

# Arctic zooplankton do not perform diel vertical migration (DVM) during periods of midnight sun

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**ABSTRACT:** Diel vertical distribution patterns of dominant zooplankton taxa were studied during a period of midnight sun (May 1999) in the Marginal Ice Zone (MIZ) of the Barents Sea along 2 transects across the ice edge. Eight stations were sampled every 6 h over 24 h at 5 depth intervals. Our study confirmed that copepod nauplii (most probably *Calanus hyperboreus* and *C. glacialis*) together with *Pseudocalanus* spp. preferred the surface water layer. The herbivores *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* concentrated in the upper 50 m depth interval, whereas the omnivores *Metridia longa* and *Microcalanus* spp. were generally found in deeper waters. As a result of vertical distribution patterns of the numerically abundant taxa, a bulk of zooplankton was concentrated within the 0–50 m layer. Vertical distribution patterns of all examined taxa/groups varied in time as a result of habitat changes (with respect to water mass distribution and sea depth) as well as random patchiness. Based on our data and on a comprehensive literature survey on Arctic zooplankton diel vertical migration (DVM), we postulate that common zooplankton taxa in the MIZ of the Barents Sea do not perform DVM under the midnight sun. Arctic *C. glacialis* in May 1999 occupied deeper layers at stations with more ice cover and less melt water. This distribution pattern was probably related to the species' reproduction. At the same time, Atlantic *C. finmarchicus* was concentrated further away from the ice edge and chlorophyll *a* maximum, and presumably had not begun its seasonal reproduction.

**KEY WORDS:** Zooplankton · *Calanus* · Diel vertical migration (DVM) · Marginal Ice Zone · Barents Sea

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## INTRODUCTION

The Marginal Ice Zone (MIZ) of the Barents Sea is the transitional area between open ocean and permanent ice cover. It is characterised as one of the most dynamic and ecologically important regions in the world's oceans because it represents a highly productive area in the Arctic (Hegseth 1992, Dayton et al. 1994, Slagstad & Stokke 1994). Zooplankton play a vital role in the Barents Sea ecosystem and the production of pelagic zooplankton supports, both directly and indirectly, large stocks of commercially important

fishes such as Arctic cod *Boreogadus saida*, capelin *Mallotus villosus*, and herring *Clupea harengus* (Dragesund & Gjørseter 1988). Precise knowledge of the diel distribution pattern of pelagic animals in a dynamic marine environment is of fundamental importance for understanding the trophic relationships between organisms.

Diel vertical migration (DVM) is a characteristic behaviour of many zooplankton taxa (Longhurst 1976a). In the Arctic, studies of this phenomenon were initiated by Bogorov (1946), who reported a lack of DVM of zooplankton during periods of continuous

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daylight. This conclusion, however, was not indisputably accepted and was a starting-point for later studies on DVM carried out by Digby (1961), McLaren (1963), Hopkins & Gulliksen (1978), Kosobokova (1978), Buchanan & Haney (1980), Falk-Petersen (1981), Groendahl & Hernroth (1986), Runge & Ingram (1988, 1991), Conover & Huntley (1991), Hays (1995), Hattori & Saito (1997), Dale & Kaartvedt (2000), Fortier et al. (2001), Arashkevich et al. (2002), and Head et al. (2003). Despite extensive research, the question of whether Arctic zooplankton migrate diurnally during periods of constant illumination has not been resolved.

In addition to light, environmental factors such as ice cover and hydrographic conditions are very important in determining the vertical distributions of zooplankton (Buchanan & Haney 1980). However, in the Barents Sea, the influence of hydrographic parameters on zooplankton distributions in ice-covered waters has only been addressed in a few studies (Unstad & Tande 1991, Pedersen et al. 1995a,b, Hansen et al. 1996, Falk-Petersen et al. 1999, Søreide et al. 2003). Thus, our investigation in the Arctic Barents Sea provided a unique, but challenging, opportunity for studying the relationship between DVM of zooplankton and hydrography during periods of continuous sun.

The purpose of the present study was to describe short-term vertical distribution patterns of zooplankton across the MIZ of the Barents Sea, and also address the question of DVM. While previous studies on DVM phenomenon focused either on 1 species/genus or total zooplankton biomass/abundance, or were based on 2 daily hauls (i.e. day and night), our investigation allowed us to examine diel changes in vertical distribution of all the numerically dominant zooplankton taxa in the central Barents Sea, (1) under typical and variable MIZ hydrological and ice cover conditions, and (2) during constant illumination.

## MATERIALS AND METHODS

**Study area.** The Barents Sea is a continental shelf sea with an average depth of 230 m. The physical conditions of the sea have been previously described (Loeng 1991, Rudels et al. 1991, Steele et al. 1995), so only a brief description of the hydrographic features prevailing at the time of the survey is provided.

Typically, in the central Barents Sea, warm Atlantic water from the south encounters cold water from the north over the Hopen Trench, forming the Polar Front at around the 250 m isobath. The inflowing warm and saline Atlantic water is advected northwards by the Norwegian Atlantic Current that splits at the Bear Island Channel. The branch that flows into the Barents Sea flows partly north along the axis of the Hopen

Trench, to the west and north of the Central Bank. In the northern Barents Sea and over the Great Bank, the upper 150 m of the water column is colder and less saline and is defined as Arctic water (Loeng 1991). This cold Arctic water layer is, initially, formed by freshening of Atlantic water by ice melt, by net precipitation, and perhaps also by mixing with less saline water advected from the Kara Sea (Rudels et al. 1991, Steele et al. 1995). It is subsequently homogenised during winter by haline convection in the area of origin, in the northern Barents Sea. Then, due mainly to the prevailing northerly winds during winter and spring, it is transported south to form the northern component of the Polar Front (Vinje & Kvambekk 1991).

**Description of transects.** This study was a part of the programme "Spatial and temporal variability of the ice-ocean system in the MIZ of the Barents Sea" carried out by the Norwegian Polar Institute (Hop & Falk-Petersen 2003). The investigated area was at the inner part of the Hopen Trench and surrounding banks of the Barents Sea, from 76°03'N to 77°31'N, and from 26°53'E to 33°08'E (Fig. 1). Zooplankton and hydrographic parameters were collected during a cruise with the ice-strengthened research vessel 'Lance' between 9 and 22 May 1999. Two transects (A: eastern at 33°E, and B: western at 27°E near Hopen), each consisting of 4 stations, were sampled from north to south across the MIZ. Transect A started at the southern Great Bank (<200 m deep) and ended up over deeper water in the Hopen Trench (~300 m), whereas Transect B started north of Hopen (~200 m) and extended south over the shallower areas of the Spitsbergen Bank (<100 m). Geographical coordinates of each sample are given in Hop & Falk-Petersen (2003). The distances between the stations varied between 5 and 35 nautical miles because the primary criterion for their location was difference in ice cover condition. Thus, Stns A31 and B49 were in compact pack ice (100%), Stns A33 and B50 were in about 60 to 70% ice cover, Stns A34 and B51 were near the ice-edge in about 10% ice cover, and Stns A35 and B52 were located in the 'open water' (Fig. 1). The open water station at the end of the eastern Transect A was located south of the Polar Front; therefore, both 'across-ice-edge' and 'across-Polar-Front' conditions were sampled there. Transect B was located entirely in Arctic water north of the Polar Front. Further details with regard to the ice conditions are described in Engelsen et al. (2002).

**Environmental background sampling.** Ice concentration, ice thickness and floe size were recorded every 3 h from the ship and documented using a digital camera (Hop & Falk-Petersen 2003).

Water mass properties (salinity, temperature and density) were measured at each station with a Sea-Bird Electronics SBE 911 + CTD (conductivity, temperature,

depth profiler) deployed vertically to the bottom approximately every 3 h. The CTD data were assigned to a grid in MATLAB version 5.3 and contoured by linear interpolation (Fig. 2). The water masses were identified according to salinity and temperature properties (Loeng 1991, Harris et al. 1998). Information on chlorophyll *a* (chl *a*) concentration in the study area ( $\text{mg chl } a \text{ m}^{-2}$ , integrated for the upper 50 m) used in the discussion was collected parallel to zooplankton sampling but only once at each station. Details on sample collection and measurements are described in Engelsen et al. (2002) and Søreide et al. (2003).

