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ORIGINAL ARTICLE

Vertical distribution of *Calanus* spp. and *Metridia longa* at four Arctic locations

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Abstract

We investigated the vertical distribution of *Calanus finmarchicus*, *C. glacialis*, *C. hyperboreus* and *Metridia longa* at four locations around the archipelago of Svalbard in autumn. The older and larger copepodites of *Calanus* spp. were generally located deeper in the water column. Differences in vertical distribution between stations partly reflected a south–north gradient in developmental progress with higher abundance of older stages in the southern locations. The *C. finmarchicus* and *M. longa* observations were consistent with the hypothesis that the developmental stages distributed according to certain preferences for light intensity, and different optical properties at the four locations are likely to have affected the vertical distributions. Diel vertical migration was only observed for older developmental stages of *M. longa* while young stages of *M. longa* remained in deep waters both day and night. A mortality index indicated that non-migrating *Calanus* spp. suffered higher mortality than migrating *M. longa*.

Key words: Calanus, Metridia longa*, mortality, optics, vertical distribution*

Introduction

The depth distribution of many copepods in cold-temperate regions is characterized by a strong seasonality that is closely related to the annual cycle in primary production (Vinogradov 1997). Phytoplankton production peaks in spring and summer and is accompanied by peak abundances of herbivorous zooplankton in the surface layers (Smith & Sakshaug 1990). Few larger, mainly herbivorous calanoid species dominate the copepod community at high latitudes in terms of biomass (Smith & Schnack-Schiel 1990; Conover & Huntley 1991). These species descend to deeper layers when phytoplankton production decreases in late summer and autumn. They overwinter at greater depth in a state of dormancy, surviving on large lipid reserves accumulated during the summer (Conover & Huntley 1991; Hagen & Auel 2001).

Adjustments in vertical position are considered an efficient strategy for coping with the highly variable depth gradients in resource availability and predation risk (Longhurst 1976). Environmental variability along the vertical axis in the sea is to some extent due to the rapid attenuation of light in water (Jerlov 1968). This sets up thermal stratification and limits the depth range available for positive primary production (Sverdrup 1953). Thus, optical properties of the water column structure the depth distribution of food for herbivores, but may also change the efficiency of predators that rely on visual cues for locating prey (Eiane et al. 1997; Onsrud & Kaartvedt 1998; Aksnes et al. 2004). Indeed, the seasonal variability in depth distribution of many cold-temperate zooplankton species (e.g. Conover 1988) is believed to reflect the sub-surface light conditions (Miller et al. 1991) and its combined effect on food availability (Unstad & Tande 1991; Hirche 1996) and distribution of predators (Fiksen & Carlotti 1998; Dale et al. 1999; Bagøien et al. 2001). Common zooplankton strategies such as periodic avoidance of surface layers through diel vertical migration (DVM) were early recognized as adaptations to cope with the depth-specific variations in food availability and mortality risk (Cushing 1951; Longhurst 1976). Although relatively little studied at

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high latitudes, where seasonal variability in light levels differs from that at lower latitudes, DVM is considered less important at high latitudes compared to the pronounced seasonal migrations found here (Kosobokova 1978; Longhurst et al. 1984; Falkenhaug et al. 1997).

Recent studies show that the vertical distribution of both zooplankton and its predators is affected by optical properties of the water column (Aksnes et al. 2004; Aksnes 2007; Sørnes et al. 2007). The higher seasonality in irradiance at high latitudes may be a particularly important element of the environmental variability, and it is therefore of interest to test for potential effects of optical properties here.

Data on vertical distribution of zooplankton in high latitudes from seasons without midnight sun are scarce. Here we present information on the vertical distribution of copepods during autumn at four high Arctic locations that differ in topography and hydrography. We focused our investigations on the three herbivorous *Calanus* species, *C. finmarchicus* (Gunnerus, 1765), *C. glacialis* Jaschnov, 1972 and *C. hyperboreus* Kröyer, 1838, and the omnivorous species *Metridia longa* (Lubbock, 1854), since they dominate the mesozooplankton community in Arctic–Atlantic waters in terms of biomass (Smith & Schnack-Schiel 1990). The vertical distributions are interpreted in terms of an estimated mortality index and potential effects of light attenuation with depth.

Material and methods

Study area

Four different locations around the archipelago of Svalbard were sampled (Figure 1). The northernmost station was situated within the marginal sea ice zone northwest of Svalbard beyond the continental shelf (bottom depth >1600 m). Furthermore, we sampled on the shelf north of Svalbard an area that borders to the Arctic Ocean but which is influenced by modified Atlantic waters that are transported into this region within the West Spitsbergen Current (Saloranta & Haugan 2001). A third station was located in Hinlopen, a strait between the two largest islands of the Svalbard archipelago, connecting the Atlantic-influenced northern waters of Svalbard with the more Arctic northwestern Barents Sea. The fourth station was located in Kongsfjorden, a glacial fjord at the western coast of Spitsbergen that is influenced by both Atlantic and Arctic water masses (Svendsen et al. 2002).

Sampling

Zooplankton was sampled during a cruise with RV *Jan Mayen* between 14 and 24 September 2002. At each location replicate samples were taken both at noon and at midnight in five depth intervals (300–200–150–100–50–0 m, in Kongsfjorden the depth intervals were 225–125–75–50–25–0 m) with a multiple opening/closing net (Multinet, Hydrobios Kiel, mesh size 180 µm, mouth opening 0.25 m^2). In addition the deep station in the marginal ice zone was sampled at 1200–600 and 600–300 m. Depth-specific temperature, salinity and fluorescence were measured with a ship-boarded conductivity, temperature and density profiler (Sea-Bird CTD equipped with a Seapoint fluorometer), at each location.

Net samples were preserved in a 4% formaldehyde-in-seawater solution until enumeration. *Calanus* spp. and *Metridia longa* were counted from random sub-samples containing at least 150 individuals of *Calanus* spp. To distinguish between *C. finmarchicus* and *C. glacialis* as well as younger stages of *C. hyperboreus*, the prosome length of all counted individuals of *Calanus* spp. were measured from the tip of the cephalosome to the distal lateral end of the last thoracic segment (Unstad & Tande 1991). A length frequency analysis was made to create size classes for the three species (Daase & Eiane 2007). Abundance estimates are based on filtered water volume measured with flowmeters attached in each net.

