Mar Biol (2014) 161:1931–1941
DOI 10.1007/s00227-014-2475-x

ORIGINAL PAPER

Inter- and intra-specific diurnal habitat selection of zooplankton during the spring bloom observed by Video Plankton Recorder

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Received: 17 December 2013 / Accepted: 1 June 2014 / Published online: 10 July 2014

Abstract Diel vertical migration (DVM) is a common behavior adopted by zooplankton species. DVM is a prominent adaptation for avoiding visual predation during daylight hours and still being able to feed on surface phytoplankton blooms during night. Here, we report on a DVM study using a Video Plankton Recorder (VPR), a tool that allows mapping of vertical zooplankton distributions with a far greater spatial resolution than conventional zooplankton nets. The study took place over a full day–night cycle in Disko Bay, Greenland, during the peak of the phytoplankton spring bloom. The sampling revealed a large abundance of copepods performing DVM (up during night and down during day). Migration behavior was expressed differently among the abundant groups with either a strong DVM (euphausiids), an absence of DVM (i.e., permanently deep; ostracods) or a marked DVM, driven by strong surface avoidance during the day and more variable depth preferences at night (*Calanus* spp.). The precise individual depth position provided by the VPR allowed us to conclude that the escape from surface waters during daytime reduces feeding opportunities but also lowers the risk of predation (by reducing the light exposure) and thereby is likely to influence both state (hunger, weight and stage) and survival. The results suggest that the copepods select day and night time habitats with similar light levels (~10^{-9} µmol photon s^{-1} m^{-2}). Furthermore, *Calanus* spp. displayed state-dependent behavior, with DVM most apparent for smaller individuals, and a deeper residence depth for the larger individuals.

Electronic supplementary material The online version of this article (doi:10.1007/s00227-014-2475-x) contains supplementary material, which is available to authorized users.

Communicated by M. A. Peck.

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Introduction

Theory predicts a trade-off between feeding and predator avoidance (e.g., McNamara 1987; Pearre 2003). Many herbivorous and omnivorous zooplankton respond to predators by performing classical diel vertical migrations (DVM), feeding in surface waters at night, when low light levels minimize their exposure to visual predators and spending the daytime in deeper and safer waters (Hays 2003). The pelagic environment hosts a diverse community in which complex interactions (both intra-, e.g., competition for food, and inter-specific interactions, e.g., predator-prey interactions) and trophic cascades can take place (Ohman 1990; Baumgartner et al. 2011). Furthermore, species will differ in their motivation to migrate, based on factors such as their feeding mode and predation risk. Similarly, intra-specific variability such as energy reserves, size or maturity status lead to state-dependent DVM (Hays et al. 2001) and consequently variability in the vertical distribution of individuals within a population. For example, individuals close to starvation are expected to perform a more risk-prone behavior than individuals with larger energy reserves.

Measuring the distribution of plankton in the pelagic environment is a challenging task. Vertical net tows are most frequently used. However, one disadvantage with this method is that individuals within depth intervals are pooled, weakening the precision of our knowledge of their position and thereby reducing the power when testing for differences in depth distributions between day and night (Pinel-Alloul 1995; Pearre 2003). Acoustic methods, on the other hand, can give precise depth position, but they suffer from uncertainties regarding which species that are observed (high spatial resolution but low taxonomic resolution, e.g., Berge et al. 2009).

Video and photographic techniques are alternatives to these traditional approaches. Optical sampling devices including Video Plankton Recorders (VPRs) have been developed over the past two decades and give exact information regarding the depth of individuals as well as providing quantitative estimates of plankton abundance, by imaging a given volume of water with a camera. Broughton and Lough (2006) compared the performance of nets (MOCKNESS) and VPR. There was good agreement in the results for zooplankton vertical distribution between the two instruments. VPRs and nets provide comparable information on concentrations of abundant taxa such as copepods (Benfield et al. 1996). The VPR samples a smaller volume than net and acoustic methods. However, the number of organisms counted by the VPR at a given station may actually be of the same order of magnitude as a typical net sample, because the latter would have to be sub-sampled to get a manageable number of individuals, i.e., manually countable (Davis et al. 1996, 2005). As pointed out by Davis et al., the VPR gives an unbiased estimate of mean abundance, which cannot be acquired by sub-sampling from net samples. Besides the precise depth position, an additional benefit of the VPR is the relative ease of fitting sensors that provide concurrent data on hydrography (temperature, salinity, density) and phytoplankton biomass (chlorophyll fluorescence) from the same parcel of water as imaged by the VPR, thus providing finely resolved information on zooplantkon distributions in relation to the environment. These data allow for investigation into the presence of thin layers and hot spots of predator–prey activity which can be overlooked if sampling gear does not have fine resolution (e.g., Möller et al. 2012).

Here, we report on a VPR study of the zooplankton community at the Arctic to sub-Arctic location of Disko Bay, western Greenland, during the annual spring bloom, a time of year when there are marked differences in the light levels between day and night, and the food availability for grazers is high. Disko Bay's onshore biological station has been a successful platform for investigations into Disko Bay's pelagic ecology (e.g., Nielsen and Hansen 1995; Madsen et al. 2001; Turner et al. 2001; Hansen et al. 2003; Webster et al. submitted) and therefore offers an ideal testing ground for process studies. The main aim of the study was to detect which parts of the Disko Bay plankton community perform DVM and to investigate behavioral variability of copepods from the genus *Calanus*. Furthermore, we investigated the extent of which light exposure during both day and night is implicated in behavior. We expected larger individuals (or species), which tend to be more easily detected by visual predators, to migrate deeper than smaller ones. We discuss the extent of DVM observed in relation to life cycle strategies of the different species and families, acknowledging that the motivation for predator avoidance and feeding may be state-dependent, varying with ontogenetic stages, maturity levels and reproductive strategies.

