta and Svendsen, 2001; Svendsen *et al.*, 2002). This stratification can be modified by intrusions, or destabilized because of strong winds and subsequent wave action. The confluence of water masses originating from different oceanographic domains is believed to be the main controlling factor of biological processes and results in co-occurrence of Atlantic and Arctic biota on the WSS (Piwoż *et al.*, 2009; Kwasniewski *et al.*, 2010; Hegseth and Tverberg, 2013; Kubiszyn *et al.*, 2014). During summer in the stratified water column, flagellated protists, especially ciliates, predominate numerically, whereas diatoms and heterotrophic taxa have the capacity to live in turbulent, mixed waters (Kubiszyn *et al.*, 2014). Diatoms and autotrophic dinoflagellates are transported with Atlantic-derived waters and cryo-pelagic species indicate inflow of Arctic waters (Piwoż *et al.*, 2009). A very few preliminary studies showing zooplankton composition in WSS waters near Hornsund and Magdalenefjorden (Kwasniewski *et al.*, 2010; Jakubas *et al.*, 2011, 2013; Trudnowska *et al.*, 2012) confirmed that the variation in the proportions of the co-occurring *Calanus* species (Kwasniewski *et al.*, 2010) together with the presence or absence of boreal/Arctic species (Kwasniewski *et al.*, 2003; Basedow *et al.*, 2004) is a reliable indicator of advection of different water masses.

### Zooplankton sampling

Zooplankton was collected with a Multiple Plankton Sampler (Hydro-Bios, Germany, mesh-size 180  $\mu\text{m}$ , mouth-opening 0.25  $\text{m}^2$ ) equipped with a conductivity–temperature–depth sensor and a flow meter, and all were monitored and logged in real time. The sampling resolution was refined to 10-m depth intervals, so generally five layers (50-40-30-20-10-0 m) were established. Three stations sampled in Hornsund in 2009 (H12, H13, H24) were situated in the shallow part of the WSS and thus were sampled from 40 m depth (40-30-20-10-0 m). The inconsistency of sampling station locations near Hornsund fjord in 2009 and 2010 was caused by unfavourable weather conditions during our sampling campaigns.

The zooplankton collected from each layer were preserved as individual samples in 4% formaldehyde-in-seawater buffered with borax. Qualitative and quantitative examinations were conducted in the laboratory following the protocols of Postel *et al.* (Postel *et al.*, 2000). First, larger zooplankters ( $>0.5$  cm) were picked out, identified and counted. The remaining zooplankton was suspended in a fixed volume of water, from which 2-mL subsamples were taken using a Stempel pipette and examined under a stereomicroscope so as to count and identify at least 300 zooplankton individuals per sample.

The rest of the sample was scanned in order to enumerate numerically less important taxa. *Calanus* species were identified based on morphology and size (Kwasniewski *et al.*, 2003). Zooplankton abundance was expressed as the number of individuals in a cubic meter ( $\text{ind. m}^{-3}$ ) calculated from the volumes of water filtered based on the net's flow meter data.

### Measurements of hydrographic and optical water indices

Measurements of the hydrographic and most of the optical water indices were obtained with an Integrated Optical-Hydrological Probe (IOHP), which consisted of a SBE 49 FastCat CTD probe (Sea-Bird Electronics), an ac-9 underwater spectrophotometer (WET Labs) and a CDOM fluorometer (TriOS). The measurements of light absorption and attenuation using the ac-9 spectrophotometer were performed at wavelengths of 412, 440, 488, 510, 532, 555, 650, 676 and 715 nm. The instrument was calibrated against Milli-Q water. Corrections for temperature, salinity and for scattering error were applied following Zaneveld *et al.* (Zaneveld *et al.*, 1994). The vertical profiles were performed with a resolution of  $\sim 30$  cm, and the signal values were smoothed with three-point median filter. Light scattering coefficients ( $b$ ) were obtained by subtracting absorption ( $a$ ) from the attenuation values ( $c$ ) for the corresponding light wavelengths ( $\lambda$ ). The calibration method meant that the measured attenuation, absorption and scattering coefficients did not account for pure optical water properties, but only for the water components, namely the presence of organic material and particles.

Vertical profiles of downwelling irradiance and upwelling radiance were performed with Compact Optical Profiling System (C-OPS) (Biospherical Instruments Inc.). This instrument has 19 spectral channels (340, 380, 395, 412, 443, 465, 490, 510, 520, 532, 555, 565, 589, 625, 665, 683, 710, 765 nm, and a PAR channel). The C-OPS radiometer was deployed in free-fall mode, away from the ship's shadow. The underwater measurements were supplemented with concurrent above-water measurements of the spectral downwelling irradiance,  $E_s(\lambda)$ , with a sensor mounted on the ship deck. These measurements were used to calculate the level of PAR in the profiles and the ocean colour at the stations.

To assess the potential use of and the ecological significance of various optical water properties, we analysed a set of optical water indices such as PAR, light attenuation ( $c_p555$ ), particulate scattering ( $b_p412/b_p715$ ), light absorption to attenuation ratio ( $a_p676/c_p650$ ) and reflectance ( $R_{rs555}/R_{rs665}$ ). The subscript p stands for particles, and the number represents the wavelength in



nm. The rationale for these selections of ratios of absorption, attenuation, scattering and reflectance at two wavelengths was because well-chosen spectral ratios are mainly dependent on one desired coefficient and are independent or quasi-independent from the others. Such an approach is also less sensitive to the uncertainties in the measurements resulting from natural variability rather than single (monochromatic) coefficients (Morel and Maritorena, 2001).

PAR was measured as a photon flux density (photons per second per square meter) within the wavelength range of 400–700 nm. Availability of PAR at a particular depth is one of the key factors determining rates of photosynthesis and living conditions for marine autotrophs. For higher values of PAR, more light was available for photosynthesis.