**Zooplankton sampling and examination.** During sampling the ship was drifting together with the ice and the underlying near-surface water masses. The longest distance between start and end sampling a single station, 94 km at Stn A35 (Fig. 2), was caused by return of the ship to the original start sampling location after the ship had drifted away in bad weather conditions. Stratified vertical hauls were performed using a multiple plankton sampler (Hydro-Bios) consisting of 5 closing nets with  $0.25 \text{ m}^2$  square opening and  $0.180 \text{ mm}$  mesh. Generally 5 layers were sampled: 0–10, 10–30, 30–50, 50–100 m and 100 m–bottom, except for 2 stations, Stn A34 at 02:15 and Stn B51 at 23:20, where only 4 layers were taken: 0–12, 12–50, 50–100 m and 100 m–bottom or 0–10, 10–30, 30–50 m, 50 m–bottom, respectively. The lower limit of the deepest (bottom) layer sampled was set a few m off the sea bed (typically 5 m off the bottom depth indicated by the ship's echo sounder) to avoid damaging of the net. However, because the location of the net in the water column was determined from the wire length, the accuracy of setting the distance between the net and the bottom varied depending on weather and sea current conditions. Each station was sampled every 6 h (5 times) during a 24 h period, and a total of 198 zooplankton samples were obtained. The amount of water filtered was calculated based on flow meter measurements for individual samples. Zooplankton samples were preserved in 4% borax-buffered formaldehyde immediately after sampling. Organisms were identified and counted under a stereomicroscope equipped with

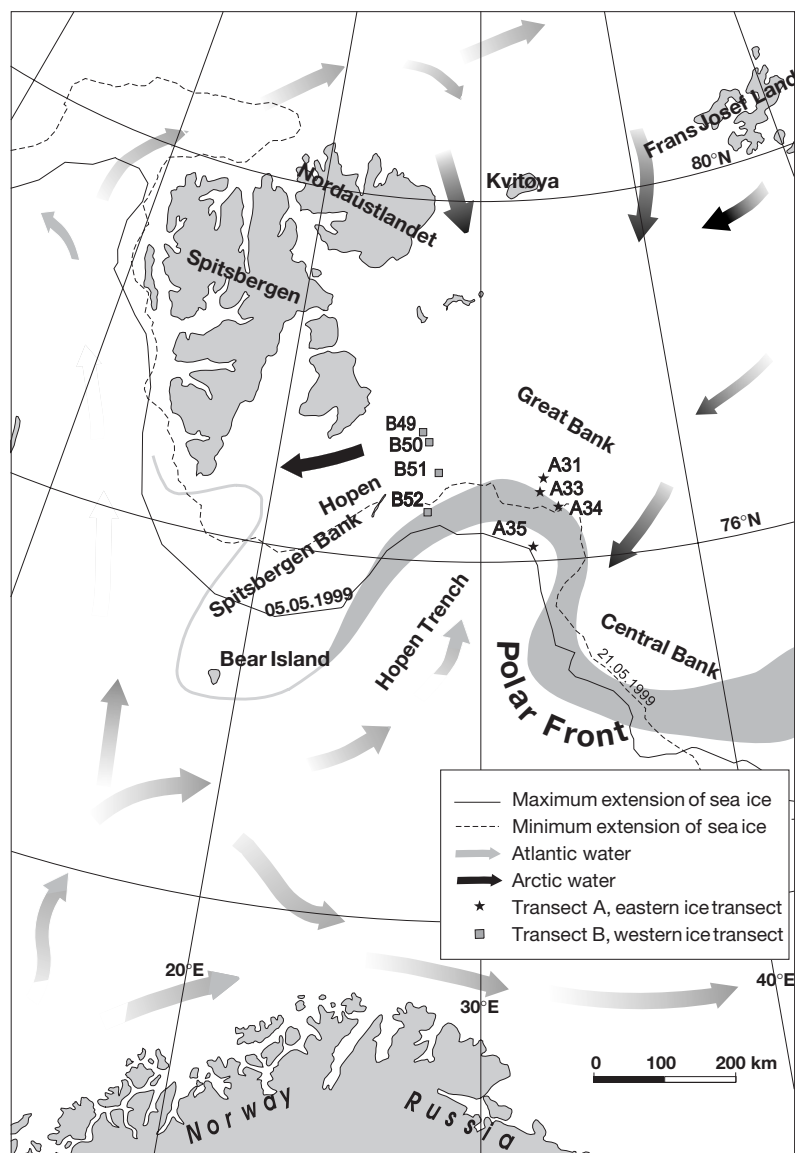


Fig. 1. Sampling stations and ice extent in the investigated area: Transect A eastern (Stns A31, A33, A34 and A35) and Transect B western (Stns B49, B50, B51 and B52) during May 1999. Dates given as d/mo/yr

an ocular micrometer, following standard procedures (e.g. Harris et al. 2000).

The examination of short-term distribution patterns was conducted for the most abundant and frequent species (*Oithona similis*, *Calanus finmarchicus*, *C. glacialis*, *Metridia longa*) and genera (*Pseudocalanus* spp, including *P. minutus* and *P. acuspes*, and *Microcalanus* spp., including *M. pusillus* and *M. pygmaeus*), as well as for copepod nauplii and for total zooplankton. It was also conducted for *C. hyperboreus* and *Triconia borealis* (= *Oncaea borealis*) (Böttger-Schnack 1999). We did not consider the appendicularian *Fritillaria borealis* and Euphausiacea larvae because they

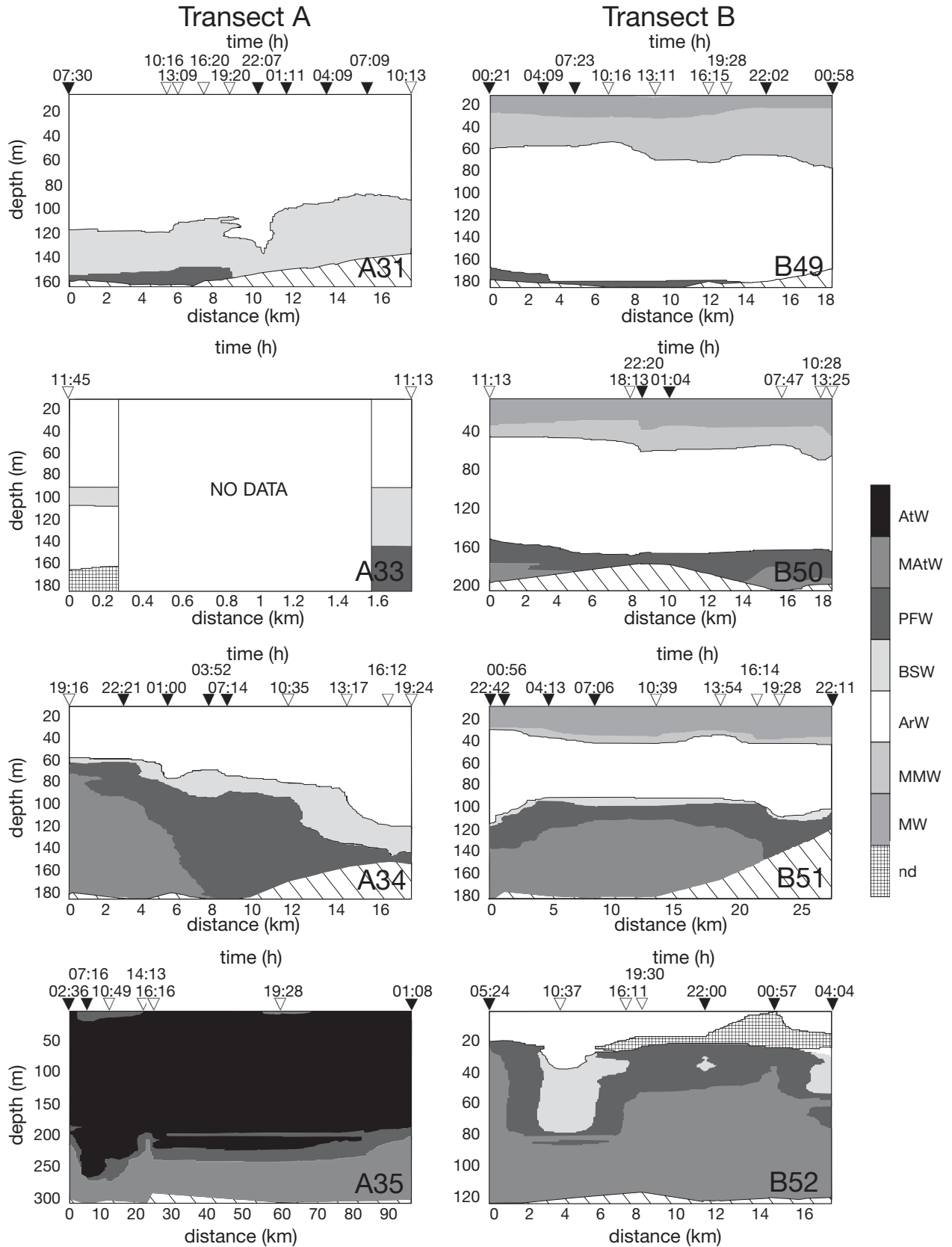


Fig. 2. Water masses determined from CTD casts along the 2 transects (A and B) in the Marginal Ice Zone (MIZ), May 1999. Identified water masses were: Atlantic water (AtW), Arctic water (ArW), Polar Front water (PFW), mixed Atlantic water (MAAtW), melt water (MW), mixed melt water (MMW), and Barents Sea water (BSW). nd: water masses of not determined type. Bottom contour indicated by oblique line pattern. ▽: 'day' hauls, ▼: 'night' hauls