Materials and methods

Sampling

Sampling was conducted from the RV *Porsild* in Disko Bay 69°15'N, 53°33'W on April 28–29, 2012. A map of the area is available in appendix A (Fig. A.1) and in Nielsen and Hansen (1995). A digital autonomous VPR from Seascan Inc., with attached SBE-49 Seabird CTD and Wetlabs ECO Puck, fluorometer/turbidity sensor was used to study the DVM of zooplankton. The VPR was supplied with a

Table 1 The VPR was deployed four times encompassing day and night-time sampling from R/V *Porsild* in Disko Bay, Western Greenland in April 2012

Cast	Date	Local time	Depth (m)	Bottom depth (m)	Number of tows	Total sampling volume (10^3 m^3)
Day 1	28/04/2012	13:02–14:24	0–291	343	1	0.24
Night 1a	28/04/2012	23:03–00:01	0–318	339	4	0.93
Night 1b	29/04/2012	01:25–02:40	0–311	345	6	1.10
Day 2	29/04/2012	13:00–14:17	0–315	341	6	1.10

camera (Uniq model UC-1830CL) with 1 megapixel resolution (1,024 × 1,024), 10 bit color depth and a frame rate of compressed images of ~15 s^{-1}. The VPR was lowered slowly (~0.5 m s^{-1}, i.e., similar speed as previous studies using vertical VPR tows, e.g., Norrbin et al. 2009) from the surface and to near the sea floor (~300 m depth; Table 1). Samples were obtained on four occasions, two daytime samplings and two night-time samplings. Each sampling event (cast) had three down tows and three up tows, except the first night-time sampling when two down tows and two up tows were made (Table 1). Due to a technical problem, only data from the first down tow were available on Day 1. Sea water temperature, salinity, density, fluorescence and light intensity (PAR) were measured by the VPR's CTD and by a stand-alone Seabird SBE25-01 CTD. The CTD casts were made just before Day 1, Night 1b and Day 2 samplings. The Seabird CTD was lowered to near the seafloor and then raised to the surface again. The PAR measurements of relative light intensity were used to find the light attenuation coefficient in the water column.

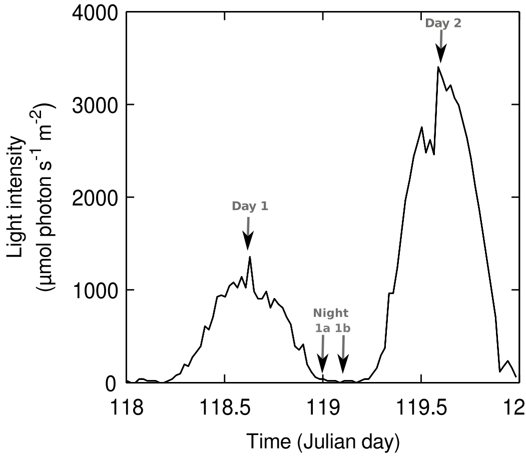

Fig. 1 Surface light intensity throughout the study. *Arrows* indicate when the sampling took place

VPR specifications

Each VPR tow produces a file consisting of compressed images and the ancillary CTD and fluorescence data. Regions of interest (ROIs) were extracted from the images employing a set of extraction parameters (e.g., segmentation threshold and focus) using the software AutoDeck (Seascan Inc). Calibration of imaged volume used calibration files and calibration software (VPR_Cal) provided by the manufacturer. The principle behind the calibration process is that a transparent plate with an evenly distributed series of holes is moved from the camera side to the strobe side of the VPR. The focus detection program (VPR_Cal) was run with the same settings as used when extracting ROIs from the field data. By observing at what distance from the camera images (holes) are being extracted, the depth of field can be worked out. From this value and the field of view, the imaged volume can be calculated. When deploying the VPR, a setting with a field of view of 24 × 24 mm was used. The settings used in AutoDeck for extracting the images gave a depth of field of 32.3 mm, and thus, the imaged volume was 18.6 ml (24 mm × 24 mm × 32.3 mm). The imaged volume and counts of manually sorted images were used to calculate abundances (individuals per m^{-3}). The names of the ROIs reflect when they were taken (time in milliseconds within the day). Mathworks (MATLAB 2012) was used to link the pictures to time and depth of observation via time stamp. The hydrographic parameters (temperature and salinity) were also time stamped and could be related to the observations. For the stand-alone CTD, we used depth and sampling events to link the data.