The light attenuation coefficient ( $c_{p555}$ ) was a measure of the light reduction by all optically significant water constituents of green light ( $\lambda \approx 555$  nm); it is a measure of the light beam attenuation by all the water components, which absorb and/or scatter the incident light. Because  $c_{p555}$  is inversely proportional to the transparency of the water, it is often used as an indicator of underwater visibility (Zaneveld and Pegau, 2003). High  $c_{p555}$  coefficient values indicated that the seawater contained a high concentration of particles and had low transparency.

The fraction of phytoplankton of the total suspended particles in the water ( $a_{p676}/c_{p650}$ ) was evaluated with the ratio of a coefficient of light absorption by particles for  $\lambda = 676$  nm ( $a_{p676}$ ) to a coefficient of light attenuation for  $\lambda = 650$  nm ( $c_{p650}$ ). Light absorption at  $\lambda = 676$  nm depends almost entirely on the amount of chlorophyll *a* (Sakshaug and Slagstad, 1991; Wozniak and Dera, 2007), while light attenuation at  $\lambda = 650$  nm is the product of light absorption and scattering by all the particles suspended in the water. Thus, a high index value indicated that the relative concentration of phytoplankton cells in the total particles was high.

The dominant size of suspended particles ( $b_{p412}/b_{p715}$ ) was acquired with the ratio of particulate scattering coefficients  $b_p$  at the shortest and longest visible light wavelengths ( $\lambda = 412$  nm and  $\lambda = 715$  nm). This is based on the spectral dependency of  $b_p(\lambda)$  to weakly or non-absorbing spherical particles as described by the theory of Mie. The light scattering by marine particles is inversely proportional to the wavelength,  $b_p \sim \lambda^{-1}$  (Morel, 1973). The volume-specific beam attenuation (and so light scattering) is three to four times greater for a blue light ( $\lambda \approx 420$  nm) than for red light ( $\lambda \approx 660$  nm) for small particles (1–10  $\mu\text{m}$  diameter), but it does not have spectral dependency for the particles larger than 10  $\mu\text{m}$  (Boss *et al.*, 2001). As a consequence, the

scattering by larger particles ( $>10 \mu\text{m}$ ) tends to be spectrally flat,  $b_p \sim \lambda^0$  (Barnard *et al.*, 1998; Gould *et al.*, 1999; Stramski *et al.*, 2004). Therefore, the ratio  $b_{p412}/b_{p715} \approx 1$  points to the prevalence of large particles or phytoplankton cells ( $>10 \mu\text{m}$ ), while higher values indicated the dominance of small particles ( $<10 \mu\text{m}$ ).

The selected ocean colour index ( $R_{rs555}/R_{rs665}$ ) was calculated as a ratio of remote sensing reflectance at  $\lambda = 555$  nm to  $\lambda = 665$  nm. The 665 nm is a spectral band of the second chlorophyll *a* absorption peak, for which the contribution from other phytoplankton pigments is minimal, contrary to the absorption at 555 nm. This ratio can be used for remote retrieval of the synthetic information about phytoplankton content. Because the reflectance ( $R_{rs}$ ) is inversely proportional to absorption, a higher ocean colour index value indicated that there was less phytoplankton in the water.

The simultaneous measurements of hydrographic and optical water characteristics were performed in vertical casts at each zooplankton station and were averaged into the 10 m depth bins, to be complementary to the vertical zooplankton net hauls intervals. For circumstances beyond our control, there were no measurements at station M12 in 2009, and there were no ocean colour and PAR measurements at station H24 in 2009.

## Statistics

The abundance data obtained from 62 zooplankton samples were log-transformed to stabilize the variances and to allow the less abundant taxa to influence the statistical results. All identified species, as well as copepodid stages of common copepods, were accounted for Bray–Curtis similarity coefficient calculations. Zooplankton composition and abundance in the samples were analysed by hierarchical cluster analysis to determine whether individual samples represented similar or different assemblages. The one-way analysis of similarities (ANOSIM) procedure was performed to test whether zooplankton composition in the defined groups of samples differed significantly. For comparison of independent groups of samples, the non-parametric Mann–Whitney *U*-test was used because the data did not meet the assumptions necessary for parametric tests. To compare the population age structure of selected copepods in the zooplankton community, a *G*-test of independence was applied. Additionally, the relation between variability in zooplankton composition and in water characteristics was modelled and tested by redundancy analysis (dbRDA). The dbRDA allowed for a model response of various zooplankton species to multiple predictor environmental variables. The dbRDA also identified the variables that best explained the patterns of

variation in the zooplankton data. The statistical analyses were computed in PRIMER V.6 + PERMANOVA and STATISTICA 9.0 packages.