were not present at all stations and their distributions were very patchy, limited to open water stations and surface layers. Examination of the vertical distribution pattern of *C. hyperboreus* was made because it is the third of the *Calanus* species often indicated as key species in the Barents Sea (e.g. Eilertsen et al. 1989, Tande 1991). *Triconia borealis* was selected because it is also regarded as an important zooplankton component in the Barents Sea and other Arctic seas (e.g. Arashkevich et al. 2002); however, in our study, although present at all stations, it was not particularly abundant. This species was also indicated by Groen-dahl & Hernroth (1986) as performing DVM in the Arctic.

Visualisations of the short-term distribution patterns were completed using Surfer software (Version 7, Surface Mapping System). Isolines were based on zooplankton abundance (ind.  $m^{-3}$ ) in water layers, using kriging to determine the distance between lines. Although variations in light intensity were not measured during the spring cruise (May), diel fluctuations in irradiance would have occurred (Fig. 3). On this basis, we arbitrarily designated 19:30 to 07:30 h Central European Time (CET) with lowest photosynthetically active radiation (PAR) values as 'night' for this study. This was in agreement with distinction of day/night that was applied by Hattori & Saito (1997) in their DVM study from similar latitudes in the Canadian Arctic in May 1992.

**Statistics.** Multiple regression analyses were applied using the depth interval ( $D_{max}$ ) at which the maximum

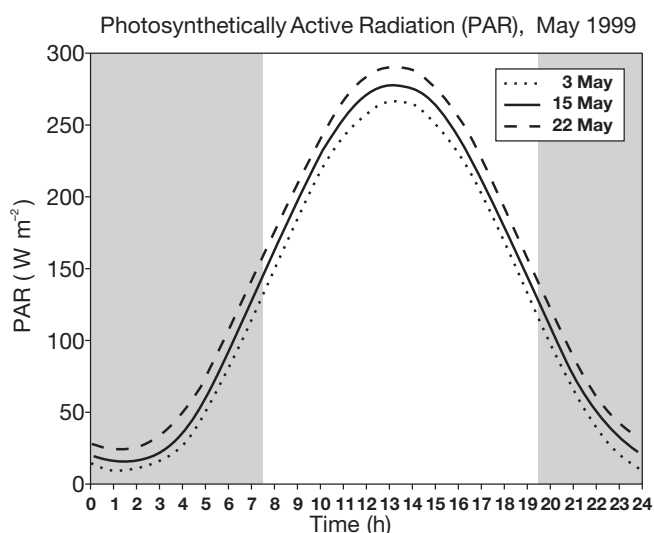


Fig. 3. Photosynthetically Active Radiation (PAR) measured at Bjørnøya (74°N, 20°E) for the period 9 to 22 May 1999, with albedo 0.8 (open sea) and no overcast. Grey areas represent designated 'night'

abundance (ind.  $m^{-3}$ ) of selected zooplankton categories occurred as the dependent variable, and time ('day' and 'night': distinction according to Fig. 3), ice cover (Group 1: Stns A31, A33, B49, B50 with >50% of ice cover; Group 2: Stns A34, A35, B51, B52 with <10% of ice cover) and transect (Transect A, Transect B) as predictors. Samples were pooled in this way in order to create 'replicates' to enable statistical analysis. Multiple regression tests were also conducted separately on each transect. Statistical analyses were conducted with the Statistical Package of Social Science (SPSS 10.0).

A frequency distribution of  $D_{max}$  was constructed for every dominant zooplankton selected by counting the number of observations of maximum abundance in each depth interval (0–10, 10–50, >50 m). Sample size added up to 40 by pooling samples across transects, stations and sampling times. Chi-square goodness of fit test was used to determine whether maximum abundance depths of each zooplankton were evenly distributed amongst layers. Next, a crosstabs chi-square test was used to test for overall similarity between the distributions, followed by pairwise crosstabs chi-square tests to determine possible grouping of categories based on their frequency distribution of  $D_{max}$ . A significance level of 1% was chosen for the pairwise crosstabs chi-square tests in order to keep the statistical analyses conservative focusing on the general pattern.

The possible relationship between distribution of zooplankton and phytoplankton was tested by linear correlation between daily mean abundance (ind.  $m^{-2}$ ) of selected zooplankton and chl *a* values (mg chl *a*  $m^{-2}$ ) at station. Additionally, the possible relationship between 'day' and 'night' weighted mean depths (WMD) of all dominant zooplankters and chl *a* values (mg chl *a*  $m^{-2}$ ) at station was examined by linear correlation.

The non-parametric Mann-Whitney *U*-test was used to test a possible relationship between zooplankton maximum abundance (ind.  $m^{-3}$ ) at stations and ice conditions (Group 1, Group 2).

## RESULTS

### Hydrography and sea ice

The water masses of the MIZ were categorised into the following types: Atlantic water (AtW), Arctic water (ArW), Polar Front water (PFW), mixed Atlantic water (MAW), melt water (MW), mixed melt water (MMW), and Barents Sea water (BSW) (Fig. 2). During the sampling period, the ice edge was located near the Polar Front in the inner part of the Hopen Trench. On Transect A, Arctic water dominated the upper 80 to 100 m

within the ice-covered area (Stns A31, A33, A34), whereas mixed and modified waters occurred down to the bottom. The open water station (A35) was mainly characterised by AtW down to 170 m, and mixed/modified waters below that depth. On Transect B, the 3 ice stations (B49, B50, B51) were characterised by MW at the surface and ArW in deeper areas. At the open water station (B52), ArW was present at the surface, whereas mixed or modified water masses occupied the depths below 40 m.

The ice conditions at each station changed continuously, depending on wind and tides. The tidal effect was very pronounced over the banks and the divergence of the tidal wave opened or closed the ice pack on a regular basis. The ice was less than 2 m thick and was characterised as first-year ice.

### Taxonomic composition

Forty-one zooplankton taxa were identified along Transect A, whereas 36 taxa were found on Transect B. The most abundant species in the area was *Oithona similis*, comprising about 46% on both transects, followed by copepod nauplii and copepods of different stages of the genera *Calanus*, *Pseudocalanus*, *Microcalanus*, and also *Metridia*. Of the non-copepod taxa, *Fritillaria borealis* and Euphausiacea nauplii were frequently found, and were particularly abundant at Stn B52. Among adult Euphausiacea, 4 species were identified: *Thysanoessa inermis*, *T. raschii*, *T. longicaudata* and *Meganyctiphanes norvegica*, but they were treated together because of their low abundances. Echinodermata larvae and Chaetognatha were of less importance numerically, while remaining taxa were scarcely present (Table 1).

### Short-term distribution of zooplankton taxa

The statistical model tested whether the 3 predictors (time, ice cover, transect) influenced the  $D_{\max}$ . The overall multiple regression was significant only for *Calanus glacialis* (Table 2). Partial regression was significant for *C. glacialis* and ice cover and transect (ice cover: partial  $r = 0.37$   $p < 0.05$ ; transect: partial  $r = -0.37$ ,  $p < 0.05$ ).

The frequency distributions for  $D_{\max}$  of all examined species/groups were non-random ( $\chi^2_2 > 8.45$ ,  $p < 0.05$ ) and differed between species/groups ( $\chi^2_{16} = 326.8$ ,  $p < 0.01$ ). Based on the result of the pairwise crosstabs chi-square tests (Table 3), the dominant species/groups were divided into 3 distributional groups according to their  $D_{\max}$  interval: (1) 0–10 m: *Pseudocalanus* spp., copepod nauplii; (2) 10–50 m: *Oithona similis*, *Calanus finmar-*

*chicus*, *C. glacialis*, *C. hyperboreus*; (3) >50 m: *Microcalanus* spp., *Metridia longa*, *Triconia borealis* (Fig. 4).