Statistics of the vertical distribution

Similar to Sørnes et al. (2007), we characterized the vertical distributions by the mean depth (Z_m) and the standard deviation (Z_s) of the frequency distribution along the depth axis using the method of Manly (1977):

$$Z_m = \frac{1}{2}\sum_{j=1}^{n} f_j d_j z_j / O \tag{1}$$

$$Z_s = \sqrt{\frac{1}{2}\sum_{j=1}^{n} f_j d_j z_j^2 / O - Z_m^2} \tag{2}$$

where n is the number of depth intervals, d_j = lower sample – upper sample depth (m) of sample interval j, z_j is the midstrata (m) of sample interval j, f_j is the density of individuals (per m^3) observed in depth interval j, and O corresponds to the area under the frequency curve (i.e. the estimated surface integrated abundance):

$$O = \frac{1}{2}\sum_{j=1}^{n} d_j \times f_j \tag{3}$$

The deepest layer was not sampled all the way to the bottom. When calculating the mean depth (Z_m) the mid-strata (z_j) of the deepest layer was chosen as

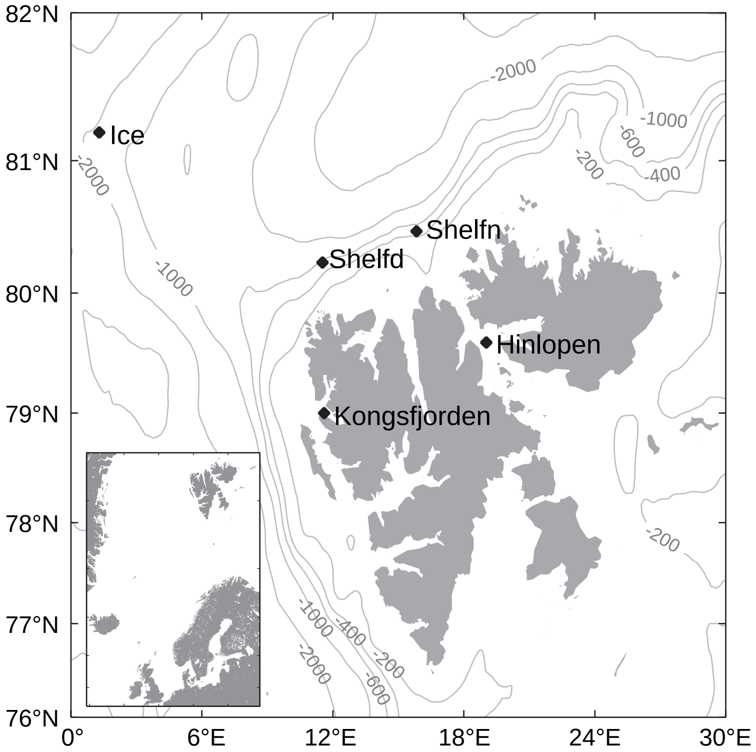

Figure 1. Map of study area and sampling sites. Shelf n/d, position of station on shelf sampled at night (n) and day (d).

the midpoint between the upper sample depth of the deepest sample interval and bottom depth. This was done under the assumption that the zooplankton abundance in the not sampled layer between lower sample depth of the deepest sample interval and the bottom does not differ from the estimates of the deepest sample interval.

Tests of possible optical effects on the vertical distribution

Following Aksnes & Samuelsen (forthcoming), we tested whether observed variations in the vertical distributions (i.e. variations in Z_m and Z_s) were consistent with expectations from models of optical regulation of vertical distribution (Miller et al. 1991; Aksnes 2007; Sørnes et al. 2007). If it is assumed that the individuals of a species or a developmental stage have a preference for ambient irradiance (which could be an average irradiance) so that they avoid irradiance levels higher than $E_u = E_0 e^{-KZu}$ and irradiance levels lower than $E_l = E_0 e^{-KZ_l}$, where E_0 is surface irradiance, K is the attenuation of downwelling irradiance, Z_u and Z_l are depths that correspond to the upper and the lower irradiance preference threshold, then the range of the vertical distribution (H) should be $H = Z_u - Z_l = \ln(E_u/E_l)/K$. Since the observed Z_s (Equation 2) is a measure of the narrowness (m) of the vertical distribution it will be proportional to H, we obtain the hypothesized prediction:

$$Z_s = c_1 K^{-1} \tag{4}$$

Additionally, the above assumptions also yield the prediction that the mean depth of the vertical distribution is proportional to the light attenuation:

$$Z_m = c_2 K^{-1} \tag{5}$$

where c_1 and c_2 are constants. Thus, if planktonic organisms distribute vertically according to optical preferences we would expect the width of the distribution to scale linearly with the population's mean depth:

$$Z_s = cZ_m \tag{6}$$

To test for this relationship we used linear regression analysis. All statistical analyses were done using R, version 2.2.1 (R Development Core Team, 2005).

Mortality index

In analysing relationships between vertical distribution patterns and mortality we used estimates of mortality rates for stage combinations obtained from each replicate net haul as an index of mortality rate. Estimates were obtained by the vertical life table approach (Aksnes & Ohman 1996), by solving

$$\frac{e^{d_i a_i} - 1}{1 - e^{-d_i a_{i+1}}} = r_i \tag{7}$$

iteratively for the combination of two juvenile stages and, for the combination of the last juvenile and an adult stage, from

$$d_{q-1} = \frac{\ln(r_{q-1} + 1)}{a_{q-1}} \qquad (8)$$

Here d is the combined mortality estimate for two consecutive developmental stages, r is the abundance ratio between two consecutive stages, a is the stage duration of a stage, and subscripts i and q denote juvenile and adult developmental stages, respectively. To estimate stage duration we used temperature-dependent functions for *C. finmarchicus* (Campbell et al. 2001), and for *C. glacialis* and *C. hyperboreus* (Arnkvaern et al. 2005). As stage durations in *M. longa* are not available we have used temperature functions of copepodite stage durations for *M. pacifica* (Padmavati & Ikeda 2002; Liu & Hopcroft 2006). To test for biases in mortality estimates caused by factors other than temperature restricting developmental rate, a comparison was made with estimates obtained by allowing stage duration to increase by 100%. This led to a significant (at the 95% level) reduction in mortality estimates for CV/adult females in all species, and for CIV/CV, in *C. hyperboreus*, but an increase in CI/CII of *M. longa*. A reduction in stage duration by 50% in *M. longa* did not result in significant different mortality estimates.

Similarly, we tested for the effect of arrested development in *Calanus* spp. by re-estimating mortality with a 180-day addition to the duration of potential overwintering stages (CV in *C. finmarchicus*, CIV and CV in *C. glacialis*, and CIII–CV in *C. hyperboreus*; Hirche 1983; Conover 1988). This resulted in significantly lower mortality rates for CV/adult females in all *Calanus* spp., and for CIV/CV in *C. hyperboreus*. Thus we conclude that our mortality index is relatively robust to biases in stage durations for early developmental stages, but that estimates for the oldest developmental stages should be interpreted with care. However, given the low number of replicate samples (four) at each location we acknowledge that our mortality estimates may be biased due to patchiness in the distribution of zooplankton (Aksnes & Ohman 1996), thus estimates of mortality presented here are used for comparison and should not be interpreted as true rates.

Results

Hydrography

The water mass in the upper 100 m at the marginal ice zone station had Arctic characteristics (<0°C, <34.7 psu; Schlichtholz & Houssais 1999). Below 100 m, temperature increased sharply to >3°C and salinity reached 35 psu indicating modified Atlantic water (Schlichtholz & Houssais 1999) (Figure 2). Deeper in the water column salinity remained constant and temperature decreased below 0°C below 750 m. In Hinlopen the water column was relatively well mixed with little variation in temperature and salinity (>1°C, <35 psu; Figure 2). The shelf station sampled at daytime (bottom depth = 520 m) was located further west than the night station (344 m). Temperature and salinity in the nighttime station increased from 3.1°C and 34.2 psu in surface waters to >5°C and 34.9 psu at 50 m. At the daytime (western) station temperature and salinity were lower in the surface (1.7°C, 33.4 psu) but reached >5°C and >35 psu at 50 m. Below this depth temperature gradually fell towards 2.3°C at 300 m at both locations. Temperature was generally lower and more variable in the daytime (western) station, while salinity was higher at the daytime station below 50 m (>35 psu) than at the nighttime station where it remained at 34.9 psu. In Kongsfjorden temperature increased from 3°C in surface waters to 6°C at 50 m depth, and below this depth it gradually decreased towards 3°C at 200 m. Salinity increased from 32.5 psu in surface waters to 35 psu at 50 m, and remained constant below this depth (Figure 2).