## RESULTS

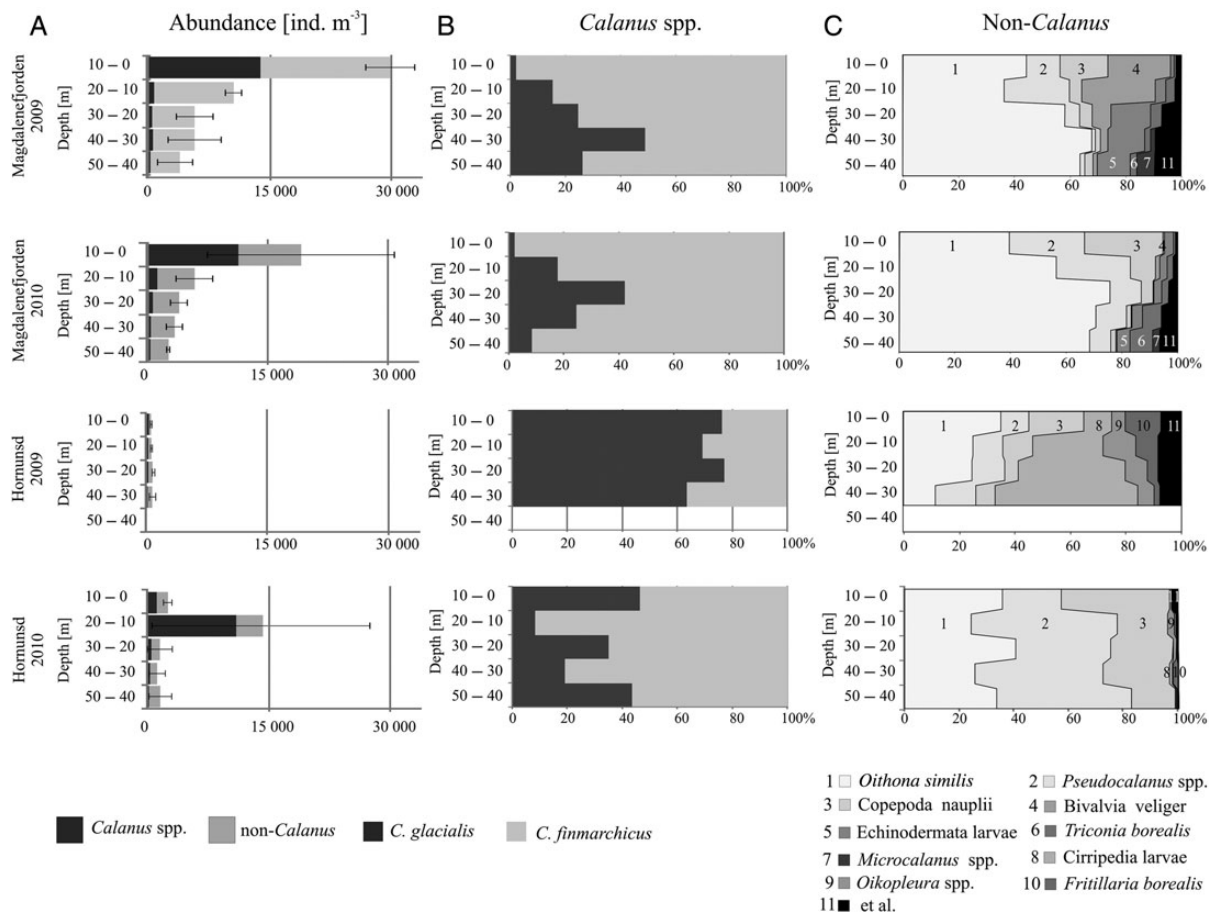
### Patterns of vertical zooplankton distribution in the upper 50 m

The zooplankton in the Magdalenefjorden region were less abundant in 2010 than in 2009 ( $U = 33.00$ ,  $P = 0.011$ ), were concentrated mainly in the upper 10-m layer and decreased in abundance gradually with depth (Fig. 2A). The zooplankton in the Hornsund region were distributed quite uniformly within the upper 50 m of the water column, with one notable exception of a very dense zooplankton concentration (24 026 ind.  $m^{-3}$ ) between 20 and 10 m at station H2 in 2010. On average, the total zooplankton abundance was lower in the Hornsund

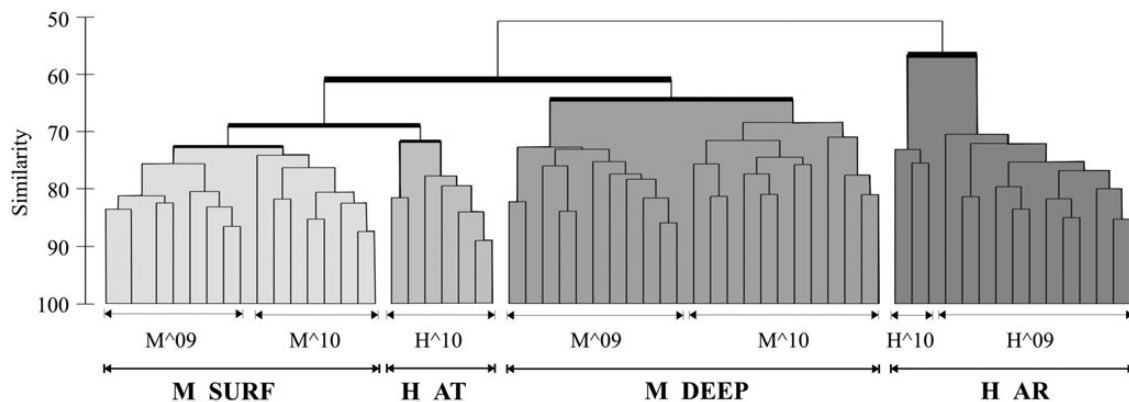
region than in the Magdalenefjorden region ( $U = 94$ ,  $P < 0.001$ ).

*Calanus* spp. individuals constituted  $\sim 50\%$  of the zooplankton community in the surface 10 m layers in both regions (Fig. 2A). Their contribution to the total abundance in the deeper layers was only  $\sim 9$  and  $25\%$  in Magdalenefjorden and Hornsund regions, respectively. The boreal species *C. finmarchicus* was the predominant *Calanus* species at the Magdalenefjorden stations (Fig. 2B), particularly in the upper 10-m layer. The relative abundance of *C. glacialis*, however, was higher in the deeper layers at Magdalenefjorden ( $>40\%$  of *Calanus* population at the 40–30 m in 2009 and at the 30–20 m in 2010). Of the two co-occurring *Calanus* species at the Hornsund stations, the Atlantic *C. finmarchicus* predominated in 2010, while in 2009 the Arctic *C. glacialis* was more than  $60\%$  of the *Calanus* spp.

