Caught in broad daylight: Topographic constraints of zooplankton depth distributions

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Abstract

For visual predators, sufficient light is critical for prey detection and capture. Because light decays exponentially with depth in aquatic systems, vertical movement has become a widespread strategy among zooplankton for avoiding visual predation. However, topographical features such as seamounts have been shown to block their descent, trapping them in illuminated waters with potential feeding benefits for visually searching fish. Here, we present an extensive and previously unpublished dataset on the vertical distribution of zooplankton in the topographically rugged Barents Sea, a continental shelf region hosting some of the largest fish stocks in the world. By modeling the ambient light exposure of zooplankton in relation to the bathymetry, we find support for a similar blockage mechanism. During daytime, zooplankton are exposed to four orders of magnitude more light above shallow banks than in the deeper water surrounding the banks. We show that zooplankton depth distributions are highly related to zooplankton size and that the bottom constrains the vertical distributions. Consequently, zooplankton remain in the planktivores' visual feeding habitat over the banks but not in deeper areas. Bottom topography and light absorbance are significant determinants of the seascape ecology across continental shelves with heterogeneous bathymetry.

Space is the stage for ecology. Spatial structures and gradients form the landscape where organisms compete, predate and reproduce. In terrestrial systems, the study of ecology with spatial structures and patterns is known as landscape ecology, while the concept of seascape ecology is still debated (Manderson 2016; Bell and Furman 2017; Manderson 2017). How do spatial gradients in the environment, such as fading light, seamounts, or bottom depth and topography, structure marine pelagic communities of small organisms drifting with the currents?

Interactions between vertically migrating pelagic species and ocean bathymetry may influence ecosystem structures. Trueman et al. (2014) demonstrated that the diel vertical migrating (DVM) community is accessible to bottom feeding fish only at depths < 1000 m. Demersal fish that consume prey above the seafloor (benthopelagic feeders) therefore have a competitive advantage at greater depths and proliferate between 1000 and 1800 m. Interactions between the bathymetry and vertically migrating prey may be important for pelagic feeding planktivores as well. Visual detection of individual prey is the common foraging mode in planktivorous fish (Eggers 1977), and the prey detection distance for a fish is sensitive to ambient light levels (Aksnes and Utne 1997). As light decreases exponentially in water, the vertical position of zooplankton prey is important for their foraging success. Zooplankton display a range of vertical migration strategies related to diurnal (Bollens and Frost 1991; Ohman and Romagnan 2016) and seasonal (Bandara et al. 2016) rhythms, which is an evolutionary adaptation to the trade-off between growth and survival in dynamic environments (Pearre 2003; Bandara et al. 2018). Zooplankton over shallow banks and shelves are prevented from migrating into deeper and darker waters, which increases their vulnerability to predation from fish. Advection of zooplankton onto seamounts and banks, where they are trapped and unable to seek safety in deep water, has been termed "the topographic blockage mechanism" (Isaacs and Schwartzlose 1965; Genin 2004) and is possibly an important driver of fish habitat choice.

Fish aggregation over bottom topographies such as seamounts, shelves, and banks can be linked to increased prey availability due to either enhanced productivity caused by upwelling of nutrients (Rogers 1994) or horizontal advection of resources from surrounding areas. Based on the topographic blockage mechanism, we hypothesize that the bathymetry

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Additional Supporting Information may be found in the online version of this article.

influences foraging opportunities for fish that feed on vertically migrating zooplankton in the pelagic because of topographic constraints on zooplankton depth distributions. Previous studies have demonstrated topographic blockage of zooplankton performing DVM (reviewed in Genin [2004]), where individuals ascending to surface layers at night are advected onto shallow topographies that block their morning descent to deeper waters. Seasonal migraters such as *Calanus* spp., the key herbivores in North-Atlantic ecosystems (Melle et al. 2014), will also be blocked by the topography if occupying shallow areas in periods of diapause (e.g., Krumhansl et al. 2018). Survival of *Calanus* spp. during overwintering has earlier been related to access darkness for avoiding predation (Kaartvedt 1996; Dale et al. 1999).