At all locations a fluorescence maximum was observed in the upper 50 m of the water column, and values dropped towards zero below 100 m at all stations (Figure 2). Highest levels were recorded in Hinlopen and lowest values were recorded in the marginal ice zone (ca. one-sixth of the Hinlopen peak value).

Copepod populations and vertical distribution

Calanus finmarchicus was the most abundant of the species investigated. Abundance peaked in the surface layer in the marginal ice zone, on the shelf and in Kongsfjorden. In Hinlopen *C. finmarchicus* was more equally distributed throughout the water column, but displayed a bimodal distribution pattern with abundance peaks in the upper 100 m and below 200 m (Figure 2). In the ice 50% of the population consisted of young stages (CI–III) (Figure 2) whereas older stages (CIV to adults) represented a larger part of the population at the other stations (64% in Kongsfjorden, 75% on the shelf and 90% in Hinlopen).

Young stages (CI–CIII) of *C. finmarchicus* were confined to the upper 100 m and had their center of distribution in the upper 50 m at all locations except in the marginal ice zone where CIIs and CIIIs were found down to 500 m (Figure 3). Older stages (CIV to adults) varied more in their mean depth of distribution and also tended to be spread out more in the water column (Figure 3). With the exception of adult females in Kongsfjorden there was no evidence of synchronous diel vertical migrations in

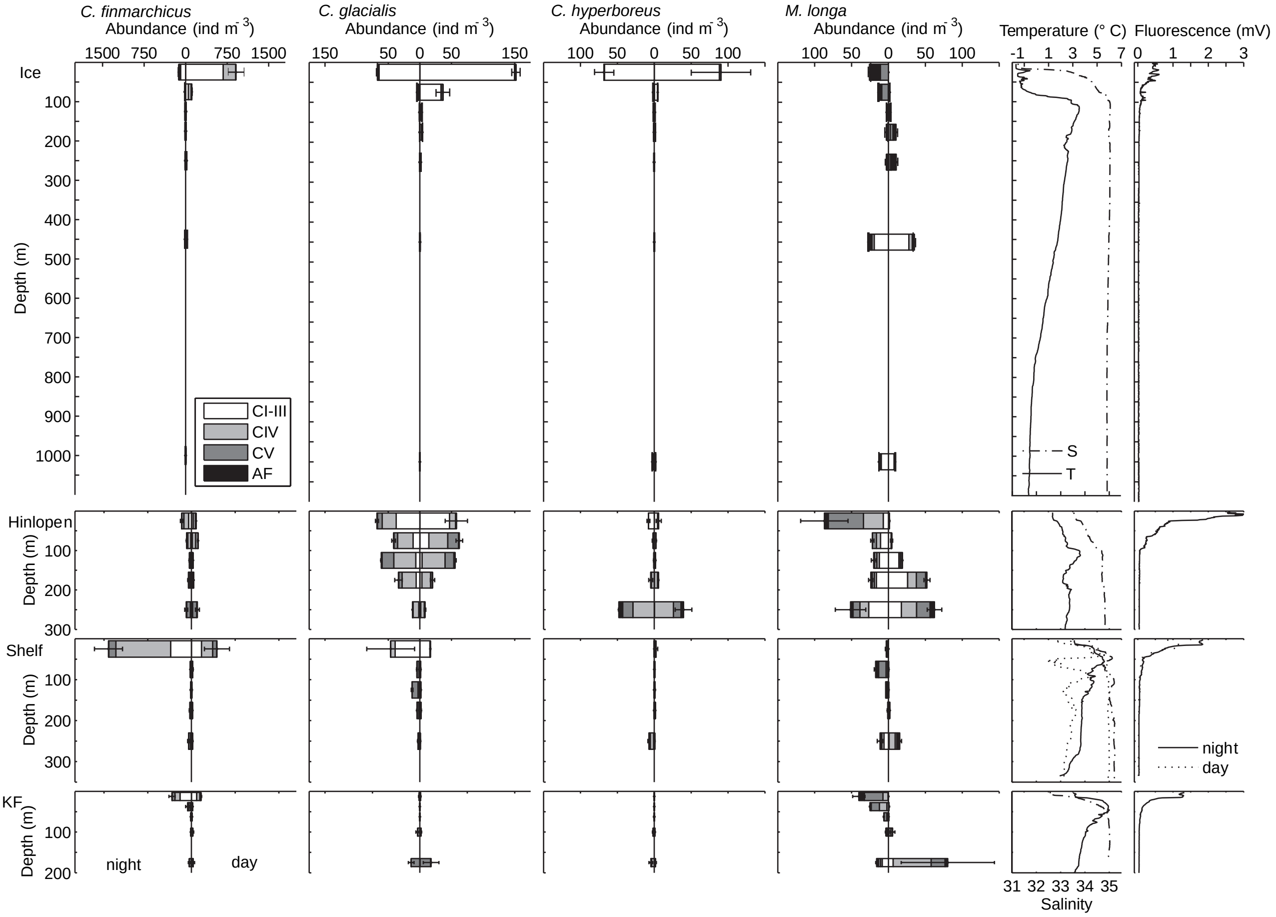

Figure 2. Vertical distribution of copodite stages of *Calanus* spp. and *Metridia longa* (individuals m^{-3}) at the four locations during day (to the right) and night (to the left). Error bars indicate standard error of the total abundance (all copepodite stages) of two replicates. Also shown are depth-specific temperature, salinity and fluorescence values. AF, adult females. KF: Kongsfjorden; T: temperature; S: salinity.

C. finmarchicus. In the marginal ice zone, however, the mean depth was generally shallower during day than night, but only in CIVs were there diel differences in the vertical spread of organisms (Figure 3).

Calanus glacialis abundance was highest in Hinlopen where it was distributed throughout the upper 200 m, and in the upper 50 m in the marginal ice zone (Figure 2). In Kongsfjorden highest abundance was observed in the deepest layer sampled (150–200 m). In the ice and on the shelf young copepodite stages (CI–III) dominated the population of *C. glacialis* (90 and 63%, respectively) while older stages (CIV to adults) dominated in Hinlopen and Kongsfjorden (70 and 99% of the population, respectively).

Calanus glacialis CIs and CIIs were mostly concentrated in the upper 50 m, while CIIIs were located slightly deeper in Hinlopen, on the shelf, and in Kongsfjorden. Older stages were centered in the upper 200 m at these locations, and occasionally the distribution of CIII–CVs spread below that depth, mainly on the shelf. Also in the marginal ice zone the center of distribution was found within the upper 200 m with notable exceptions for the daytime distribution of CIVs and the nighttime distribution of CVs, which were found deeper in the water column spreading from 100 to 800 m and from 50 to 1100 m, respectively (Figure 3). Day and nighttime distribution varied in adult females in Kongsfjorden, CIIIs and CIVs on the shelf, and in CIVs and older developmental stages in the marginal ice zone.