In addition to the *Calanus* spp., small copepods such as *Oithona similis* and *Pseudocalanus* spp., and Copepoda nauplii



**Fig. 2.** Vertical patterns of zooplankton distribution in the upper 50 m layer. Individual graphs show integrated zooplankton data for discrete groups of stations located in different study sites (Magdalenefjorden, Hornsund) and years (2009, 2010). (A) Mean total abundance (ind.  $m^{-3}$ ) of zooplankton (*Calanus* and non-*Calanus* taxa indicated by different shades of gray), bars indicate min. and max. abundance. (B) Proportions of *C. glacialis* and *C. finmarchicus*, and (C) proportions of taxa other than *Calanus*.



**Fig. 3.** Group-average hierarchical clustering of the Bray–Curtis similarity index of all taxa present in the samples. M\_SURF (samples from the surface 30/20 m in the Magdalenefjorden region), H\_AT (samples collected in the Hornsund region in 2010), M\_DEEP (samples collected from deeper than the 20 m depth layers in the Magdalenefjorden region), H\_AR [samples collected in the Hornsund region in 2009 together with three samples (50–40, 40–30 and 30–20 m) from the H2 station sampled in 2010].

were relatively abundant at each sampling station (Fig. 2C), and sometimes they even predominated numerically (e.g. Hornsund stations sampled in 2010). Bivalvia veligers were also very abundant ( $3103 \text{ ind. m}^{-3}$ ), particularly in the upper layers (20–10 and 10–0 m) at the Magdalenefjorden stations in 2009, while in the most numerous meroplankton the deeper layers were Echinodermata larvae. The contribution of Echinodermata larvae and copepods such as *Triconia borealis* and *Microcalanus* spp. as well as rare taxa increased with depth in the Magdalenefjorden region in both years. Cirripedia larvae were 28% of the zooplankton community below 10 m at the Hornsund stations in 2009. Appendicularians (*Oikopleura* spp. and *Fritillaria borealis*) contributed markedly to the zooplankton community at the Hornsund stations in 2009 in the three upper depth strata (30–20, 20–10 and 10–0 m).

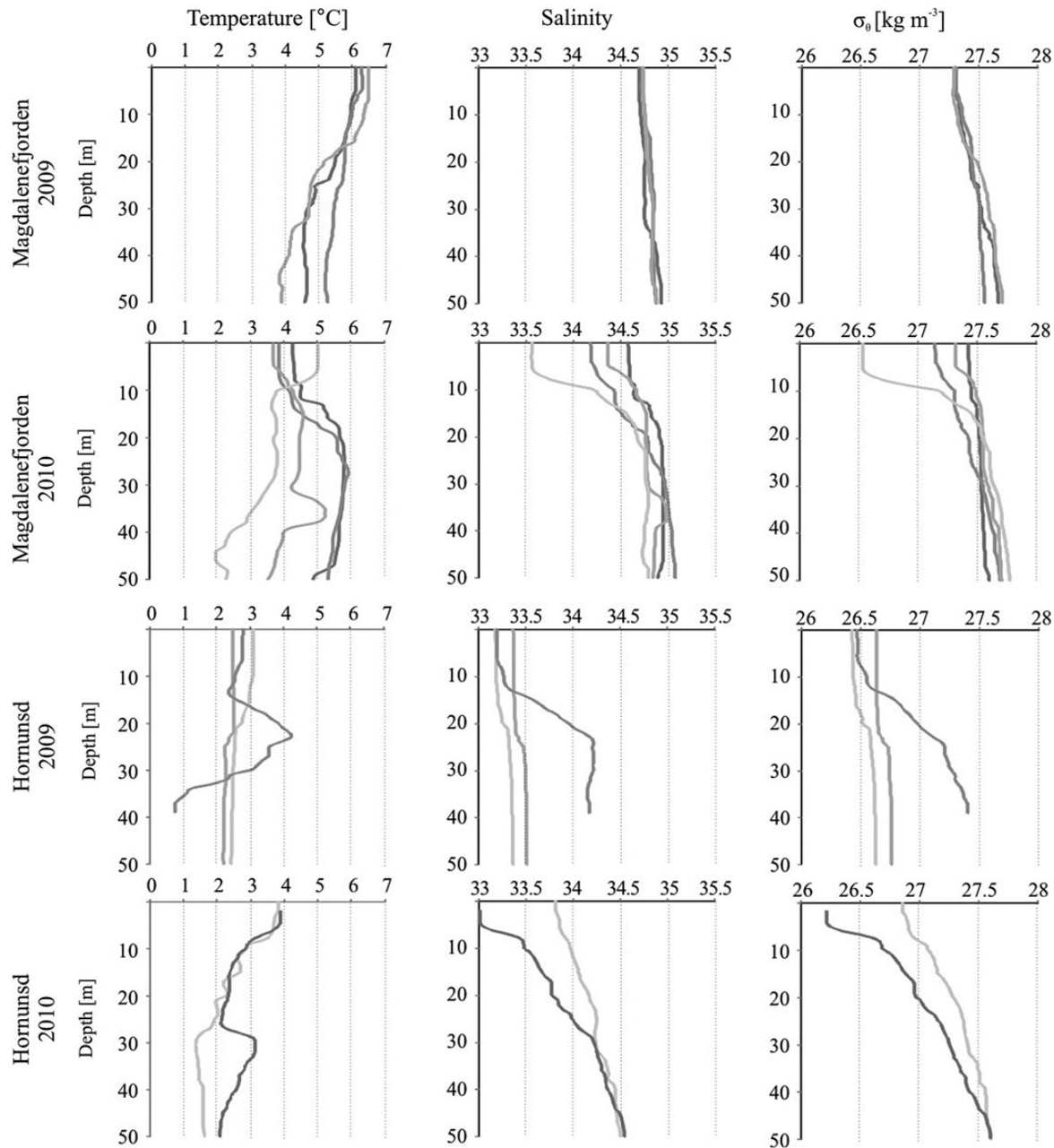
Analysis of the population age structure of the two *Calanus* species indicated that younger stages (CI–CIII) were generally concentrated in the upper layers while older stages (CIV–CVI) predominated in the deeper layers, especially at the Magdalenefjorden stations (data not shown). There were significant differences between populations from Hornsund and Magdalenefjorden ( $G$ -test,  $P < 0.05$ ) for age structure, with younger populations in the southern region (Hornsund). The inter-year comparison demonstrated that the *C. finmarchicus* population was younger in 2009 at both sites ( $G = 31$  and  $G = 2$ ,  $P < 0.001$ ), whereas the *C. glacialis* population differed only in the Magdalenefjorden region, i.e. it was older in 2009 than in 2010 ( $G = 18$ ,  $P = 0.003$ ).