As a result of depth preferences of the numerically predominating taxa, zooplankton were concentrated in upper layers of the water column (0–50 m) (Fig. 5). The maximum concentrations of total zooplankton at stations fluctuated from 899 ind.  $m^{-3}$  at Stn A35, to 6815 ind.  $m^{-3}$  at B49. The distributions of individual

Table 1. Relative abundance (%) of identified zooplankton along 2 transects in the MIZ of the Barents Sea in May 1999. Examined taxa in **bold**

Transect A		Transect B	
Taxon	%	Taxon	%
<b><i>Oithona similis</i></b>	<b>46.54</b>	<b><i>Oithona similis</i></b>	<b>46.13</b>
<b>Copepod nauplii</b>	<b>18.72</b>	<b>Copepod nauplii</b>	<b>12.69</b>
<b><i>Pseudocalanus</i> spp.</b>	<b>10.19</b>	<b><i>Calanus glacialis</i></b>	<b>9.02</b>
<b><i>Microcalanus</i> spp.</b>	<b>9.42</b>	<b><i>Pseudocalanus</i> spp.</b>	<b>7.34</b>
<b><i>Calanus finmarchicus</i></b>	<b>3.20</b>	<i>Fritillaria borealis</i>	5.81
<b><i>Calanus glacialis</i></b>	<b>3.15</b>	<b><i>Calanus finmarchicus</i></b>	<b>4.53</b>
<i>Fritillaria borealis</i>	2.94	<b><i>Microcalanus</i> spp.</b>	<b>4.00</b>
<b><i>Metridia longa</i></b>	<b>2.21</b>	Euphausiacea larvae	3.69
<i>Oithona atlantica</i>	0.64	Echinodermata larvae	0.89
<i>Oikopleura</i> spp.	0.48	<b><i>Calanus hyperboreus</i></b>	<b>0.75</b>
Echinodermata larvae	0.44	<b><i>Metridia longa</i></b>	<b>0.49</b>
<b><i>Triconia borealis</i></b>	<b>0.35</b>	<i>Oikopleura</i> spp.	0.21
Euphausiacea larvae	0.32	<b><i>Triconia borealis</i></b>	<b>0.20</b>
<b><i>Calanus hyperboreus</i></b>	<b>0.24</b>	<i>Oithona atlantica</i>	0.10
Polychaeta n. det.	0.20	Mollusca larvae	0.07
Chaetognatha	0.20	Harpacticoida n. det.	0.07
Hydromedusae	0.15	Chaetognatha	0.06
Amphipoda	0.12	Hydromedusae	0.06
<i>Clione limacina</i>	0.10	<i>Clione limacina</i>	0.05
<i>Limacina helicina</i>	0.09	Amphipoda	0.04
Harpacticoida n. det.	0.05	Polychaeta n. det.	0.03
Euphausiacea adults	0.04	<i>Limacina helicina</i>	0.03
<i>Bradyidius similis</i>	0.04	Euphausiacea adults	0.02
Ctenophora	0.03	Ctenophora	0.01
Ostracoda	0.03	<i>Bradyidius similis</i>	0.01
<i>Pareuchaeta norvegica</i>	0.02	<i>Scolecithricella minor</i>	0.01
Mollusca larvae	0.02	Isopoda	0.01
Harpacticoida nauplii	0.02	Ostracoda	0.01
Isopoda	0.01	Harpacticoida nauplii	<0.01
Cumacea	<0.01	Siphonophora	<0.01
<i>Oncaea</i> sp.	<0.01	<i>Pareuchaeta norvegica</i>	<0.01
<i>Scolecithricella minor</i>	<0.01	Cumacea	<0.01
Siphonophora	<0.01	Pisces larvae	<0.01
Cirripedia	<0.01	Cirripedia	<0.01
Decapoda larvae	<0.01	<i>Oncaea</i> sp.	<0.01
Pisces larvae	<0.01	Decapoda larvae	<0.01
<b>Taxa present on Transect A only</b>			
<i>Microsetella norvegica</i>	0.02		
<i>Neoscolecithrix farrani</i>	<0.01		
<i>Metridia lucens</i>	<0.01		
<i>Heterorhabdus norvegicus</i>	<0.01		
<i>Gaidius</i> sp.	<0.01		

Table 2. Results of overall multiple regression between  $D_{max}$  of main zooplankton and selected predictors

Taxon	$r^2$	$F_{3,28}$	p
<i>Pseudocalanus</i> spp.	0.069	0.7	0.56
Copepod nauplii	0.10	1.03	0.39
<i>Oithona similis</i>	0.022	0.21	0.89
<i>Calanus finmarchicus</i>	0.18	2.0	0.14
<i>Calanus glacialis</i>	0.25	3.16	0.04
<i>Calanus hyperboreus</i>	0.092	0.95	0.43
<i>Microcalanus</i> spp.	0.106	1.11	0.36
<i>Metridia longa</i>	0.097	1.0	0.41
<i>Triconia borealis</i>	0.12	1.26	0.31

groups are illustrated in Fig. 5 and Appendix 1 (available at: [www.int-res.com/articles/suppl/m308p101-116\\_app.pdf](http://www.int-res.com/articles/suppl/m308p101-116_app.pdf)).

**Taxa with maximum abundances in surface water layer (0–10 m)**

*Pseudocalanus* spp. (consisting of *P. acuspes* and *P. minutus*) showed highest abundances in the upper water layer (0–10 m) except at 2 stations (A31, B52), where the greatest numbers were found at depths of 10–30 m (Appendix 1a). The highest abundance of these copepods (938 ind.  $m^{-3}$ ) was found at Stn A34.

Copepod nauplii demonstrated a similar, but more pronounced, pattern of distribution with depth to *Pseudocalanus* spp. The only exception was Stn A31, where the maximum density occurred within the 10–30 m depth interval (Appendix 1b). The maximum abundance (3240 ind.  $m^{-3}$ ) was observed at Stn A34.

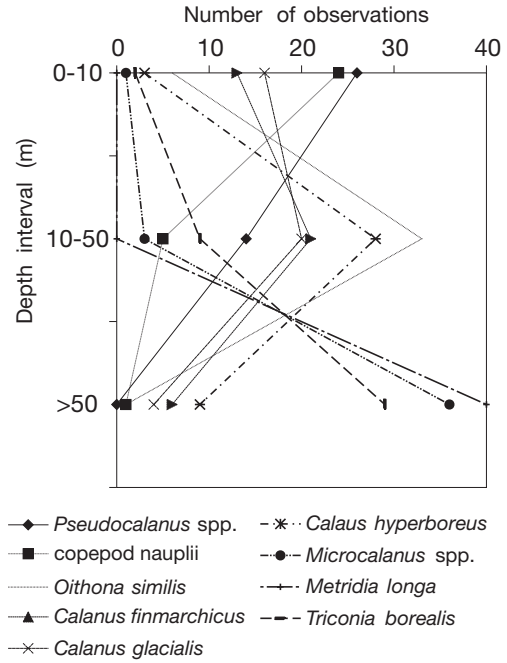


Fig. 4. Maximum abundance depth ( $D_{max}$ ) of main zooplankton

**Taxa with higher abundances above 50 m**

The highest concentrations of *Oithona similis* were mainly found at 10–30 and 30–50 m (Appendix 1c). *Oithona similis* was most abundant at the ice cover stations (maximum density 1932 ind.  $m^{-3}$  at Stn B50), and decreased in abundance at the open water stations (A35, B52).

Maximum concentrations of *Calanus finmarchicus* occurred within 2 depth ranges: 0–10 and 30–50 m.