Calanus hyperboreus reached highest abundance in the upper 50 m in the marginal ice zone and below 200 m in Hinlopen (Figure 3), but its abundance on the shelf and in Kongsfjorden was very low (=3 individuals m^{-3}). The population in the ice was dominated by young copepodite stages (CI–III, 65% of the population; Figure 2). Young stages were absent in Kongsfjorden and also at the two other locations older stages (CIV to adults) dominated (66% on the shelf, 95% in Hinlopen).

Calanus hyperboreus developmental stages CIs and CIIs were centered in the upper 50 m, while CIIIs were located at intermediate depths in the marginal ice zone, but relatively deep in Hinlopen and on the

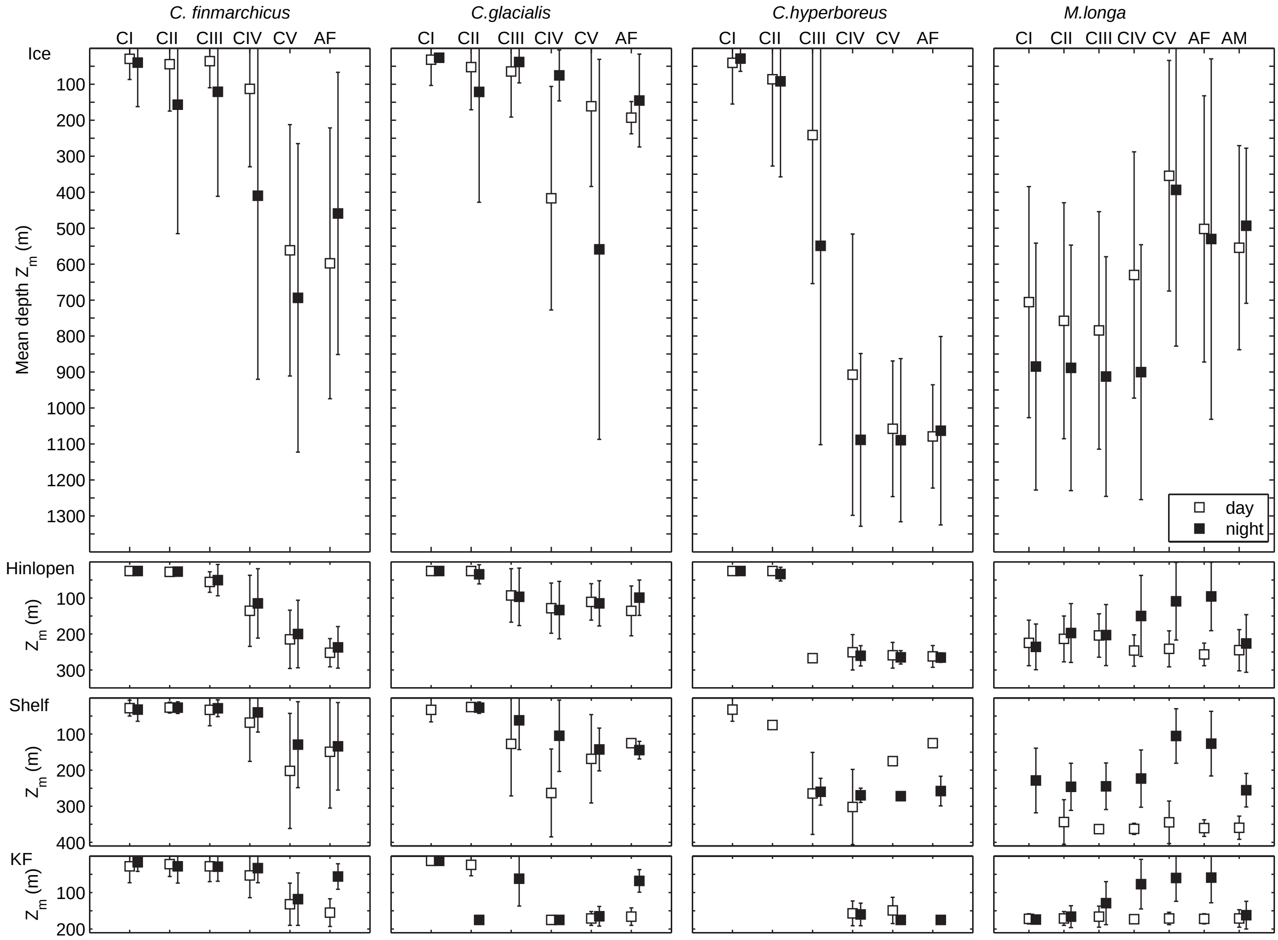

Figure 3. Mean depth (Z_m) of copepodite stages of *Calanus* spp. and *Metridia longa* at the four locations during day (☐) and night (■). Error bars show spread (Z_s). AF, adult females; AM, adult males; KF, Kongsfjorden.

shelf. Older copepodite stages (CIV, CV and adult females) were located deep in the water column both at daytime and nighttime, perhaps with an exception for the shelf stations where daytime distribution of CVs and adult females were at ca. 150 m. However, abundance was very low here (<1.6 individuals m^{-3}), thus we remain unsure as to whether this reflects DVM or patchiness. Marked differences between day and night distributions were only evident for CIIIs and CIVs in the marginal ice zone, where they were located at shallower depth during the day than during the night (amplitude ca. 300 and 180 m, respectively; Figure 3).

Metridia longa was most abundant in Hinlopen (~40 individuals m^{-3}) and least abundant on the shelf (~9 individuals m^{-3}; Figure 2). The population in the ice consisted of 70% younger copepodite stages (CI–III). At the other locations older stages (CIV to adults) made up a larger proportion of the population, representing 57% in Hinlopen, 72% on the shelf and 83% in Kongsfjorden (Figure 2).

The distribution of young stages of *M. longa* (CI–CIII) was always centered relatively deep in the water column (mean depth >130 m; Figure 3), while older stages differed more in their mean depth between daytime and nighttime. CIVs, CVs and adult females were located closer to surface during night than during day at all stations except for in the marginal ice zone (Figure 3), where CVs and adult females showed no signs of DVM while developmental stages CI–CIV were located higher up in the water column at day than during the night.

Mean depth (Z_m) differed significantly between the stations for *C. finmarchicus* CII, CIV to adult females (AF), *C. hyperboreus* CIV–AF and for all stages of *M. longa* (one-way ANOVA, $P < 0.05$). The differences were mainly due to differences between the ice station and the other locations (Tukey HSD test, $P < 0.05$; Table I).

Evidence for light preference

Linear regression analyses between the range of the vertical distribution (Z_s) and the mean depth (Z_m) were statistically significant for most of the developmental stages of *Calanus* spp. and *M. longa*

Table I. Results of ANOVA and Tukey HSD test to test for significant differences in mean depth (Z_m) between stations.