Light conditions

Surface light intensity was recorded on an onshore biological station approximately 12 km from the sampling site, throughout the sampling period. The VPR casts were made near the high and low peaks of daily light variation (Fig. 1). The decline of light in the water column was measured by the PAR sensor of the CTD deployed prior to each VPR sampling. These data were used to calculate the light attenuation coefficient (Beer–Lambert's law, Crouch and Ingle 1988) by fitting an exponential decay function over the depth:

$$I(d) = I_0 \exp(-\alpha d), \tag{1}$$

where $I(d)$ is the light intensity at depth d, l_0 the light intensity at the surface and α the attenuation coefficient. α was estimated using a nonlinear (weighted) least-squares fitting procedure. We then calculated the model fit (R^2) by correlating model prediction and observed values from Day 2. Day 2 was used as a reference because the light intensity at the surface was highest, thus providing the largest variation in light intensity over depth. The surface light measurements were converted from watts per squre meter (W m^{-2}) to photon irradiance (μmol photon s^{-1} m^{-2}) using a 4.39 conversion coefficient, corresponding to a wavelength of 525 nm (standard lighting radiation conversion method).

Species identification and measurement

Sixteen taxa, genera or particle types were identified, with most of the copepods being identified to genus (see Fig. 2 for examples of species photographed). The categories used were amphipods, euphausiids, *Calanus* spp., *Metridia longa*, *Pseudocalanus* spp. carrying egg sac, *Paraeuchaeta* spp. carrying and without egg sac, unidentified copepods, chaetognaths, ctenophores, crustaceans, fecal pellets (most likely fecal strings of euphausiids), marine snow, jellyfish, ostracods and others, i.e., either unidentified or non-listed (Table 2). Note that a general category (called "copepods") has been added to Table 2, containing all copepods: *Calanus* spp., *Metridia longa*., *Pseudocalanus* spp. with egg sac, *Paraeuchaeta* spp. with and without egg sac and unidentified copepods. Partial images of individuals were included in the data set, but only when positive identification was possible. The most abundant categories of animals were used in analyses (more than 25 detections over the four samplings events and present in all).

We compared the day/night distributions among groups, using a linear mixed model. Depth was square-root transformed and included in the model as the dependent variable, while species and time of day (Day, Night) were taken as independent factors. Interactions between time of day and species groups were allowed. "Tows" nested in "cast" was used as random factor to account for sampling variability.

In addition, we investigated what appeared to be a daytime surface avoidance behavior. We therefore calculated the depth below which 75 % of the population was found for each tow and tested the difference between day and night using an ANOVA.

We also tested whether light level at which the individual copepods were found differed between day and night by using a Kruskal–Wallis rank sum test.

Using the software ImageJ (Rasband 1997), we measured the prosome length of the abundant *Calanus* spp. category whenever possible, i.e., when the prosome was aligned parallel to the image plane. The measurements were converted to micrometers using the known pixel size (1 pixel = 23.4 μm). The role of length on the depth distribution was analyzed using a generalized additive model (GAM). The best model was selected based on the Akaike Information Criteria (AIC, Akaike 1974), including models

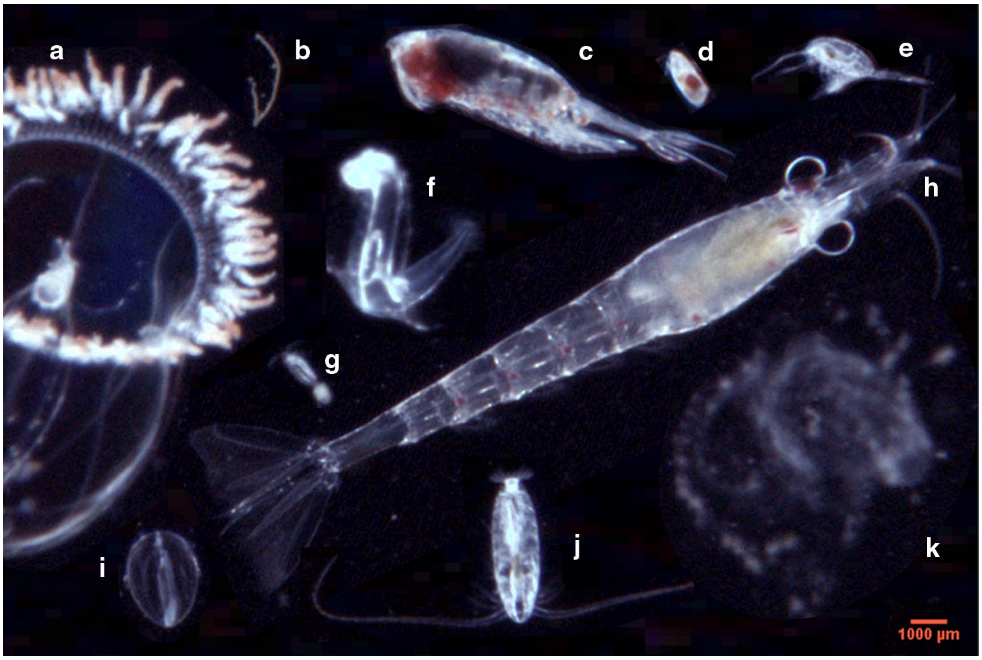

Fig. 2 A selection of images taken by the Video Plankton Recorder as part of the study. The collage includes a jellyfish (**a**), fecal pellet (**b**), *Paraeuchaeta* spp. without eggs (**c**), ostracod (**d**), *Metridia* spp. (**e**), chaetognath (**f**), *Pseudocalanus* spp. with an egg sac (**g**), euphausiid (**h**), ctenophore (**i**), *Calanus* spp. (**j**) and irregular marine snow (**k**)

Table 2 Abundance of groups observed, averaged for all four deployments of the VPR