Table 3. Results of pairwise crosstabs chi-square tests ( $\chi^2_2$  and p) for possible grouping of species based on frequency distribution of maximum abundance depth (May 1999). Significant values shown in **bold**

	<i>Calanus hyperboreus</i>	<i>Calanus glacialis</i>	<i>Calanus finmarchicus</i>	<i>Pseudocalanus</i> spp.	<i>Microcalanus</i> spp.	<i>Metridia longa</i>	<i>Oithona similis</i>	<i>Triconia borealis</i>
<i>Calanus glacialis</i>	12.2 <0.002							
<i>Calanus finmarchicus</i>	<b>7.8</b> <b>0.02</b>	<b>0.74</b> <b>0.69</b>						
<i>Pseudocalanus</i> spp.	31.9 <0.0005	<b>7.44</b> <b>0.02</b>	11.7 0.003					
<i>Microcalanus</i> spp.	37.4 <0.0005	51.4 <0.0005	45.2 <0.0005	66.3 <0.0005				
<i>Metridia longa</i>	50.6 <0.005	65.5 <0.0005	59.1 <0.0005	80.0 <0.0005	<b>4.2</b> <b>0.122</b>			
<i>Oithona similis</i>	<b>7.8</b> <b>0.02</b>	9.5 0.009	<b>8.8</b> <b>0.012</b>	21.2 <0.0005	61.7 <0.0005	76.1 <0.0005		
<i>Triconia borealis</i>	20.48 <0.0005	34.0 <0.0005	28.0 <0.0005	50.7 <0.0005	<b>4.1</b> <b>0.13</b>	12.7 0.002	41.8 <0.0005	
Copepod nauplii	48.4 <0.0005	17.3 <0.0005	22.8 <0.0005	<b>6.3</b> <b>0.042</b>	64.7 <0.0005	76.0 <0.0005	40.2 <0.0005	55.7 <0.0005

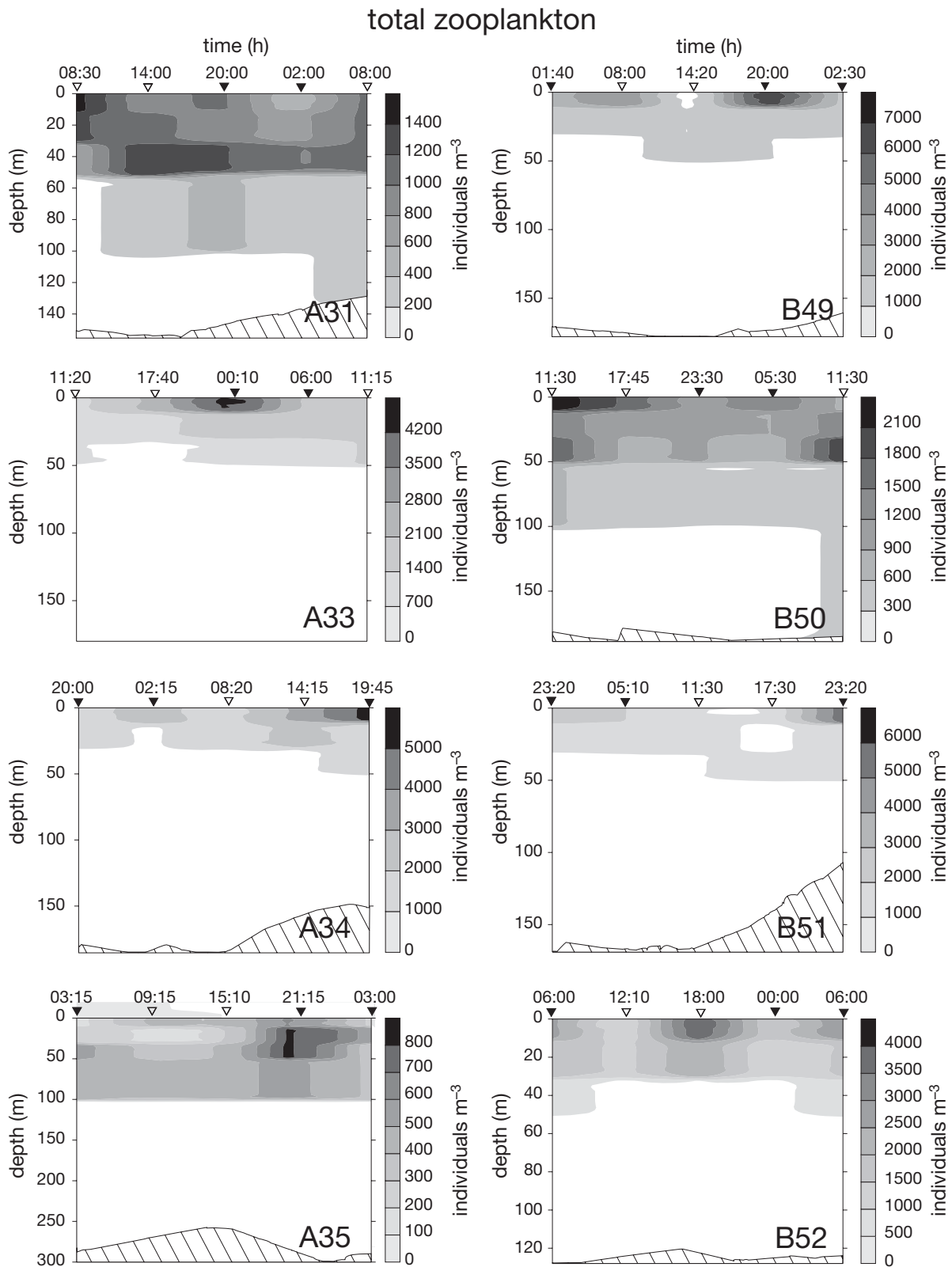


Fig. 5. Diurnal (24 h) changes in abundance (ind. m<sup>-3</sup>) of total zooplankton at stations along Transect A and B. Note changes in scale for abundance. Bottom contour indicated by oblique line pattern. Water layers sampled: 0–10, 10–30, 30–50, 50–100 m, and 100 m–bottom. Triangles indicate exact time of sampling. ▽: 'day' hauls, ▼: 'night' hauls according to division from Fig. 3



The maximum abundance at stations fluctuated from 11 ind. m<sup>-3</sup> at Stn B52, to 1259 ind. m<sup>-3</sup> at Stn B49 (Appendix 1d).

The vertical distribution pattern of *Calanus glacialis* (Appendix 1e) was very similar to that displayed by *C. finmarchicus*. The highest abundances at stations ranged from 60 ind. m<sup>-3</sup> at Stn A33 to approximately 2400 ind. m<sup>-3</sup> at Stn B49.

*Calanus hyperboreus* was more vertically dispersed in comparison with the other 2 *Calanus* species, but this observation may have been influenced by the low numbers recorded in the study (data not shown). It was numerous at only 2 stations (B51, B52) on Transect B (maximum densities 95 and 68 ind. m<sup>-3</sup>, respectively).

### Taxa with highest abundances below 50 m

*Microcalanus* spp. showed greatest densities below 50 m, except at 1 station (A34), where the maximum abundance occurred in the 30–50 m depth range (Appendix 1f). The maximum abundance (283 ind. m<sup>-3</sup>) of this species was observed at Stn A34.

*Metridia longa* displayed a clear preference for the deepest water layer (100 m–bottom) at all stations. Its highest abundance (71 ind. m<sup>-3</sup>) occurred at ice-covered Stn A31 (Appendix 1g).

*Triconia borealis* was more vertically dispersed than the other copepods studied. The maxima of *T. borealis* abundances were noted in the 50–100 m depth range (data not shown). The species contributed only little to total zooplankton numbers observed here (maximum abundance 10 ind. m<sup>-3</sup> at Stn B52).

A comparison of instances (8 stations) of maximum abundance during 'day' and 'night' hauls yielded equal numbers for *Microcalanus* spp. (4:4), *Oithona similis* (4:4), copepod nauplii (4:4), and very similar ones for *Metridia longa* (3:5), whereas visibly higher numbers were observed for 'night' hauls for *Calanus finmarchicus* (2:6), *C. glacialis* (1:7), *C. hyperboreus* (2:6), *Pseudocalanus* spp. (2:6), and *Triconia borealis* (2:6).

## DISCUSSION

The phenomenon of DVM of zooplankton was described about 50 yr ago as one of the greatest puzzles of pelagic natural history (Hardy & Bainbridge 1954). Since the beginning, studies of this phenomenon have concentrated mainly in temperate and tropical areas, whereas less effort has been devoted to the polar regions. Bogorov (1946), who summarized earlier studies in the far north, concluded that dominant zooplankton species did not shift their vertical distribution over a 24 h period during the season of permanent day-

light. Another early attempt to tackle the problem was carried out by Digby (1961). The author emphasised the difficulty of extracting a signal of migration from the very turbulent environments examined (Svalbard fjords).