	ANOVA				Tukey HSD					
					Ice–Hin	Ice–KF	Ice–Shelf	KF–Hin	Shelf–Hin	Shelf–KF
	df	f	F	P	P	P	P	P	P	P
C. finmarchicus										
CI	3	12	1.08	ns	ns	ns	ns	ns	ns	ns
CII	3	12	5.05	*	*	*	*	ns	ns	ns
CIII	3	12	1.32	ns	ns	ns	ns	ns	ns	ns
CIV	3	12	5.18	*	ns	*	*	ns	ns	ns
CV	3	12	79.33	***	***	***	***	ns	ns	ns
AF	3	12	9.93	**	**	***	**	ns	ns	ns
C. glacialis										
CI	3	8	3.85	ns	ns	ns	ns	ns	ns	ns
CII	3	10	1.48	ns	ns	ns	ns	ns	ns	ns
CIII	3	9	0.97	ns	ns	ns	ns	ns	ns	ns
CIV	3	10	0.68	ns	ns	ns	ns	ns	ns	ns
CV	3	12	0.75	ns	ns	ns	ns	ns	ns	ns
AF	3	12	1.77	ns	ns	ns	ns	ns	ns	ns
C. hyperboreus										
CI	2	5	3.99	ns	ns		ns		ns	
CII	2	5	1.37	ns	ns		ns		ns	
CIII	2	6	0.18	ns	ns		ns		ns	
CIV	3	12	100.59	***	***	***	***	ns	ns	ns
CV	3	11	706.11	***	***	***	***	***	ns	*
AF	3	8	405.42	***	***	***	***	ns	ns	ns
M. longa										
CI	3	10	92.21	***	***	***	***	ns	ns	ns
CII	3	12	156.92	***	***	***	***	ns	ns	ns
CIII	3	12	116.33	***	***	***	***	ns	ns	**
CIV	3	12	31.99	***	***	***	***	ns	ns	ns
CV	3	12	4.25	*	ns	*	ns	ns	ns	ns
AF	3	12	11.63	***	***	***	**	ns	ns	ns
AM	3	12	16.38	***	***	***	**	ns	ns	ns

AF, adult females; AM, adult males; Hin, Hinlopen; KF, Kongsfjorden.
***$P > 0.001$; **$P < 0.01$; *$P < 0.05$; ns, not significant.

(Table II). This result is consistent with the hypothesis that the individuals of the different developmental stages distribute according to a certain preference for light intensity such as predicted by Equation (6).

Mortality

Mortality indices of *C. finmarchicus* and *C. glacialis* increased with developmental stage, while they decreased with stage for *C. hyperboreus* (Figure 4). Mortality indices were generally lower and less variable for *M. longa*, but also these increased with developmental stage (Figure 4). There were significant differences in mortality indices between developmental stages for *C. finmarchicus*, *C. glacialis* and *M. longa* (one-way ANOVA, $P < 0.05$), but not for *C. hyperboreus* (one-way ANOVA, $P < 0.05$). These differences were mainly due to variations in the

Table II. R^2 values and significance level of linear regression of the observed vertical range (Z_s) of the vertical distribution versus the observed mean depth (Z_m) of the distribution of each copepodite stage of all four species.

	Calanus finmarchicus		*Calanus glacialis*		*Calanus hyperboreus*		*Metridia longa*	
Stage	R^2	P	R^2	P	R^2	P	R^2	P
CI	0.00	ns	0.59	**	0.84	**	0.61	**
CII	0.95	***	0.37	*	0.57	*	0.60	***
CIII	0.82	***	0.16	ns	0.58	*	0.66	***
CIV	0.91	***	0.73	***	0.75	***	0.74	***
CV	0.95	***	0.73	***	0.58	**	0.61	***
AF	0.71	**	0.20	ns	0.81	***	0.61	**

AF, adult females.
***$P > 0.001$; **$P < 0.01$; *$P < 0.05$; ns, not significant ($P > 0.05$).

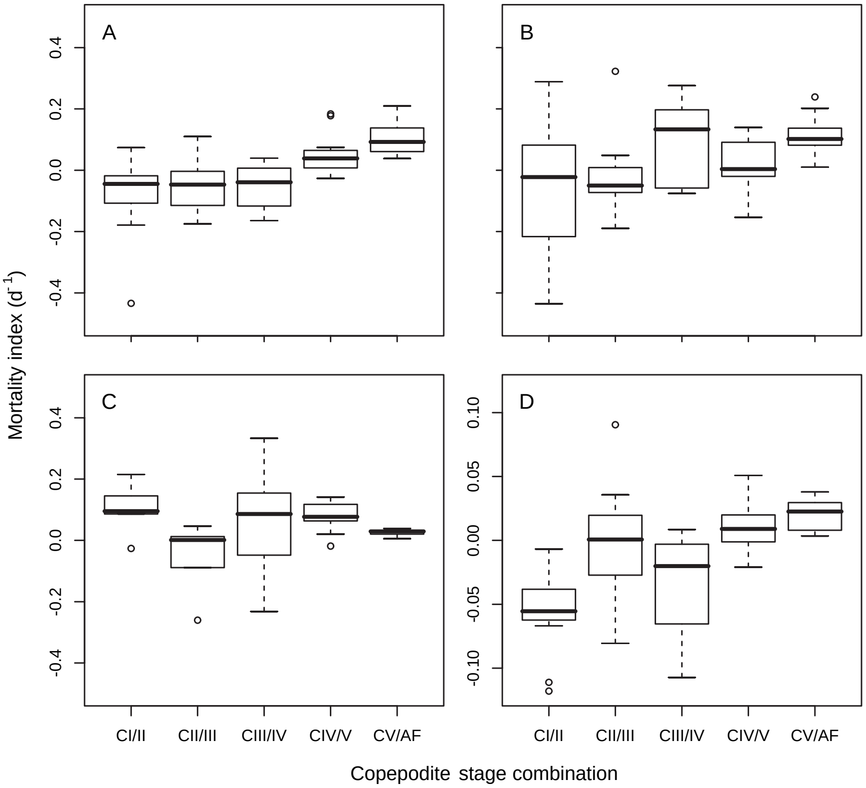

Figure 4. Mortality index for (A) *Calanus finmarchicus*; (B) *C. glacialis*; (C) *C. hyperboreus*; (D) *Metridia longa*. Mortality indices have been estimated for stage combinations CI and CII (CI/II), CII and CIII (CII/III), CIII and CIV (CIII/IV), CIV and CV (CIV/V), CV and adult females (CV/AF). See Material and methods for details. Horizontal line shows the median, the bottom and top of the box show the 25 and 75 percentiles, respectively, whiskers extend 1.5 times the interquartile range of the sample. Values outside this range are marked by circles. Note different scale on y-axis for *M. longa* (D).

mortality of young stages (CI/II, CII/III, CIII/IV) compared to older stages (CIV/V, CV/AF) (Tukey HSD test, $P < 0.05$; Table III).

Mortality indices correlated positively with mean depth of *C. finmarchicus* and *C. glacialis*, and slightly negatively with mean depth of *M. longa* (Figure 5). Also, mortality correlated with average prosome length of *C. finmarchicus* (Pearson's correlation $R = 0.63$, $t_{57} = 6.12$, $P < 0.001$) and *C. glacialis* (Pearson's correlation $R = 0.43$, $t_{52} = 3.45$, $P < 0.01$)

Table III. Results of ANOVA and Tukey HSD test for differences in mortality indices between copepodite stages of each species.