	Abundance (m^{-3})		
	Mean	SD	Range
Fecal pellets	529.5	131.8	[254.5– 807.3]
Copepods	201.9	84.9	[98.7–480.2]
Calanus spp.	150.6	64.8	[85.8–371.4]
Unidentified Copepods	33.8	25.4	[5.7–96.0]
Ostracods	17.3	11.4	[0.0–33.7]
Irregular marine snow	14.0	12.2	[0.0–48.1]
Others	12.8	7.1	[4.1–32.5]
Metridia spp.	10.7	5.9	[4.1–22.1]
Euphausiids	7.8	6.2	[0.0–23.7]
Ctenophores	5.6	11.7	[0.0–45.0]
Jellyfish	5.5	5.7	[0.0–19.0]
Chaetognathas	4.1	4.6	[0.0–13.3]
Pseudocalanus with eggs	3.4	3.7	[0.0–11.0]
Paraeuchaeta without eggs	3.0	4.9	[0.0–16.4]
Crustacea	1.7	3.4	[0.0–10.4]
Paraeuchaeta with eggs	0.6	1.8	[0.0–5.5]
Amphipods	0.6	1.7	[0.0–4.4]

Standard deviation and range is also given

with “time of day” (day/nighttime) and “length” as fixed factors and “depth” as a dependent variable. We allowed for models having an interaction between depth and length and controlled for differences between sampling events (Day 1 and 2 versus Night 1a and 1b) by including tows as a random factor. The depth data were square-root transformed prior to the analysis to meet the normality requirement. We restricted our analyses to the copepod length interval for which we had both day and night data (1,621–5,722 µm). All statistical analyses were carried out in R v3.0.1 (R Core Team 2013) and with the package “mcgv” (Wood 2006) for general additive models.

Results

Physical conditions

The surface light intensity at noon on Day 1 (1,230 µmol photons s^{-1} m^{-2}) was almost three times lower than on Day 2 (3,400 µmol photons s^{-1} m^{-2}), due to cloud cover on Day 1 (Fig. 1). Underwater light intensity decreased exponentially with depth with a light attenuation coefficient of 0.26 m^{-1} (R^2 for the exponential model is 0.97). The relationships between depth, fluorescence and salinity were similar across the three sampling events (Fig. 3). As expected at this time of year, there was a marked peak in phytoplankton biomass in the upper 25–50 m (Fig. 3a).

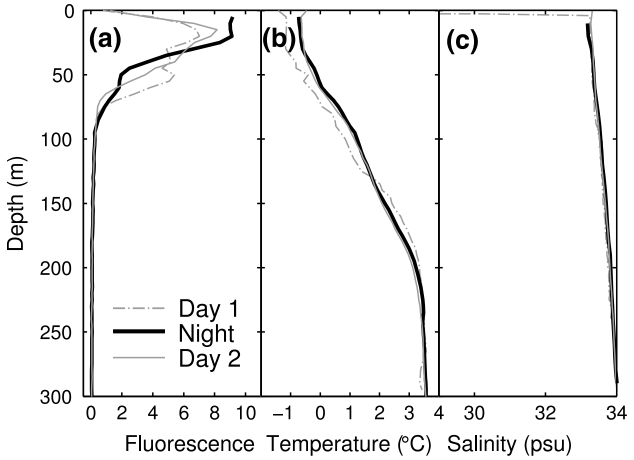

Fig. 3 Fluorescence (not calibrated) (**a**), temperature (**b**) and salinity (**c**) on the sampling site for *Day 1* (*dashed gray line*), the *night* (Night 1a and 1b combined, *black line*) and *Day 2* (*gray line*). The measurements were made by the CTD fitted on the VPR, except for the salinity on Day 1, when measurements were made by a stand-alone CTD. The cast of this stand-alone CTD has been made prior to the Day 1 VPR sampling

Water temperature increased with depth, from approximately −0.5 °C at the surface to almost 4.0 °C at 300 m depth (Fig. 3b). The thermocline was weak with an upper limit at ~50 m, while salinity increased gradually with depth (Fig. 3c).

Zooplankton community composition, abundances and migration

Fecal pellets were the most abundant particle type, and copepods were the most abundant animals consisting mostly of *Calanus* spp. (Table 2). Due to their size, fecal pellets most likely originated from euphausiids and could be used as a proxy for their behavior. However, for the rest of the analysis, we focused on the animals themselves and mostly on copepods. For each group, the exact depth and time for every category of animals observed can be found in the Appendix B (Fig. B.1 and Fig. B.2).

Depth distribution differed between the most abundant animal groups (Fig. 4). Some groups showed clear signs of DVM (e.g., euphausiids), whereas others stayed at depth both day and night (e.g., ostracods). As expected, the median depth of copepods was higher during night (88 m) than during day (103 m), although individual copepods were more widely distributed through the water column during night than during day. However, this variability decreased when considering only *Calanus* spp. or *Metridia* spp. *Calanus* spp. had a DVM signal and *Metridia* spp. did not. *Metridia* spp. were also found deeper in the water column both day and night. Overall, the depth distribution during day and night was significantly different between categories (ANOVA over *Calanus* spp., *Metridia* spp., ostracods and euphausiids: interaction time*species: $F_{(3,593)} = 5.2$, $p = 0.002$).