Later, Buchanan & Haney (1980) stated that zooplankton did not undergo DVM when exposed to continuous daylight in the Arctic. The animals tended to remain at a constant mean depth, maintaining the same vertical distribution throughout the day. Gron-dahl & Hernroth (1986), working in the Nansen Basin north and east of Svalbard, concluded that of the 5 dominating copepods in the area, only *Oncaea borealis* (= *Triconia borealis*) and *Metridia longa* were migrators, although they only supported the statement with data for *O. borealis*. In the seasonally ice-covered seas of Hudson Bay (Canada), Runge & Ingram (1988) showed that females of *Calanus glacialis* and *Pseudocalanus* spp. migrated to the food-rich ice-associated layer during the night, and carried out a diel feeding pattern similar to those observed in open water areas. In Resolute Passage (Canadian Arctic), Conover et al. (1986) observed that, under continuous sunlight, the vertical migration and diel change in ingestion rate were related to the tidal cycle. However, the above-mentioned observations of DVM and diel feeding rhythm were exclusively limited to the sub-ice layer.

Diel migration studies of Arctic and Antarctic zooplankton have been reviewed by Conover & Huntley (1991). They concluded that in the polar seas, some copepods do migrate near mid-summers day but in their opinion few, if any, studies of zooplankton distribution have been designed well enough to indisputably support this statement. A contrasting conclusion was reached by Dale & Kaartvedt (2000). These researchers claimed that they observed patterns of diel vertical distribution of *Calanus finmarchicus* during midnight sun in the Norwegian and Greenland Seas. They concluded that the differing results with regard to diel distribution patterns could indicate plasticity in DVM behaviour related to different environmental conditions, and also that some of the differences could be due to sampling design (i.e. fine vertical and temporal sampling resolutions are needed to reveal subtle changes of distribution patterns). Also, Fortier et al. (2001) stated that despite midnight sun, herbivorous copepods *Calanus hyperboreus*, *C. glacialis* and *Pseudocalanus acuspes* displayed a normal DVM under the ice cover in the Barrow Strait in spring: these copepods ascended into the chlorophyll-rich under-ice layer around maximum relative rate of change in irradiance at dusk, but returned to depth a few hours later.

Several studies on DVM in zooplankton have been recently conducted in the Barents Sea. Hansen et al. (1990) noted that *Calanus* spp. displayed no consistent

day-night vertical migration patterns during spring-summer seasons. Arashkevich et al. (2002) studied seasonal and spatial changes in biomass of zooplankton in the central Barents Sea and the MIZ during March, May and June. They interpreted the difference in day/night distribution of total zooplankton at the northern stations in May as manifestation of DVM, although this observation was based exclusively on 2 day and night hauls from the same station.

In contrast to previous zooplankton studies in the Barents Sea, we rigorously analyzed the vertical distribution pattern of the dominant taxa over a relatively large region and with respect to the sea ice cover, hydrographic conditions, and time. In the study area the dominating taxa were *Oithona similis*, copepod nauplii, *Pseudocalanus* spp., *Calanus finmarchicus*, *C. glacialis*, *Microcalanus* spp. and *Metridia longa*. In adjacent areas, similar zooplankton compositions were observed in March and May 1998 and in July 1999 by Arashkevich et al. (2002). However, in June (1995) in a nearby area of the MIZ, zooplankton was predominated by *C. glacialis* and *P. minutus* (Falk-Petersen et al. 1999).

Over the entire region in May 1999, the characteristic feature of the vertical distribution was concentration of the bulk of the zooplankton in the uppermost layer 0–10 m (Fig. 5). This observation agrees well with results of a study by Pedersen et al. (1995a). However, each of the numerically important taxa showed individual preferences for maximum abundance depth.

In the Canadian Arctic, *Pseudocalanus* spp. are mainly found in neritic waters (Conover & Huntley 1991). This agrees with our results: lowest numbers of these copepods were recorded at the deepest and open water station (Stn A35) influenced by AtW. The preference of the genus *Pseudocalanus* to upper water layers observed in our study was in agreement with Melle et al. (1987). The report of DVM in *Pseudocalanus* at high latitudes (Conover et al. 1988) was not supported by our results. On the contrary, our findings concurred with those of McLaren (1969), who demonstrated no day/night difference in vertical distribution of *Pseudocalanus* in a fjord on the Baffin Island.

The maximum concentrations of copepod nauplii in our study coincided with ice edge conditions (Stns A31, A34 and B51) This was in agreement with results of Falk-Petersen et al. (1999). With regard to depth distribution, Melle et al. (1987) reported that copepod nauplii showed preferences for the upper 50 m in the Barents Sea. We observed these developmental stages to be concentrated in the uppermost 0–10 m of the water column.

According to McLaren (1963), *Oithona similis* is a widespread and numerically important component of epiplankton, especially in the marginal seas. Our study

confirmed its preference for upper water layers in the Barents Sea during spring. We were, however, unable to confirm the suggestion that this species is associated with AtW (Melle et al. 1987), as in our study this species showed highest abundances in the area covered by sea ice and in association with ArW and MW. This observation suggests the ability of this species to take advantage of unstable environmental conditions which are typical in hydrological front areas (Wiborg 1954) and ice edge zones (this study).

Generally, calanoid copepods are regarded as the most important organisms that transfer primary production to higher trophic levels in boreal and sub-Arctic oceans (e.g. Tande 1991, Kwasniewski et al. 2003), although the role of small copepods in these waters seems to be underestimated (Arashkevich et al. 2002). Key zooplankton species in the Barents Sea are *Calanus finmarchicus*, which can be used as a tracer of Atlantic water masses, and the typically Arctic *C. glacialis* (Jaschnov 1970). Maximum concentrations of *C. finmarchicus* and *C. glacialis* in the 0–50 m depth range during our survey confirmed earlier findings from the Barents Sea region (Tande & Bamstedt 1985, Hassel 1986). However, Hansen et al. (1996) observed that vertical distributions of the 2 species during spring 1993 were more extensive than in the present study. Sparse occurrence of *C. hyperboreus* in the area that we studied agrees with findings of Hassel (1986) and points to the fact that this species, in addition to being an Arctic species, is also a deep water copepod that thrives first of all in the Greenland Sea and in the Arctic Ocean. Perhaps the reason why *C. hyperboreus* can not maintain higher population density in the shelf seas is that, because of its size, it becomes a very easy prey for benthic and hyperbenthic organisms during its wintering at depths. In the Barents Sea there is a great variety of benthic potential copepod predators that continue to forage throughout winter (e.g. deep-sea shrimp *Pandalus borealis* and fish such as polar cod *Boreogadus saida*, Northeast Arctic cod *Gadus morhua*, and Greenland halibut *Reinhardtius hippoglossoides*) (Dragesund & Gjørseter 1988).

Grice (1962) found *Metridia longa* to be the most frequently encountered copepod under the permanent sea ice, and the third most abundant over the entire Arctic Ocean. In accordance with previous data (Pedersen et al. 1995a, Hansen et al. 1996), we found this species attained maximum abundance below 100 m. In the Norwegian fjords *M. longa* is known to inhabit deep waters during both day and night (Balino & Aksnes 1993), which is similar to what we observed in the Barents Sea. In the Labrador Sea, Head et al. (2003) found higher densities of this species at night and argued this could indicate DVM. A similar conclusion (i.e. of presence of DVM basing on observation of

higher densities during night) was formulated by the same authors (Head et al. 2003) with respect to *Microcalanus* spp. According to our data, *Microcalanus* spp. showed clear preferences for deeper water layers (below 50 m) in the MIZ of the Barents Sea, and we did not perceive any indication of DVM for this species. It must be mentioned, though, that because of coarse division of the lower part of water column (50–100 and 100 m–bottom), recognition of DVM of these deep water dwellers may not have been possible given our data if they migrated only within a narrow depth range (Fortier et al. 2001).

The non-copepod zooplankton, *Fritillaria borealis* and Euphausiacea larvae, were abundant in May 1999 only on a local basis, notably at the open water station (B52). This was in accordance with previous observations of Arashkevich et al. (2002). Based on data from the literature (Wiborg 1954) and on our own observations, we feel inclined to be of the opinion that these species do not perform DVM and prefer upper layers of the water column. Euphausiacea larvae are a seasonal component of the Barents Sea zooplankton. Their high abundance during spring is strictly related to spawning, whereas their horizontal/spatial distributions are very much affected by preferences of adult Euphausiacea for AtW masses (Dalpadado & Skjoldal 1991).