		Calanus finmarchicus	*Calanus glacialis*	*Calanus hyperboreus*	*Metridia longa*
ANOVA					
	df	4	4	4	4
	F	15.51	4.37	2.53	14.58
	P	***	**	ns	***
Tukey HSD					
CI/II–CII/III	P	ns	ns	ns	***
CI/II–CIII/IV	P	ns	ns	ns	ns
CI/II–CIV/V	P	**	ns	ns	***
CI/II–CV/AF	P	***	*	ns	***
CII/III–CIII/CIV	P	ns	ns	ns	*
CII/III–CIV/CV	P	*	ns	ns	ns
CII/III–CV/AF	P	***	ns	ns	ns
CIII/IV–CIV/V	P	*	ns	ns	**
CIII/IV–CV/AF	P	***	ns	ns	***
CIV/V–CV/AF	P	ns	ns	ns	ns

***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; ns, not significant ($P > 0.05$). Mortality indices have been estimated for stage combinations CI and CII (CI/II), CII and CIII (CII/III), CIII and CIV (CIII/IV), CIV and CV (CIV/V), CV and adult females (CV/AF). See Material and methods for details.

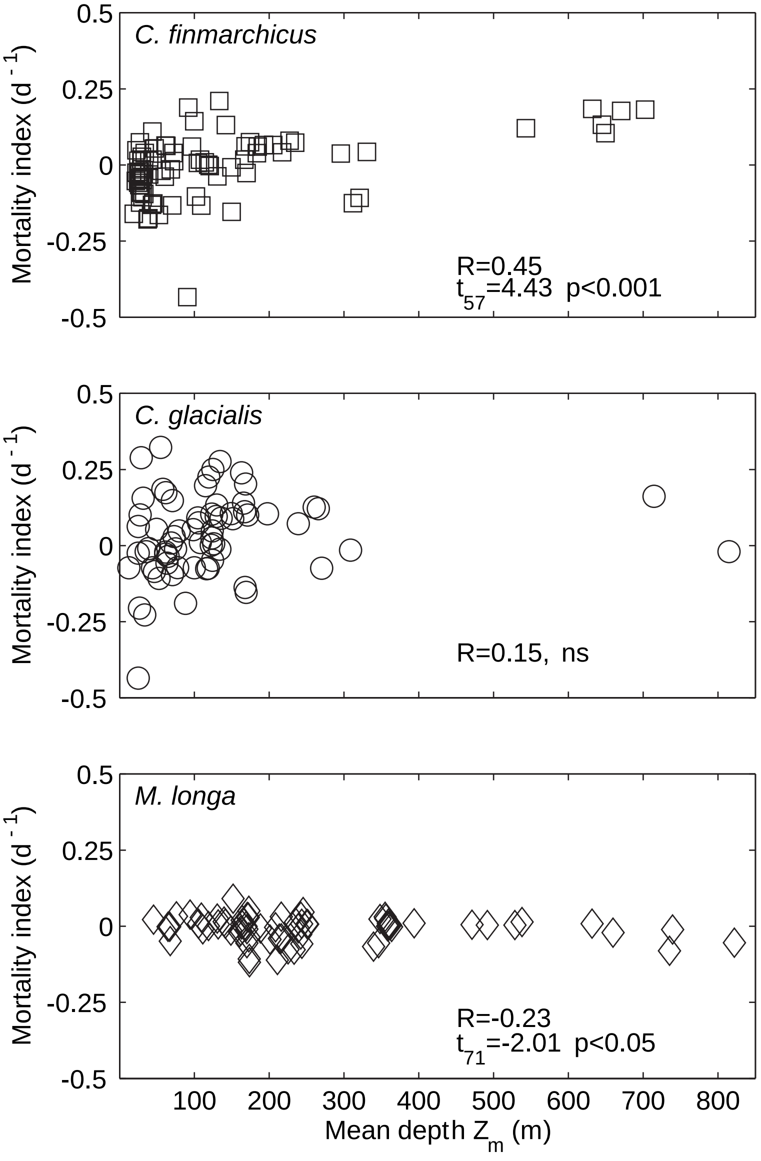

Figure 5. Plot of mortality index against mean depth (Z_m) of *Calanus finmarchicus*, *C. glacialis* and *Metridia longa*.

Discussion

At most stations *Calanus* abundance peaked in the surface layer and overlapped with the highest fluorescence recordings, presumably indicating high phytoplankton concentration. Such overlap in vertical distribution of herbivorous zooplankton and the chlorophyll maxima is in accordance with previous observations (Eilertsen et al. 1989; Thor et al. 2005), and seems to suggest that a large fraction of *Calanus* was still actively feeding at the time of study. Surface populations were dominated by young developmental stages in all stations whereas the older stages prevailed at larger depths. Similar observations have been made by e.g. Østvedt (1955) in the Norwegian sea, by Longhurst et al. (1984) in late summer in the Canadian archipelago and by Madsen et al. (2001) in early autumn in Disko Bay.

Despite variability in the day and night distribution in some copepodite stages we found little evidence for synchronous DVM in *Calanus* spp. This apparent lack of DVM is in accordance with earlier studies from high latitudes, i.e. Nansen Basin (Gröndahl & Hernroth 1986; Mumm 1993) and in northern Norwegian coastal waters (Falkenhaug et al. 1997). However, *C. finmarchicus* is observed to conduct DVM at lower latitudes (e.g. Magnesen 1989; Hays 1996; Tarling et al. 2002; Irigoien et al. 2004). Also, DVM is reported from the Canadian archipelago for *C. finmarchicus*, *C. glacialis* and *C. hyperboreus* (Sameoto 1984; Runge & Ingram 1991; Fortier et al. 2001). These studies, however, used finer depth resolution than what was used in the present study (in particular in the upper 50 m of the water column) and were focused on the upper 100–150 m of the water column (Runge & Ingram 1991; Fortier et al. 2001). Due to coarse vertical and temporal sampling intervals, possible dusk and dawn migration as well as short-range migrations (in particular in the upper 50 m) might have escaped our attention.

A number of studies indicate that the tendency to perform DVM in *C. finmarchicus* varies with season, feeding conditions and age (e.g. Tande 1988; Krause & Radach 1989; Durbin et al. 1995). In the Norwegian Sea and northern Norwegian coastal waters diel patterns in vertical distribution have been observed in some copepodite stages of *C. finmarchicus* (Tande 1988; Dale & Kaartvedt 2000). Young developmental stages (CI–CIII) were found to be confined to surface waters, which is in accordance with our observations, while older stages (CV, females) displayed DVM.

Most studies on DVM at high latitudes have focused on the summer season during which there is continuous daylight (i.e. Bogorov 1946; Fortier et al. 2001) and less is known about vertical distribution patterns during early spring or autumn when day lengths are similar at high and low latitudes. Kosobokova (1978) reports diel migrations of females of *C. glacialis* during summer and autumn from the central Arctic Basin. Our data indicated DVM in adult females of *C. finmarchicus* and *C. glacialis* in one station only (Kongsfjorden; Figure 3). However, females of both species occurred in relatively small numbers in this station, thus results should be interpreted with care. Cottier et al. (2006) record asynchronous DVM during periods of midnight sun in Kongsfjorden but conclude from the distribution of acoustic backscattering layers that synchronized migrations begin when nighttime resumes in autumn, and identify *C. finmarchicus* and *C. glacialis* as important contributors to the migratory scattering layers.