Copepods were present in most parts of the water column during both day and night, but aggregated at certain depth levels, i.e., around 60 m at Day 1, 40 and 70 m during the night and 100 m at day 2, as highlighted in Fig. 5a. Note that the abundance recorded by tows and casts is variable, probably due to patchiness (Fig. 5a; Table 2). The copepods mainly consisted of *Calanus* spp. (495 observations) and to a lesser extent of *Metridia* spp. (35 observations). *Metridia* spp. were found 62 m deeper (difference in the day/night weighted mean) than *Calanus* spp. Note that 110 copepod observations remained unidentified (blurry or incomplete pictures). Most of the ostracods were also found in deep water (>150 m) during both day and night (Fig. 5b). Euphausiids performed clear DVM and were approximately 100 m shallower during night (~20 m) than day (~150 m; Fig. 5c).

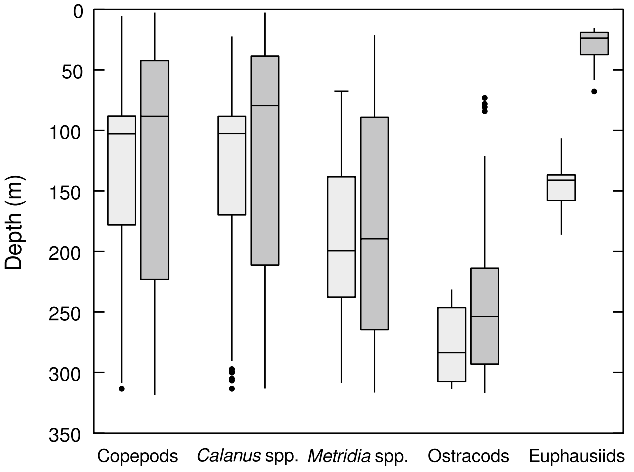

Fig. 4 *Boxplot* showing the depth distribution of groups with at least 25 observations, and separated by day (*light gray*) and night (*dark gray*). The *shaded boxes* represent the first and third quartile with the middle bar being the median. The end of the whiskers extends from the hinge to the lowest and highest value within a 1.5 inter-quartile range. The *dots* represents outliers

The depth below which 75 % of the copepods were found was 91 ± 4 m ($n = 6$) during day tows and 46 ± 10 m ($n = 10$) during night tows (Fig. 6). Copepods were thus significantly deeper at day than at night (ANOVA, $F_{(1,15)} = 82.9$, $p < 0.0001$). This is a result of a day-time surface avoidance behavior (Fig. 5). The single tow from Day 1 (at 65 m depth) differed from all the tows of Day 2 as highlighted in Fig. 6. This suggests that copepods were avoiding a larger depth layer during Day 2, when the light intensity at the surface was higher than during Day 1.

Disparity in the surface avoidance depth could be explained by the differences in surface light level between the two days. Instead of avoiding a fixed depth level, individuals avoided a fixed light intensity level, even if the comparison between the two days remains difficult due to the low sampling volume in Day 1 (Appendix C, Fig. C.1). The copepods median light exposure during day (7.7×10^{-9} μmol photon s^{-1} m^{-2}) was close to the one at night (1.1×10^{-9} μmol photon $s^{-1}m^{-2}$), suggesting that the copepods select day- and night-time habitats with similar light levels (order of 10^{-9} μmol photon $s^{-1}m^{-2}$; Fig. 7).

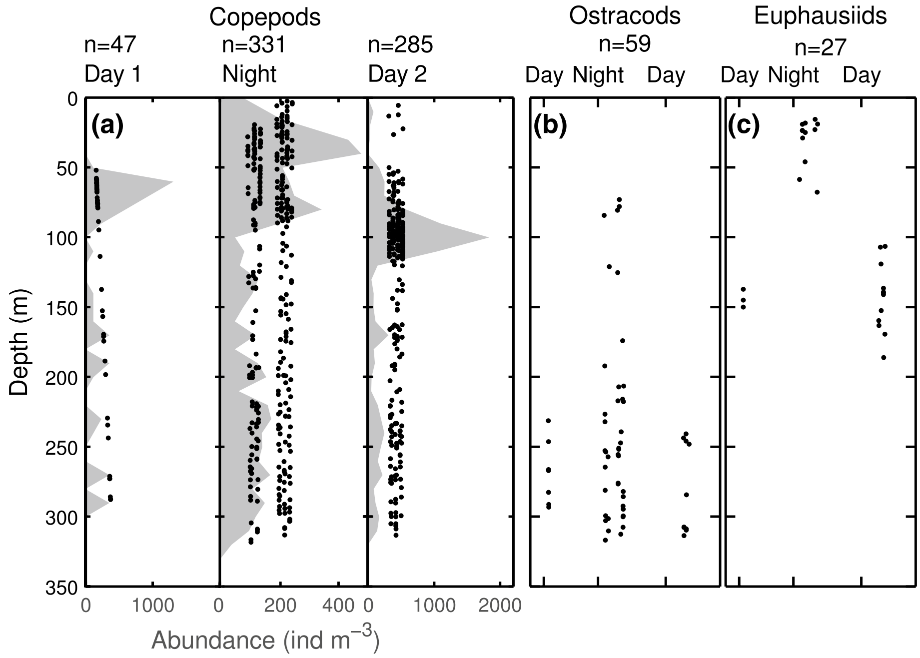

Fig. 5 Position (*dots*) of all copepods (**a**), ostracods (**b**) and euphausiids (**c**) by depth and time (Day 1, Night 1a and 1b combined, and Day 2). *Each dot* represents an individual observation. Please note the different scales of the *x*-axes between the panels of **a**. For the copepods, abundance in 10 m depth bins is also illustrated (*gray shaded areas*)