A complete study of an ecological phenomenon such as DVM should include a proximate and an ultimate aspect (Ringelberg & Van Gool 2003). The proximate aspect must answer questions on how animals migrate and what physiological and behavioural mechanisms are involved in migration. The ultimate aspect must answer why migrations occur, and what adaptive significance can be attributed to the phenomenon. Such an approach is, however, not simply realised, and confusion of proximate and ultimate aspects easily occurs in practice (Ringelberg & Van Gool 2003). Four proximate factors are considered the most important in this respect: light changes, fish presence, food concentration, and temperature. Several authors agree that the most important adaptive significance of DVM is avoidance of visual predators (McLaren 1963, Gliwicz 1986, Lampert 1989, Ohman 1990, Dagg et al. 1998, Ringelberg 1999). They argue that zooplankton, such as copepods, are complex organisms which must balance risk of predation and necessity of feeding. Seeking a refuge from predators in deeper dark water layers during the day and moving to the upper, food-rich layer at night are considered the main evolutionary benefits achieved by performing DVM.

High zooplankton abundance often coincides spatially with high chl *a* concentration (Hansen et al. 1990), and food concentration may stimulate diel migratory behaviour (Conover 1988, and citations therein). Herman (1983) observed that peaks of *Calanus glacialis*

and *C. finmarchicus* occurrence in north-eastern Baffin Bay were commonly situated 3 to 4 m above the chl *a* maximum, whereas the distribution pattern of *C. hyperboreus* coincided with the chl *a* peak. However, in some regions, the relationship between *Calanus* spp. and chl *a* distributions has been found to be negative (Woodd-Walker et al. 2001). Flint et al. (2002) even stated, based on investigations of frontal regions, that in such environments high zooplankton biomass areas were located away from the phytoplankton peaks.

In this study, the highest chl *a* concentration in upper 50 m water layer was observed at the open water stations (Stns A35 and B52) and near the ice edge (Stns B51 and A33). Chl *a* decreased with distance into the ice covered region (Engelsen et al. 2002). A similar observation was made in June 1995 in the MIZ (Falk-Petersen et al. 1999), when the chl *a* concentrations were the highest in the ice edge area. Unfortunately, during our study, sampling of chl *a* was carried out in a different manner (only once at a station) to sampling of zooplankton (5 times at a station), and the only available information on chl *a* were integrated biomass for the upper 50 m layers. This did not allow complex statistical comparison of possible relationship between zooplankton and chl *a* (phytoplankton) depth distribution.

We tried, nonetheless, to test for possible relationships on more a general level, by calculating linear correlation between chl *a* ( $\text{mg chl } a \text{ m}^{-2}$ ) and daily mean zooplankton abundance ( $\text{ind. m}^{-2}$ ) at stations. As a result, significant negative correlations were found between chl *a* and integrated abundances of *Oithona similis* ( $r = -0.927$ ,  $p = 0.003$ ) and *Calanus finmarchicus* ( $r = -0.853$ ,  $p = 0.015$ ). There were no significant correlations for any other species/group tested. These findings corroborate the results of Mann-Whitney *U*-test for maximum zooplankton abundance and ice conditions (see below), which suggested that these 2 species were less abundant at the ice edge and open water stations than further off under the ice. In our opinion, these results may indicate that in the MIZ of the Barents Sea in May 1999, *C. finmarchicus* and *O. similis* did not utilize the phytoplankton bloom related to MIZ, probably because of different timing of their life cycles. Another possible explanation for the negative correlations might be inverse correlation between zooplankton and phytoplankton precisely because of intensive grazing by herbivorous zooplankters, as suggested previously by Longhurst (1976b).

Pearre (2003) emphasized the role of food density on the vertical distribution of zooplankton. According to Pearre (1979), when animals were in poor condition due to low food abundance, they were likely to be found near the surface even in daylight; however, because of the increased risk of predation in upper waters, they would make short and unsynchronised

escapes to deeper water if they had fed. Conversely, when in good condition at times of high food abundance, they need to spend little time actively foraging and would thus spend more time at the deepest end of their migration range (Pearre 2003). To verify whether there was any correlation between the mean population depth and food, we tested for a possible relationship between chl *a* values ( $\text{mg chl } a \text{ m}^{-2}$ ) and 'day' and 'night' WMD of all dominant zooplankters at station. The significant linear correlations were found only for *Calanus glacialis* ('day':  $r = 0.843$ ,  $p = 0.017$ ; 'night':  $r = 0.845$ ,  $p = 0.017$ ) and *C. finmarchicus* ('day':  $r = 0.880$ ,  $p = 0.010$ ; 'night':  $r = 0.892$ ,  $p = 0.007$ ). Interestingly, a negative correlation was found for *Triconia borealis* only when 'night' WMD ( $r = -0.946$ ,  $p = 0.001$ ) was considered. These findings suggest that mean populations depths of herbivores *C. glacialis* and *C. finmarchicus* might increase in direct proportion to food richness (high chl *a* values) during both 'day' and 'night'; in contrast, the inverse case may apply to the omnivore *T. borealis* during 'night'. After Pearre (1979, 2000, 2003 and citations therein), the most obvious migrations—and the only migration easily detectable by conventional methods (stratified sampling)—would occur at intermediate food densities, when the population migrated more or less as a unit (termed 'synchronous migrations').

According to Riley (1976), perceiving DVM of zooplankton can also be obscured by the fact that only part of a population is migratory. He claimed that, in general, only adult and older stage copepodids are migratory, and estimated that approximately only half of a population undertook migration. Kosobokova (1978) observed a weak tendency for migration by adult females of *Calanus glacialis* in the central Polar Basin during summer. Hays (1995) noted that CV-VI of *C. hyperboreus* exhibited a diel variation in depth distribution in near-surface layers at temperate latitudes, although not in the Arctic. Enright & Honegger (1977) reported strong DVM by CV and adults of *C. pacificus* during spring and summer, whereas Dale & Kaartvedt (2000) concluded that only CV and females of *C. finmarchicus* displayed distinctive migrations.

Dale & Kaartvedt (2000) also suggested that the vertical distribution pattern may be affected by an individual's size. Furthermore, Pearre (1979) argued that the swimming capability of zooplankton is directly proportional to size. According to Hays et al. (1994), large copepod taxa from the northeast Atlantic showed significantly stronger DVM than small taxa (<1 mm wide). Haney (1988) explained that immature animals may remain in illuminated waters during the day because their small size makes them difficult to see. Also, Hays et al. (1994) suggested that copepod size, rather than colour, is the principal factor influencing

the probability of perception of copepods by predators relying on vision to find their prey. Summing up, all the above-mentioned authors argued that size would be an important factor in determining whether the zooplankton exhibit DVM. In the present study we looked for patterns in vertical distribution for the entire populations of dominant taxa/group. We were not able to examine differences in depth distribution pattern for individual developmental stages/size classes; we were not able to collect all stages because of (1) selectivity of the sampling tool, and (2) specifics of the species' life cycles. Possibly, we could have examined the relationship between depth distribution and size for populations of *Calanus finmarchicus* or *C. glacialis*; however, our samples were predominated by copepodite CIII and CIV (data not shown), which previous research has suggested to be non-migratory.

In DVM studies, the commonly used determinant of location of the studied population or selected representative in the water column is WMD (Dale & Kaartvedt 2000, Irigoien et al. 2004), sometimes called zooplankton centre of mass of the vertical distribution (ZCM) (Fortier et al. 2001). In our study, use of this determinant proved inappropriate because of the coarse division of depth layers, especially in the lower part of the water column. Instead, we examined the vertical distribution pattern using  $D_{\text{max}}$ .

Changing light level is, generally, regarded as the most likely cue stimulating vertical migration of zooplankton in the water column (Masson et al. 2001). Under continuous light, the rhythm of migratory activity has been shown to persist for several days before disappearing (Andrewartha & Birch 1967). During the Arctic spring and summer with continuous sunlight, the day/night changes in light levels are reduced to changes in radiation due to inclination of the sun. Digby (1961), working in the Svalbard area, concluded that the extent to which DVM occurred during high Arctic summer depended on the extent of the change of light intensity as well as on locality. Groendahl & Hernroth (1986) stated that the diurnal variation in irradiance during the polar summer is large enough to produce a pattern of vertical migration similar to that found in temperate latitudes, although DVM may still not occur or only be present in some species.

Neither the multiple regression nor the partial regression revealed any possible relationship between  $D_{\text{max}}$  and time of day (light level) for the predominant zooplankton in our study. This allowed us to assume that there is no DVM in the MIZ of the Barents Sea during spring, discernible within the layers distinguished. We assumed that the observed variability in zooplankton abundance could result from sampling at a station at different times under changing environmental conditions (bottom depth or water masses), as a

result of the ship drifting, and from water mass movement (for example, change in abundance of *Metridia longa* parallel to change in bottom depth at Stns A34 and B49). Thus, we consider that the observed variability in zooplankton vertical distribution was related to habitat changes rather than to diel migration pattern.