There were clear differences in the zooplankton composition between the two study sites (ANOSIM,  $R = 0.70$ ), especially in 2009 (ANOSIM,  $R = 0.98$ ). The composition also varied between the 2 years in the Hornsund region ( $R = 0.76$ ), but it did not in Magdalenefjorden ( $R = 0.41$ ).

Four zooplankton community assemblages were distinguished with the use of hierarchical clustering of the zooplankton samples. There were two assemblages at the Magdalenefjorden stations associated with the upper and lower layers (M\_SURF and M\_DEEP) and two assemblages at the Hornsund stations associated with Atlantic- and Arctic-type waters (named accordingly H\_AT and H\_AR) (Fig. 3). The M\_SURF zooplankton assemblage was characterized by high total zooplankton abundance (mean  $15\,557 \pm 10\,855 \text{ ind. m}^{-3}$ ) and the predominance of *O. similis*, *C. finmarchicus*, *Pseudocalanus* spp. and juvenile forms of copepods, bivalves and echinoderms. The H\_AT assemblage was similar to the M\_SURF for both high abundance ( $11\,619 \pm 15\,783 \text{ ind. m}^{-3}$ ) and major taxonomic composition, but it differed substantially because of the greater contribution of *C. glacialis*. The M\_DEEP zooplankton assemblage was characterized by higher taxonomic diversity but lower total zooplankton abundance ( $3992 \pm 2098 \text{ ind. m}^{-3}$ ) than the M\_SURF assemblage. The distinct H\_AR assemblage was characterized by the lowest zooplankton abundance (mean  $1260 \pm 875 \text{ ind. m}^{-3}$ ), in which the most numerous taxa were *O. similis*, Copepoda nauplii, *Pseudocalanus* spp., *C. glacialis*, Cirripedia larvae and appendicularians.

### Patterns of vertical distribution of hydrographic and optical water characteristics

Water temperature and salinity varied significantly within the upper 50 m of the sea (Fig. 4). Generally, temperatures ( $U = 21$ ,  $P < 0.001$ ) and salinities ( $U = 17$ ,  $P < 0.001$ ) were lower in the Hornsund than in the Magdalenefjorden region. The highest temperatures ( $6.0$ – $6.5^\circ\text{C}$ ) were recorded in the upper 10–0 m in the