Metridia longa displayed a broader vertical distribution than *Calanus* which is in accordance with observation of Longhurst et al. (1984) and Sameoto (1984). We also observed clear variability in depth distribution of *M. longa* between day and nighttime samples confirming previous observations of DVM in *M. longa* (Gröndahl & Hernroth 1986; Diel 1991; Mumm 1993; Falkenhaug et al. 1997). As in our study, it is normally the younger stages (CI–CIII/IV) and adult males that tend to be stationary while CVs and females migrate upwards during the night.

Causes for observed differences in vertical distribution

The abundance of overwintering stages (i.e. CV for *C. finmarchicus*, CIV and CV for *C. glacialis* and CIII–CV for *C. hyperboreus*) increased with depth (Figure 3), indicating that parts of all populations had initiated the descent to overwintering depth at the time of sampling, while younger stages were still mostly concentrated closer to the surface. Such seasonal migrations can start in midsummer in *Calanus* spp. (Pedersen et al. 1995; Hirche 1996), but are typically not synchronized in that older stages descend while younger individuals remain in surface waters until late autumn (Hirche 1996).

South–north gradient in developmental progression. The observed variability in the vertical distribution of *Calanus* spp. reflects in part a geographic trend in the population age structure between study locations. It is likely that variability in water temperature, ice cover, and timing of the spring phytoplankton bloom between the stations have resulted in differences in seasonal succession in the zooplankton community. Thus copepod development probably started earlier in the relatively warmer and ice-free southern locations and therefore had progressed further than in the northern stations at the time of sampling. For instance, the peak abundance of overwintering stages (CIV–CV) of *C. hyperboreus* occurred deep (200–300 m) in Hinlopen (Figures 2 and 3), indicating that these organisms had migrated to their overwintering habitat. In the marginal ice zone, however, the *C. hyperboreus* population consisted mainly of CIs accumulating in the upper 50 m, indicating that the development here was delayed compared to the more southern locations. Higher abundance of *C. glacialis* in the deepest layer in Kongsfjorden (mainly CV) indicates a similar pattern for that species. This is supported by the dominance of overwintering stages (CIV and older) in Hinlopen and Kongsfjorden, representing 70 and 99% of total *C. glacialis* population, respectively.

Also the stage structure of *M. longa* was skewed towards older stages in the more southern location. *Metridia longa* is an omnivore (Haq 1967) that does not overwinter in diapause, but is found to continue feeding throughout the winter (Båmstedt et al. 1985). Hirche & Mumm (1992) and Diel (1991) postulate that older stages of *M. longa* spend the winter close to the surface and migrate into deeper layers for the summer, whereas young stages remain at greater depth for most of the year. This is supported by observations from off eastern Greenland (Ussing 1938; Digby 1954) and from the Polar basin (Geynrikh et al. 1980; Vinogradov 1997), and agrees with our observation of a deep distribution of developmental stages CI–CIII (Figure 3). However, this seasonal migration pattern may vary as Pavshtiks (1983) reports that young stages of *M. longa* in the Arctic Ocean are located close to the surface all year round while older stages tend to be distributed deeper during winter than summer. Similar observations are reported from northern Norwegian fjords (Grønvik & Hopkins 1984; Falkenhaug et al. 1997).

Evidence for optical effects. Pearre (2003) pointed out that vertical location of pelagic organisms should be considered with regard to changes in light conditions and not with regard to depth per se. Several recent studies suggest that optical properties are important in shaping abundances and vertical distributions in plankton and fish (Aksnes et al. 2004; Sørnes & Aksnes 2006; Aksnes & Samuelsen forthcoming). We observed a positive linear relationship between the vertical range of the depth distribution and the mean depth for most of the copepodite stages (Table II). This is consistent with the hypothesis that the organism distributes according to a preference for ambient light of the water column (Equation 6), although we cannot eliminate that other possible mechanisms may account for this observed relationship such as preferences or avoidance of certain water masses, avoidance of non-visual predators or avoidance of bottom. Whether optical properties of the water column were important for shaping the vertical distribution of the different species and developmental groups can be tested more effectively by relating the two observed statistics, Z_m and Z_s, directly to the light attenuation coefficient as given by the predictions in Equations 4 and 5. We do not have direct measurements of light attenuation, but other studies suggest that salinity (Eiane et al. 1999; Højerslev & Aarup 2002; Sørnes & Aksnes 2006) and chlorophyll concentrations (Morel 1988) are important determinants for light attenuation. Hence, we have approximated light attenuation from the observed salinity and fluorescence profiles and related Z_m and Z_s to the reciprocal light attenuation (Table IV) as suggested by Equations 4 and 5. Similar to the previous and independent analysis provided in Table II, also the overall results from these analyses (Table IV) are consistent with the hypothesis that the developmental stages have a preference for a certain light intensity range as given by Equations 4 and 5. Copepodite stages of *C. finmarchicus* show highest consistency with the hypothesis, while less consistency was found for *C. glacialis* and *C. hyperboreus*. *C. finmarchicus* had high abundances at all stations, and this provided higher accuracy of the estimates of the mean depth Z_m and the vertical range Z_s. For the other species these estimates were more uncertain. This applies in particular to the estimate of the third moment (Z_s) of the frequency curve which also provided the highest number of non-significant relationships (Table IV). Another uncertainty in our analysis is the approximation of the light attenuation coefficient K.

The evidence provided here clearly suggests that three factors should be addressed in future studies of vertical distributions in copepods. First, vertical distributions should be measured in locations with different light attenuation. Second, direct measurements of light attenuation need to be conducted, and third a finer depth resolution than used in the present study should be applied in order to obtain more accurate Z_s estimates. This should enable more effective tests of whether a particular organism distributes according to a preference for light intensity.

Diel vertical migration in M. longa. The adaptive significance of DVM has been widely discussed (Lampert 1989; Aksnes & Giske 1990; Ohman 1990; Fortier et al. 2001; Hays 2003) and is currently understood primarily as a survival-optimizing strategy to reduce detection by visual predators in well-lit surface layers (Lampert 1989). This ‘predator avoidance hypothesis’ is supported by numerous studies in marine and freshwater habitats (e.g. Zaret & Suffern 1976; Gliwicz 1986; Bollens & Frost 1989; Hays et al. 1994; Tarling et al. 2002). Possible predators on copepods in our study area are polar cod (*Boreogadus saida*), the amphipod *Themisto libellula*, the cephalopod *Gonadus fabricii* as well as the chaetognaths *Eukrohnia hamata* and *Sagitta elegans* (unpublished data) but unfortunately we lack quantitative data on the predator regime to assess variability in predation risk.

The marked differences in observed vertical behavior between *Calanus* spp. and *M. longa* can be based on behavioral and morphological differences which affect their susceptibility to visual predators (Hays et al. 1997; Torgersen 2001), and on differences in food preferences and life-history strategies of these copepods. Given the highly seasonal primary production at high latitudes it is important for herbivorous species such as *Calanus* spp. to synchronize their position in the water column with layers of maximum primary production (Fiksen & Carlotti 1998). Such synchronization to phytoplankton productivity is probably less essential for omnivorous species such as *M. longa* (Haq 1967) which might therefore be more flexible in choosing their vertical position. Thus factors other than food abundance may influence their choice of vertical position. For example, being more conspicuous for predators than *Calanus* spp. (Hays et al. 1997; Torgersen 2001) might create a higher demand to adapt

Table IV. R^2 values and significance level of linear regressions of Z_m (observed mean depth) and Z_s (observed vertical range) against the approximated reciprocal light attenuation coefficient K (K^{-1}).