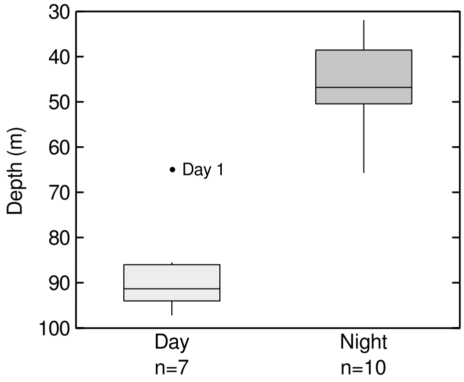

Fig. 6 *Boxplot* of the depth below which 75 % of the copepods where found per sampling tows. This represents the surface depth layer that most of the population avoid during day and night. The outlier at 65 m during the Day is the sampling made during Day 1, while the rest of the *Day box* represent the *six tows* sampled during Day 2. The *shaded boxes* represent the first and third quartile with the middle bar being the median. The end of the whiskers extends from the hinge to the lowest and highest value within a 1.5 inter-quartile range

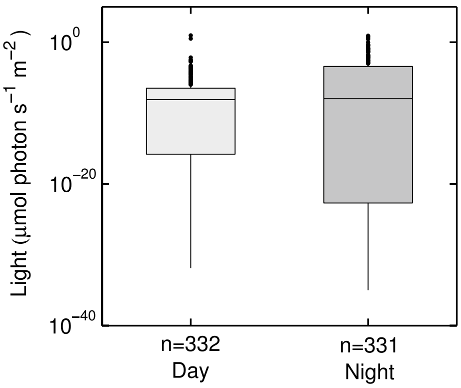

Fig. 7 *Boxplot* of the light exposure of copepods during Day and Night. Light is a function of the copepods' precise depth and time when observed by a Video Plankton Recorder. For category "*Day*," Day 1 and Day 2 are combined. For category "*Night*," Night 1a and Night 1b are combined. For further explanation on the calculation refer to the Materials and methods section. The *shaded boxes* represent the first and third quartile with the middle bar being the median. The end of the whiskers extends from the hinge to the lowest and highest value within a 1.5 inter-quartile range. The *dots* represents outliers

The light exposure during day and night was statistically similar (Kruskal–Wallis rank sum test: $\chi^2_1 = 0.1481$, p value $= 0.70$).

Length versus depth distribution in the *Calanus* group

Calanus spp. body size influenced both depth position and the extent of DVM. Smaller individuals performed extensive DVM, while individuals larger than 3,000 µm stayed in deep water (~120 m). The GAM with the highest explanatory power was the one allowing for two different smooth terms for day and night and included time of the day as a fixed factor, cf. Appendix D, Table D.1. The day and night smooth terms were significant, and the intercept of night was significantly different from the intercept of day. Figure 8 shows the model fit for both day and night. Although the model only explained 21.1 % of the variation, smaller *Calanus* spp. showed classical DVM behavior. Larger *Calanus* spp. were not observed performing such a clear upward movement during night, although there are fewer data points for large individuals (only 42 observations of individuals between 4,400 and 5,722 µm prosome length, which could be assumed to be *C. hyperboreus*).

Discussion

We have shown a large diversity of DVM behavior that can be found in the zooplankton community of a sub-Arctic shelf ecosystem. Specifically, euphausiids displayed clear DVM, ostracods stayed at depth and copepods performed DVM but with some variability, including state dependence. We observed a clear surface-water avoidance by copepods during daytime but a wide depth-range below this upper zone. The extent of the surface zone that copepods avoided seemed to depend on surface light intensity. The migration of the most abundant copepod genus (*Calanus* spp.) was size dependent, with smaller individuals performing clear migrations and larger individuals staying mostly at depth.

DVM strategies of zooplankton in Disko Bay

Zooplankton adopt DVM in the presence of food and when light levels are sufficient to allow visual predators to hunt effectively (Pearre 2003). This is the case during our study as the peak of fluorescence was found at 25–50 m depth, and fish (not studied by us) can be assumed to be an abundant predator on copepods in the system (e.g., Arctic cod *Boreogadus saida*, sand lance *Ammodytes* spp. and Atlantic poacher *Leptagonus decagonus*, Munk et al. 2000; Hamilton et al. 2003; Stenberg 2007). In Disko Bay, light levels at the surface were higher on Day 2 than Day 1 of sampling and the resulting elevated risk at shallow depth may partially explain the deeper depth distribution of the copepods on Day 2 compared with Day 1. Previous observations have also suggested that light is probably the most important factor controlling daily migration, with animals responding to intensity changes (Clarke 1933, 1934). By avoiding the topmost part of the water column, the copepods were reducing the risk of visual predation (light) but were