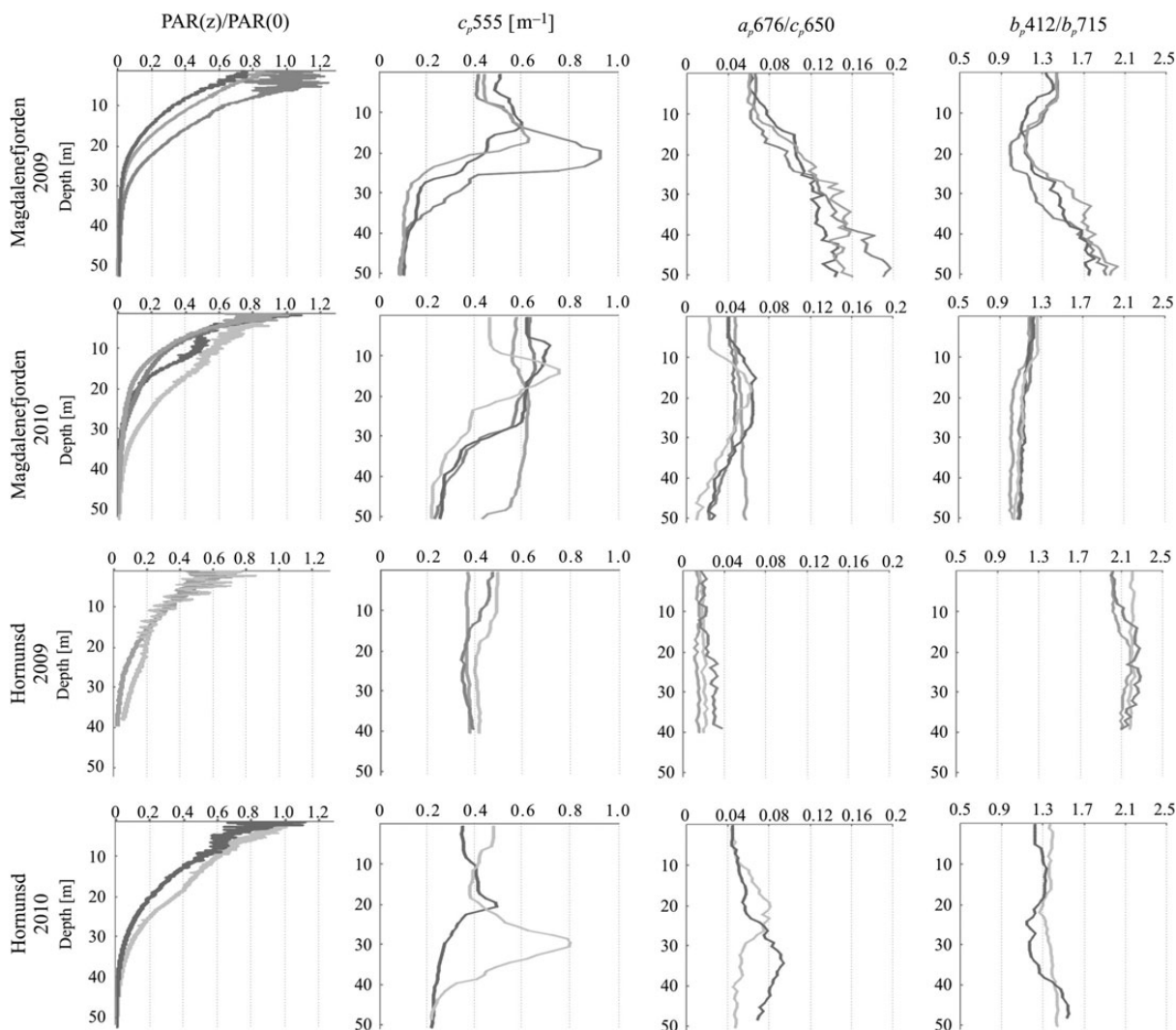


**Fig. 4.** Vertical profiles of hydrography (temperature, salinity, potential density  $\sigma_{\theta}$ ), data 1-m averaged. Each separate graph includes profiles from discrete groups of stations located in different study sites (Magdalenefjorden, Hornsund) and years (2009, 2010).

Magdalenefjorden in 2009. The temperature at the sites in the Hornsund region was below  $4^{\circ}\text{C}$  in both years. There were clear vertical gradients in temperature, salinity and potential density at some stations, especially in 2010. The gradients were absent or very weak in 2009, at stations in both the Magdalenefjorden and Hornsund regions, except for the H24 station.

The vertical distribution of the optical water indices in the upper 50 m of the water column showed various patterns (Fig. 5). High values of PAR occurred only within the upper few meters. PAR was the highest at the surface of the Magdalenefjorden stations in 2009 and the lowest at the Hornsund stations also in 2009. Light attenuation coefficients of the water at 555 nm ( $c_{p555}$ ) varied from





**Fig. 5.** Vertical profiles of optical water properties: PAR (Photosynthetically active radiation),  $c_{p555}$  (light attenuation),  $a_{p676}/c_{p650}$  (phytoplankton fraction index) and  $b_{p412}/b_{p715}$  (particle size index). Each graph includes profiles from discrete group of stations located in different study sites (Magdalenefjorden, Hornsund) and years (2009, 2010).

0.1 to almost  $1.0 \text{ m}^{-1}$ . The relatively high, though variable,  $c_{p555}$  values (i.e. low transparency) coincided with the low values for the particle size index,  $b_{p412}/b_{p715}$  (1.0–1.3) at the corresponding water layers at all Magdalenefjorden stations and at the Hornsund stations in 2010. This indicated the occurrence of relatively large particles, presumably of organic origin, which was further supported by the high  $a_{p676}/c_{p650}$  index values (relative contribution of phytoplankton to all particles in the water). Increasing with depth, the  $a_{p676}/c_{p650}$  and  $b_{p412}/b_{p715}$  index values at the Magdalenefjorden stations in 2009 indicated the higher content of small phytoplankton particles within the depth layers of 50–40–30 m. Very different optical characteristics were observed at the

Hornsund stations in 2009, where the water column seemed optically homogenous (Fig. 5). The low proportion of phytoplankton particles ( $a_{p676}/c_{p650}$ ) and the high values of the scattering index ( $b_{p412}/b_{p715}$ ) suggested the prevalence of particles of mineral origin.

The highest ocean colour index ( $R_{rs555}/R_{rs665}$ ) values noted at the Hornsund stations in 2009 (10.1 and 13.0) confirmed the low content of phytoplankton. The ranges of ocean colour index values in the Magdalenefjorden region in both years ( $R_{rs555}/R_{rs665}$ : 6.8–8.1 in 2009 and 6.7–8.6 in 2010) and at the Hornsund stations in 2010 ( $R_{rs555}/R_{rs665}$ : 7.6–9.6) were similar and suggested a higher content of phytoplankton in those waters.

## Relations between zooplankton community structure and water characteristics

The dbRDA analysis indicated clear relationships between the zooplankton community structure and water characteristics (Table I, Fig. 6). The model showed that the hydrographic and optical characteristics together explained 52% of the total variation observed among the zooplankton communities for their composition and abundance. Salinity was the most important explanatory variable, followed by PAR and the indices characterizing the type of particles present in the water ( $b_{p412}/b_{p715}$

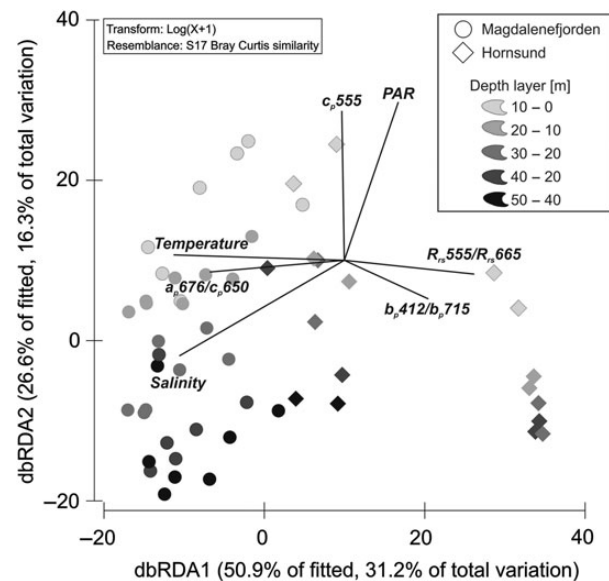
*Table I: Statistics for each explanatory variable tested in the redundancy analysis (dbRDA)*