A possible source of variability in zooplankton abundance could be natural patchiness. Dagg (1977) postulated that, in heterogeneous pelagic environments, there is a tendency for zooplankton and their food to be patchily distributed on any spatial or temporal scale. According to Roe (1972), zooplankton is more or less randomly distributed and there is no reason to suppose that day and night catches should be equal. Day and night hauls differed during our study, for example with respect to maximum abundance of the studied taxa. Frequencies of maximum abundance during day and night were equal for *Microcalanus* spp., *Oithona similis*, copepod nauplii, and *Metridia longa*, indicating no relationship with time of sampling (light regime) and suggesting patchiness or distribution related to other environmental parameters. On the other hand, frequencies were remarkably higher during the night for *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus*, *Pseudocalanus* spp., and *Triconia borealis*, suggesting a systematic difference related to time of sampling. However, a closer examination of the instances of higher abundance during 'night' shows that in 2 out of 6 instances for *C. finmarchicus*, *C. glacialis* and *Pseudocalanus* spp., this observation coincided with a significant change in another environmental condition (i.e. decreasing sea depth at Stns A34 and B51), which supported our previous conclusion that there is no DVM in these taxa and that distribution is influenced by other environmental parameters as well as species' response to them, rather than light. Additionally, the results of Mann-Whitney *U*-tests revealed no difference in the maximum abundance values between 'night' and 'day' hauls for any analysed taxa.

It is also noteworthy that almost all the dominant zooplankton considered here had diel peaks of concentration at individual stations at the same time during the 24 h period. (cf. Appendix 1 & Fig. 5). This suggests that patchiness related to heterogeneity in a pelagic environment, rather than synchronised migration of various taxa related to time (light level), accounted for observed differences in zooplankton abundance. The phenomenon of DVM is now known to be more complex than first assumed. Recently, Pearre (2003) presented an excellent review of the influence of hunger/satiation state of animals on their vertical movements. Hunger/satiation migrations seem to be controlled by individual's hunger/satiation state, and due to its individual character, these migrations generally do not result in overall population movement

(Pearre 2003). Similarly, Ohman (1990) concluded that the DVM phenomenon is dynamic rather than a fixed, invariant behavioural trait within a population of a species, and that many individuals within single population may perform either reverse, normal, or no DVM. According to these conclusions, it seems rather unlikely to expect to observe all dominant taxa migrating synchronously in this study.

Another difficulty in investigating zooplankton DVM using conventional equipment (net sampling) is determining the number of individuals that remain in close association with the seabed. Due to net construction, a small portion of the water column (usually about 5 m) close to the bottom was left unsampled during our study. Concentration of some zooplankton close to the bottom is a known phenomenon and may concern hyperbenthic zooplankton, which were beyond the scope of our study, or typical water column dwellers. In the latter case, the concentrating taxa would be, for example, overwintering herbivorous copepods such as *Calanus finmarchicus* (e.g. Kaartvedt 1996). We consider that this inaccuracy would not influence our sampling and would not affect results, because our study took place in spring when all the taxa that could possibly exhibit such a behaviour were higher in the water column as a result of seasonal ontogenetic migration towards the surface for reproduction. Recently, some studies revealed that vertical migration can occur in some taxa on much smaller amplitudes (Falkenhaug et al. 1997). If this would be the case, our sampling design did not allow us to detect such a behaviour.

Our investigation revealed a statistically significant negative relationship between *Calanus glacialis* maximum abundance depth and ice cover as predictor, in both the multiple regression as well as in partial regression analysis. The results suggest that  $D_{\max}$  of *C. glacialis* was located at lesser depths in the water column in areas with less ice cover. The influence of sea ice cover on zooplankton is complex, species specific, and differs among regions and seasons. Smith (1988) concluded that in summer in Fram Strait, the ice edge had a positive effect on herbivorous zooplankton abundances because of elevated concentrations of plant biomass. However, Hirche et al. (1991) did not find any enhanced biological activities along the ice edge in Fram Strait during the same season, although he mentioned considerable regional variability related to physical mesoscale processes. Similar complex and inconsistent relationships may occur in the Barents Sea where, due to dynamic interactions of sea, ice and atmospheric systems, zooplankton can be exposed to unusual conditions.

While Hansen et al. (1996) generally observed much lower zooplankton biomasses in the ice edge area compared to ice cover and open waters in the Central

Barents Sea in May, they recorded the highest egg production rate for *Calanus finmarchicus* at the ice edge station. In Disco Bay (West Greenland), which can be regarded as a less unpredictable ecosystem, Hansen et al. (2003) also found no response by *Calanus* spp. (all 3 species) to ice cover conditions. We believe that a plausible explanation for the generally shallower distribution of *C. glacialis* in waters with less ice in the MIZ of the Barents Sea in May can be movement of *C. glacialis* towards the surface, related to the species' life cycle (Kosobokova 1999, Kwasniewski et al. 2003).

In addition, the results of the multiple regression and partial regression analysis for transect as predictor seem to support our hypothesis that the vertical distribution of *Calanus glacialis* was predetermined by the species' life cycle. Both analyses yielded significant negative relationships between the maximum abundance depth of *C. glacialis* and transect, thus indicating that  $D_{\max}$  for this species was greater on Transect A than on Transect B. Samples on Transect A were collected earlier (9 to 14 of May) than on Transect B (17 to 21 of May), and there was less melt water on Transect A. We postulate that *C. glacialis* on Transect A was generally located deeper in the water column than on Transect B, because the species was less advanced in its seasonal vertical migration towards the surface.

The non-parametric Mann-Whitney *U*-test indicated a possible relationship between ice conditions and maximum abundance of copepod nauplii ( $p = 0.027$ ), *Oithona similis* ( $p = 0.001$ ), *Calanus finmarchicus* ( $p = 0.002$ ), and *C. hyperboreus* ( $p = 0.018$ ). Copepod nauplii and *C. hyperboreus* were generally more abundant at the ice edge and open water stations than at the ice cover stations (mean maximum abundance 952 versus 510 and 26 versus 2 ind.  $m^{-3}$ , respectively). Although not confirmed by correlation analyses, higher abundances of copepod nauplii and *C. hyperboreus* (mostly copepodids CI) coincided with generally higher chl *a* values at the ice edge and open water stations; this corroborates with earlier findings that suggested a positive relationship between copepod reproduction and the amount of available food (Herman 1983). On the contrary, *O. similis* and *C. finmarchicus* were less abundant at the ice edge and open water stations (631 versus 1079 and 43 versus 220 ind.  $m^{-3}$ , respectively). We presumed that at the time of our study, reproduction of *C. hyperboreus* and *C. glacialis* was already taking place, whereas it had not started yet for *C. finmarchicus*. Such a temporal separation in reproduction in areas of co-occurrence most likely allows for avoidance of competition for food among offspring, and has been observed in other locations (e.g. Kwasniewski et al. 2003).

In summary, our investigation provided evidence that zooplankton in the Barents Sea MIZ in spring are distributed unevenly in the water column, with the abun-

dance peak concentrated within the upper 0–50 m layer. Pairwise crosstabs chi-square tests revealed 3 distributional groups amongst the examined species/taxa according to depth preferences. *Pseudocalanus* spp. and copepod nauplii were concentrated within the uppermost water layer (0–10 m). *Oithona similis*, *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus* preferred the 10–50 m depth interval, whereas *Microcalanus* spp., *Metridia longa*, and *Triconia borealis* predominantly inhabited waters below 50 m. Vertical distribution patterns varied over time, but neither the multiple regression nor the partial regression revealed any possible relationship with time of day (light level). We hypothesized that the studied taxa do not perform DVM in the MIZ of the Barents Sea in spring. We assumed that both habitat changes (in respect of water mass distribution and sea depth) and random patchiness could account for observed variability in zooplankton vertical distribution. The results of multiple regression and partial regression indicate that, in the MIZ in spring, *C. glacialis* occupied deeper layers at stations with more ice cover and less melt water. Such behaviour is most likely related to the species' life cycle. Among other examined species/taxa, statistically significant relationships were found only among the distributions of *C. finmarchicus* and *O. similis* and ice and chl *a*. In the MIZ in spring, both species were concentrated further away from the ice edge and chl *a* maximum. We presumed that this was related to differences in the timing of their life cycles. We also observed significantly higher abundances of copepod nauplii and *C. hyperboreus* (mostly CI) in relation to ice edge. All the mentioned above findings allowed us to hypothesize that, during our study, the reproducing copepods were *C. hyperboreus* and *C. glacialis*, whereas *C. finmarchicus* had not yet begun reproduction.

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