	Calanus finmarchicus		*Calanus glacialis*		*Calanus hyperboreus*		*Metridia longa*	
	R^2	P	R^2	P	R^2	P	R^2	P
Z_m vs. K^{-1}								
CI	0.92	***	0.60	**	0.47	ns	0.52	**
CII	0.92	***	0.91	***	0.65	*	0.43	**
CIII	0.71	***	0.70	***	0.41	ns	0.51	**
CIV	0.75	***	0.61	**	0.36	*	0.54	**
CV	0.52	**	0.45	**	0.51	**	0.50	**
AF	0.44	*	0.39	*	0.60	**	0.54	**
Z_s vs. K^{-1}								
CI	0.00	ns	0.24	ns	0.19	ns	0.32	*
CII	0.86	***	0.19	ns	0.36	ns	0.20	ns
CIII	0.77	***	0.26	ns	0.22	ns	0.31	*
CIV	0.85	***	0.21	ns	0.29	*	0.29	*
CV	0.64	***	0.25	*	0.24	ns	0.24	ns
AF	0.46	*	0.02	ns	0.50	*	0.19	ns

***$P > 0.001$; **$P < 0.01$; *$P < 0.05$; ns, not significant ($P > 0.05$). Regression analyses were conducted for each copepodite stage of each species. The light attenuation coefficient (K) for a particular set of Z_m and Z_s observations was calculated as the average light attenuation of the water column between the surface and the mean depth. The light attenuation at a particular depth (K) was approximated from the observed salinity (S) and the observed chlorophyll concentration (C) that was derived from the observed fluorescence according to $K = f(S) + g(C)$ where we used $f(S) = 1.3076 - 0.036S$ (Eiane et al. 1999) and $g(C) = 0.121C^{0.428}$ (Morel 1988).

predator-avoiding behavior such as DVM than for *Calanus* spp.

The indicated reverse DVM pattern in *M. longa* in the marginal ice zone (Figure 3) is likely due to the greater depth here compared to the other stations since this was the only station in our study that was situated in deep water beyond the shelf break. *Metridia longa* is characterized as a bathypelagic species (Brodskii 1967), but is typically found closer to the surface in Arctic waters (Geynrikh et al. 1980). However, in areas influenced by Atlantic waters its abundance typically peaks at greater depth (Wiborg 1954; Smith 1988; Diel 1991; Hirche & Mumm 1992). Such was the case below ca. 100 m in the marginal ice zone station investigated in the present study (Figure 2) where *M. longa* abundance peaked below 300 m. Below this depth abundance did not differ much between day and nighttime, indicating that a large part of the *M. longa* population remained below this depth both at day and nighttime. Focusing on the upper 300 m only (Figure 6) reveals that the shallow component of the *M. longa* population engages in DVM also on this location. The stage-specific pattern was similar to what was observed in the other stations (Figure 3).

On the shelf the young stages of *M. longa* seem to be distributed shallower during nighttime than during daytime. This is likely an artifact caused by difference in bottom depth between the daytime and nighttime station (bottom depth is 525 and 344 m, respectively) which pushes the mean depth down for the population observed at the deeper station sampled during the day.

Mortality

The mortality indices for the diel migrating *M. longa* were lower than for *Calanus* spp. (Figure 5). Thus in accordance with predictions from the predator-avoidance hypothesis *M. longa* seems to profit from DVM relative to *Calanus* spp. However, *M. longa* mortality tended to increase with age, and peak mortality was recorded in the migrating developmental stages. Also, we found a significant relationship between *M. longa* DVM amplitude and the

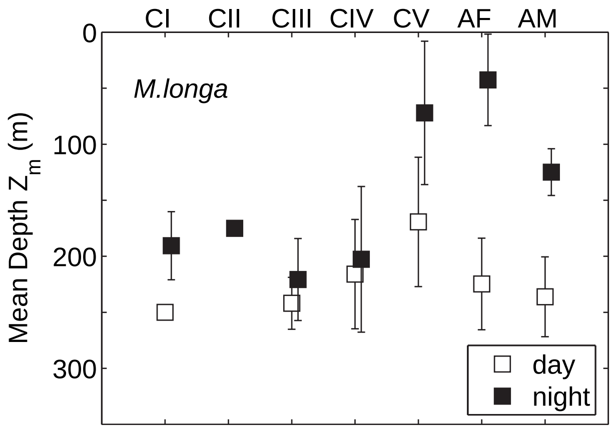

Figure 6. Mean depth (Z_m) of copepodites of *Metridia longa* in the upper 300 m of the ice station during day (□) and night (■). Error bars show spread (Z_s).

mortality index (Pearson's correlation: $R = 0.38$, $t_{71} = 3.45$, $P < 0.001$). DVM behavior in older stages of *M. longa* might have evolved from a trade-off between predation risk and risk of starvation (Pearre 2003) and although the migrating stages experience greater mortality risk they still suffer lower mortalities than the non-migrating *Calanus* species.

Mortality indices of *Calanus* spp. generally peaked in the overwintering stages (Figure 5). We did not observe significant relationships between mortality and mean depth for *C. glacialis*, but a somewhat unexpected increase in mortality estimates for *C. finmarchicus* with depth. The positive relationship between size and mortality of *C. finmarchicus* and *C. glacialis* is in contrast to findings by Kiørboe & Sabatini (1995) and Huntley & Lopez (1992) who describe size-independent mortality in copepods, and also with Hirst & Kiørboe (2002) who found that mortality decreased slightly with size in broadcast spawning copepods. Correlation of mean depth against size of copepodites was significant for both *C. finmarchicus* ($R = 0.66$, $t_{58} = 6.65$, $P < 0.001$) and *C. glacialis* ($R = 0.44$, $t_{55} = 3.66$, $P < 0.001$), reflecting the increase in older (and larger) stages with depth. Thus it seems likely that the observed increase in mortality with mean depth in *C. finmarchicus* and with size reflects the increase in mortality with age. This might reflect higher susceptibility to predators of larger stages, and possibly senescence for the adult stages.

Concluding remarks

The results presented here suggest that the vertical distribution of the four copepod species during the end of the productive season varies with the developmental progression and potentially also the optical properties of the water column. Factors not addressed here are likely to add to this. Observations of DVM of *Calanus* at high latitude remain inconclusive. We do recommend that future studies on vertical distribution and migration should include finer sample intervals than we used, particularly close to the surface. Also, the seasonal and ontogenetic variations in the intensity of DVM (Durbin et al. 1995; Falkenhaug et al. 1997; Cottier et al. 2006) underline the need for a finer temporal resolution of the transition time when the light regime changes from constant daylight via a period of normal day and night rhythm to polar night. This, in addition to studies of the vertical distribution throughout Arctic autumn and winter, could give further insight into how light and optical properties affect vertical behavior and distribution as well as the life history of *Calanus* spp. and *Metridia longa*.

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