Variable	df	$R^2$	Pseudo-F	$p$ (Perm)	%
Salinity	51	0.28	19.5	0.0001	28
PAR	50	0.39	9.6	0.0001	12
$b_{p412}/b_{p715}$	49	0.47	7.2	0.0001	20
$a_{p676}/c_{p650}$	48	0.53	6.5	0.0001	16
Temperature	47	0.57	4.3	0.0001	20
$c_{p555}$	46	0.61	4.0	0.0001	10
$R_{rs555}/R_{rs665}$	45	0.61	0.6	0.8607	23

The variable that best explained the variability in zooplankton community structure was ranked first, and the following variables were ranked according to their additional explanatory power.

and  $a_{p676}/c_{p650}$ ). The explanatory power of individual indices such as salinity, water colour ( $R_{rs555}/R_{rs665}$ ), temperature and particle size ( $b_{p412}/b_{p715}$ ) was very high ( $>20\%$ ), while it was high ( $>10\%$ ) for the phytoplankton fraction ( $a_{p676}/c_{p650}$ ), light attenuation ( $c_{p555}$ ) and PAR.

The dbRDA model revealed two ecological gradients (*horizontal* and *vertical*) in the variability of zooplankton composition and environmental variables. The *horizontal* gradient, which can also be regarded as the manifestation of regional differences between the two study sites, is expressed along the first axis in the diagram (Fig. 6) and is related to the differences in hydrography and types of particles (particle size  $b_{p412}/b_{p715}$ ) and phytoplankton fraction ( $a_{p676}/c_{p650}$ ). The *vertical* depth related gradient is depicted along the second ordination axis and it is related to the gradients in light conditions expressed by PAR and light attenuation ( $c_{p555}$ ). The dbRDA model suggested that the zooplankton in the Magdalenefjorden region experienced conditions of higher salinity, temperature and relative phytoplankton concentration ( $a_{p676}/c_{p650}$ ), compared with those experienced by the zooplankton in Hornsund that were characterized by higher ocean colour ( $R_{rs555}/R_{rs665}$ ) and particle size ( $b_{p412}/b_{p715}$ ) indices, which suggested lower phytoplankton concentrations and the presence of high concentrations of suspended small particles of mineral origin.



**Fig. 6.** Biplot of the redundancy analysis (dbRDA) relating the structure of zooplankton community at each depth layer and station (samples from station M12 from 2009 are lacking). Different symbols indicate different study sites (Magdalenefjorden, Hornsund) and their grey shadows indicate the depth layer of samples. The positions of markers are centroid scores of zooplankton community structure in each sample, whereas arrows point to the direction of increasing values of the explanatory variables: temperature, salinity, PAR,  $c_{p555}$  (light attenuation),  $b_{p412}/b_{p715}$  (particle size index),  $a_{p676}/c_{p650}$  (phytoplankton fraction index) and  $R_{rs555}/R_{rs665}$  (ocean colour index) (for statistics, see Table I).

## DISCUSSION

Our study clearly demonstrates that as a result of the heterogeneous distributions of hydrographic and optical water characteristics, the surface waters of the WSS provided different micro-habitats in discrete water layers and these had substantial influence on the vertical structure of the zooplankton community. Because of the refined sampling resolution (10-m depth intervals), it was possible to distinguish specific zooplankton distribution patterns in the upper 50-m layer of the WSS for these discrete micro-habitats. These patterns included distinct depths containing high abundances of *C. finmarchicus* and small copepods, and others in which there were relatively high proportions of *C. glacialis*. The pattern of the bimodal vertical separation of the developmental stages of *Calanus* spp. as well as the zones of relatively even zooplankton distributions were also identified. It is hypothesized that the uneven fine-scale vertical distribution of zooplankton was generated by behavioural responses of the zooplankters in selecting preferred water characteristics determined by water stratification, advection or even by the weather conditions (Haury *et al.*, 1990; Checkley *et al.*, 1992; Norrbin *et al.*, 1996; Folt and Burns, 1999;

Pinel-Alloul, 1995; Ambler, 2002; Pearre, 2003). Because light, temperature, food availability and predation risk all vary with depth within the ocean water column (Banse, 1964), these fine-scale vertical distribution patterns of zooplankton can be explained by zooplankton habitat selection (Falkenhaug *et al.*, 1997; Pearre, 2003).