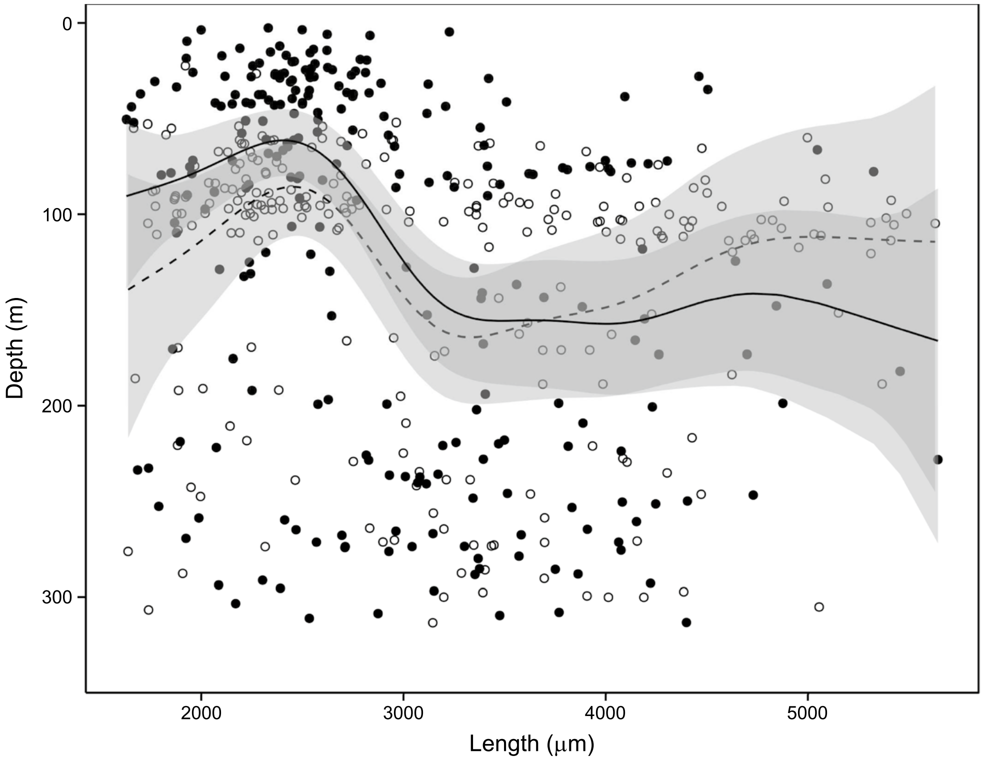

Fig. 8 Prosome length of *Calanus* spp. during day (*open symbols*) and night (*filled symbols*). The fitted general additive model is shown by *dashed line* for the day, and in *whole line* for the night, with their standard deviations (*gray shading*)

consequently some distance away from the phytoplankton peak concentrations. This is in accordance with the predator avoidance hypothesis suggesting that DVM is a beneficial strategy for zooplankton only when reduced predation risk counterbalances lost feeding opportunities. For example, using a game theory approach played between grazers and visual predators, Sainmont et al. (2013) showed that DVM is an emergent strategy when the losses due to predation are higher than the gain provided by extra feeding during daylight hours, which is also found in our study.

Among the *Calanus* spp., we found that small individuals performed DVM with a wide range of variability. In addition to size, the variability in the depth distribution could potentially be explained by other individual states, for example gut fullness, energy reserves or differences in life-history strategies between the three *Calanus* species (Hays et al. 2001). For instance, the five copepods found at shallow depth during day could be individuals risking fast ascent to the surface to feed in the phytoplankton layer and sink while digesting as suggested in other studies (Lopez and Huntley 1995; Pearre 2003) during both day and night, but with a lower frequency during daytime. Furthermore, some copepods were found higher in the water column than the peak of the phytoplankton bloom, which seems sub-optimal as it is more risky (higher light level). However, competition for food at the peak food concentration is likely to be high, and copepods may therefore disperse over the phytoplankton layer to avoid intra-specific competition for food (cf. ideal free distribution, Fretwell 1972). Individual dispersion could also be a strategy against tactile predators (such as chaetognaths, amphipods and ctenophores that were observed in this study), or filter-feeding whales, which capture their prey during the day as well as night (Ohman 1990; Hays 2003). Such spatial distributions can easily be observed with VPRs, and we suggest that further studies should focus on the gut fullness and lipid sac variability for a deeper understanding of these observations.

DVM was not evident for larger *Calanus* spp. individuals that generally were found deeper than smaller individuals (see also Wiebe et al. 1992; De Robertis et al. 2000). Thus, food availability in the surface layers is not affecting their depth distribution. The size range of these copepods is wide with copepodites and adults *C. finmarchicus* and *C. glacialis* ranging between 1,900 and 4,400 µm in prosome length, while the larger *C. hyperboreus* can grow up to 7,400 µm in prosome length (Frost 1974; Nielsen and Hansen 1995; Hirche 1997; Madsen et al. 2001). Small individuals of the *Calanus* spp. group sampled can therefore be assumed to be copepodite stages or adult *C. finmarchicus*, *C. glacialis* or young copepodite stage of *C. hyperboreus*, while individuals larger than 4.5 mm could only be late copepodite stages or adult *C. hyperboreus*. Large size individuals are more easily detected by visual predators and because they generally have a longer life span, they have more to lose in terms of survival (Pasternak et al. 2001). They could therefore benefit from the safety of a deeper habitat. Furthermore, *C. hyperboreus* is a capital breeder (cf. Varpe et al. 2009) that spawns in winter and early spring (Conover et al. 1988; Hirche 1997; Swalethorp et al. 2011). An essential part of their life history is thus to accumulate and store reserves during the phytoplankton bloom period, but also to survive until the next winter (e.g., Falk-Petersen et al. 2009; Varpe 2012). In addition, they may encounter sufficient feeding opportunities at depth by foraging on detritus or marine snow (Alldredge and Silver 1988; Hansen et al. 1996; Möller et al. 2012). An income breeding species with a shorter life cycle, such as *C. finmarchicus* (Conover 1988), is more dependent on current food intake. *C. finmarchicus* may benefit from a risk-prone behavior to achieve high growth and egg production rates; thus, DVM is a good compromise between feeding and predator avoidance.