With the vertical thermohaline stratification, such as that observed in the Magdalenefjorden region, different zooplankton community assemblages were distinguished for the upper and lower layers of the surface 50 m of the ocean. The micro-habitat of the upper layers at the Magdalenefjorden stations was characterized by relatively high temperature, salinity and phytoplankton fraction. These conditions appeared favourable for copepod nauplii, meroplankton and young *Calanus* copepodid stages. In contrast, the micro-habitat of subsurface layers had much lower overall zooplankton abundances, but contained higher proportions of older *Calanus* spp., copepodid stages and taxa that generally avoid surface waters (e.g. *Microcalanus* spp., *Paraeuchaeta* spp., *Metridia longa*, Aetideidae, Ostracoda). The descending of the older life stages of *C. glacialis* may result from the favourable lower temperature and water transparency in the deeper layers (Kosobokova, 1999; Daase *et al.*, 2008; Weydmann and Kwasniewski, 2008; Dupont and Aksnes, 2012). The observed bimodal vertical distribution pattern of younger and older copepodid stages of *Calanus* was previously found in the Atlantic-influenced fjord of the WSS, Kongsfjorden (Kwasniewski *et al.*, 2003; Basedow *et al.*, 2004). The boreal *C. finmarchicus* was the dominant species in the top surface strata in the Magdalenefjorden region, whereas the Arctic *C. glacialis* was concentrated in the subsurface (40–30–20 m). A depth-dependent decrease in light intensity and food supply has already been suggested as critical factors determining the zooplankton distribution and community structure in the central Arctic Ocean (Auel and Hagen, 2002). Light detection occurs in most plankton organisms, and some of them exhibit phototactic behaviour, such as *Calanus* spp. (Båtnes *et al.*, 2013). Thus, in addition to temperature and water clarity, the change in the irradiance level with depth could have had an effect on the *Calanus* vertical distribution, as was suggested in earlier studies (Daase *et al.*, 2008; Dupont and Aksnes, 2012).

The vertical stratification of the upper water column was less pronounced in Hornsund in 2009 and the zooplankton were typically less numerous and more evenly distributed. The sampling in 2009 was performed after days with strong winds over the shallow part of the shelf, south of the Hornsund fjord. This may explain why the habitat was characterized by the presence of cold and less saline waters with low stratification and high contents of small, mostly mineral particles from the sea bottom that

likely were resuspended as a result of the storm and tidal mixing. Higher mineral and lower phytoplankton content in Hornsund waters were reflected in higher ocean colour index values than observed in the Atlantic-influenced waters. The zooplankton there had greater proportions of *C. glacialis*, a principal inhabitant of the Arctic shelves (Conover, 1988), and included Cirripedia larvae and appendicularians. Earlier studies found that high abundances of Cirripedia larvae were mainly recorded during the spring season in the Arctic (Blachowiak-Samolyk *et al.*, 2008; Walkusz *et al.*, 2009), although their distributions tend to be patchy in time and space. The high abundance of Cirripedia larvae, also found in this region in 2011 (Jakubas *et al.*, 2013), could be associated with the close proximity of hard bottoms to the sampling stations and the capability of cirripedes to produce repeated clutches of offspring throughout the season (Kuklinski *et al.*, 2013).

The sampling in 2010 occurred north of Hornsund fjord, near the trench in the shelf, in the pathway of Atlantic-type waters transported into the fjord. This can explain why some characteristics of the habitat differed in comparison with the ones recorded in the previous year and were similar to those recorded in the Magdalenefjorden region. The water column was homogenous rather than stratified, thus we conclude that it contained a dynamic mix of various types of waters, with different properties and various constituents, including different phytoplankton communities along with terrigenous particles originating from the fjord and the sea bed (Cunningham *et al.*, 2003; Sullivan *et al.*, 2005; Hodal and Kristiansen, 2008). Regardless of hydrography, the zooplankton assemblages found to the north of Hornsund were similar (Fig. 3) to those found in the surface layers at Magdalenefjorden, with increased proportions of *C. finmarchicus*, *O. similis* and *Pseudocalanus* spp. The increase in proportion of *C. finmarchicus* may have been due to admixture of Atlantic-type waters from the trench, whereas the increase in *Pseudocalanus* spp. supported the suggestion of an admixture of fjord waters, which generally contain numerous populations of this copepod (Walkusz *et al.*, 2009).

The analysis of the interactive influence of various water characteristics on zooplankton communities with the use of a multivariate statistical method proved to be an effective approach to advance our understanding of habitat selection by different zooplankton species and life stages. Our results showed that, even though the temperature, salinity and the resulting water stratification explained a substantial part of the variability in zooplankton distribution and community structure in the surface waters, the influence of other water characteristics described by optical indices was equally important.

Although the results presented here concur with earlier research (Daase and Eiane, 2007; Daase *et al.*, 2007; Blachowiak-Samolyk *et al.*, 2008; Estrada *et al.*, 2012) indicating that the variability in hydrography had measurable effects on zooplankton distribution and species composition in the Arctic, this was the first attempt to assess the importance of optical water properties in contributing to the variability in zooplankton community composition and distribution. The optical indices describing characteristics, such as the phytoplankton fraction and particle size, were among the main variables explaining the *horizontal* variability in the composition of zooplankton assemblages on the WSS, whereas light conditions such as PAR and light attenuation accounted mainly for the *vertical* patterns in our model. We argue that using high-resolution *in situ* measurements to determine the ratio of absorption at 676 nm to attenuation at 650 nm can be a more sensitive method for estimating the fine-scale chlorophyll *a* content than the conventional method of collecting water samples at a few predefined depth levels. Additionally, the combinations of absorption and scattering coefficients proved to be both simple and useful descriptors of the relative composition of phytoplankton and detritus in the suspended matter (Stramski *et al.*, 2001).

In situations when information on vertical stratification is not necessary, the ocean colour index, which had a very high explanatory power in our statistical model, used in combination with remote, satellite observations, might be very useful for characterizing water properties, such as temperature, light absorption, particle content and pigment composition (Bouman *et al.*, 2003), because the index contains the synthetic information on the optical properties of the upper ocean layer. High-resolution multidisciplinary *in situ* studies (e.g. Daase *et al.*, 2008; Trudnowska *et al.*, 2012) together with remote sensing (Strömberg *et al.*, 2009) data (e.g. temperature, chlorophyll *a* and water colour retrieved from satellite) are strongly recommended for further comprehensive investigations on the spatial structures of the zooplankton community.

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