Other species recorded by the VPR included euphausiids which are larger in size and have a greater swimming capability than copepods. Euphausiids had a clear DVM signal, with all individuals, found within distinct depth intervals at both day and night. No euphausiids were found below 70 m during night or above 100 m during the day. Our findings correspond well with previous studies on DVM of euphausiids (e.g., Onsrud and Kaartvedt 1998; Tarling et al. 2010). Due to their large size, euphausiids are highly vulnerable to visual predators during daylight hours, and therefore, it is not surprising to see all individuals avoiding the surface waters during daytime. During nighttime, however, their position matched with the phytoplankton bloom layer, adding an inter-specific component to the competition for food experienced by copepods (see above).

Few comparative data on vertical distribution of ostracods exist and none for Disko Bay or western Greenland. Ostracods observed in Disko Bay were located deep in the water column during the day (220–300 m), and at night, they extended their vertical distribution to a shallower depth (60–300 m). Studies from another coastal Arctic area, the waters around Svalbard, also suggest that ostracods live at depth (Baczewska et al. 2012).

Advantages of VPR for the study of DVM

One of the advantages of utilizing a VPR for studying pelagic ecology is the ability to combine concurrent measurements of environmental data (fluorescence, salinity, temperature, depth) with the precise position of individuals at any given time of sampling. This information is crucial when investigating both inter-specific and intra-specific behavioral strategies. During day 2, all copepods were found below 50 m, except for five individuals which were observed at shallower depths (Fig. 5), feeding on the phytoplankton bloom (guts could be visually identified on the images). The VPR also makes it possible to study the fine-scale spatial position of individuals, which is impossible when individuals are integrated over 50 m or longer distances as is the case with many net-sampling systems. Our application of a GAM on day and night depth positions with prosome length is only possible when precise data are available. As pointed out by Pearre (2003), information of this kind is essential if one wants to understand the causes and effects of DVM. Furthermore, the pictures taken are of good quality and properties of individuals, such as size and coloration can in many cases be extracted (e.g., Baumgartner et al. 2011). In this study, we focused on copepods, and from most of the images, we could identify genus and measure prosome length. Although our focus was not on *Pseudocalanus* spp., due to their low abundance, we could see whether or not they were carrying eggs, while they tend to lose them during net tows (Corkett and McLaren 1979). We could also see green colored algae filled guts and lipid stores in the copepods. Finally, we could calculate the amount of light individuals were exposed to, using the precise depth position and time of sampling (e.g., Appendix C, Fig. C.1 and Fig. C.2). None of the *Calanus* spp. were exposed to a light level higher than 1 μmol photon s^{-1} m^{-2}. The role of light and water clarity for copepod behavior and distributions remains understudied (as suggested by Dupont and Aksnes 2012), and we suggest that further studies on DVM more explicitly incorporate individual light exposure (such as done in Fig. 7 and Appendix C) as this is often more relevant than depth per se when understanding risk-taking and predator avoidance.

Conclusion

This study revealed the wide variability of daily migration patterns among and within groups of plankton, as resolved to the fine-scale spatial position of individuals by the VPR. The results are in agreement with the hypothesis that DVM is an adaptive behavior which increases survival by feeding at night, and avoiding surface waters at day. Our findings suggest that smaller (and thus often younger) individuals exhibit a more risk-prone behavior prioritizing food intake and growth rather than safety. On the other hand, larger individuals may benefit from safer behavior, staying at depth and potentially switching food sources. Thanks to fine-scale spatial resolution, VPR techniques have great potential in the study of individual behavior. Individual behavior has marked fitness consequences (through growth, mortality and fecundity), and precise observations of individual behavior combined with individual state and environmental conditions are valuable parameters for testing model predictions on individual behavior (e.g., Fiksen and Carlotti 1998). VPRs allow small-scale input data (e.g., depth, individual size, light exposure) that are currently lacking and hard to obtain using traditional sampling methods as net-sampling or acoustic surveys.

Acknowledgments The data have been collected during the PhD course sponsored by Nordforsk "Fate of the Arctic spring bloom" between April 25 to May 7, 2012, at the Arctic Station, Qeqertarsuaq, Greenland. A. Gislason and Ø. Varpe wish to thank Torkel G. Nielsen for the opportunity to teach during the course and to run a DVM project with one of the student groups, and we all thank him for organizing the course and giving us the opportunity to do this interesting study. We wish to thank the Arctic Station and the Geographical and Geological Institute from Copenhagen University for sharing their solar irradiance data collected at the Arctic station. J. Sainmont and Ø. Varpe also thank Mark Ohman for interesting discussions around an earlier draft of this work and André W. Visser for his support and advice. We thank Mark Payne for statistical advice and Dag L. Aksnes for valuable comments on a previous version of this manuscript. Ø. Varpe was supported by The Research Council of Norway through project CircA (214271/F20). This work was supported by the Greenland Climate Research Centre and the Centre for Ocean Life, a VKR center of excellence funded by the Villum foundation.

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