Our study area, the Barents Sea, is a relatively deep shelf sea (bottom depth up to 500 m) situated on the Arctic continental shelf adjacent to the deep Norwegian Sea to the west. Atlantic water flows through the system from the shelf edge in the southwest to the northern Kara Sea and the Arctic Ocean in the northeast (Smedsrud et al. 2013). We use an extensive dataset on the vertical distribution of zooplankton in three size classes, to examine whether their depth distributions are constrained by the bathymetry and evaluate if this improves the foraging potential for visually searching planktivorous fish. Planktivorous fish are size selective (Brooks and Dodson 1965), and large-sized prey are easier to see (Eggers 1977; Aksnes and Giske 1993) and require deeper habitats to avoid visual predators (e.g., Ohman and Romagnan 2016). We therefore expect pronounced differences between the size classes and predict that the bathymetry limits the depth distribution particularly for the large zooplankton in our data. Water clarity alters the vertical light gradient, and we expect to find zooplankton deeper in clear relative to less transparent water (Dupont and Aksnes 2012; Ohman and Romagnan 2016). The ambient light exposure of prey is important for the foraging efficiency of planktivorous fish—and here we quantify zooplankton light exposure from vertical distributions, vertical light attenuation and the bathymetry.

Materials and methods

Data

The Barents Sea is a large marine ecosystem (1.6×10^6 km^2) on the Arctic continental shelf and hosts economically and ecologically important fish stocks (Gjøsæter 1998; Eriksen et al. 2017a). It is monitored extensively each year through a joint Norwegian/Russian monitoring program by the Institute of Marine Research (IMR) and Knipovich Polar Research Institute of Marine Fisheries and Oceanography (Eriksen et al. 2018). The annual ecosystem survey takes place in autumn and covers key physical and biological components of the ecosystem using different sampling equipment. Our study is based on zooplankton data from Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) sampling gear (Wiebe et al. 1985), with 1 m^2 opening and 180 μm mesh size. The samples have

been collected at Norwegian vessels during ecosystem surveys in the period 1992–2016 and span day of year 214–280 (early August to early October). We also used salinity and chlorophyll *a* (Chl *a*) data from the same cruises and sampling stations as the zooplankton data (see below).

The MOCNESS samples zooplankton in up to eight depth strata in the water column. Samples have routinely been split in two, with one half used to determine dry weight biomass (g dw m^{-3}) in three size fractions using mesh gauzes of 2000, 1000, and 180 μm (Melle et al. 2004). Krill have been measured separately over the period and are not considered in this study, while amphipods and chaetognaths have been measured separately since 2008 and may comprise a smaller part of the > 2000 μm size fraction in samples from before 2008. Copepods, particularly of the genus *Calanus*, dominate the mesozooplankton (> 0.2 mm) biomass in the Barents Sea (Aarflot et al. 2017) and likely comprise the larger part of the data analyzed here.

Zooplankton-weighted mean depth

Only samples covering > 75% of the water column were considered suitable for our purpose of determining zooplankton depth distributions and included in the analyses, and the upper and lower depth strata were extrapolated to the surface and bottom. Similar to Daase et al. (2008), we estimated the weighted mean depth (*WMD*, m) and the standard deviation (*SD*, m), which is a measure of the compactness, of the depth distribution (Manly 1977) for each sample and size fraction (j):

$$WMD_j = \sum_{i=1}^{k} \frac{\Delta Z_i b_{j,i} Z_{m,i}}{B_j} \tag{1}$$

$$SD_j = \sqrt{\sum_{i=1}^{k} \frac{\Delta Z_i b_{j,i} Z_{m,i}^2}{B_j} - WMD_j^2} \tag{2}$$

Here, ΔZ_i is the thickness (m) and $b_{j,i}$ the zooplankton biomass (g dw m^{-3}) of size class j in stratum *i*, $Z_{m,i}$ is the stratum mean depth, k is the total number of strata sampled, and B_j is the depth integrated biomass (g dw m^{-2}) of the size class ($\sum_{i=1}^{k} \Delta Z_i b_{j,i}$). The size classes will hereafter be denoted L, M, and S, referring to the large (> 2000 μm), intermediate (1000–2000 μm), and small (180–1000 μm) size fraction. Surface irradiance was modeled with an algorithm from the HYbrid Coordinate Ocean model (HYCOM) (Bleck 2002) based on sampling time (day of year and hour at the onset of sampling) and latitude assuming 50% loss at and through the surface, and we sorted samples as day/night presuming day = surface irradiance > 1 μmol m^{-2} s^{-1}.

Light attenuation

Light absorption and scattering determine light attenuation and how deep surface irradiance penetrates the water column. In oceanic water, attenuation is largely influenced by the

Table 1. Results from regression analyses of daytime occurrences, with zooplankton WMD (WMD_j, m) and distribution compactness (SD_j, m) as functions of bottom depth (Z_b, m) and optical depth (K^{-1}, m). Both Z_b and K^{-1} were significant predictors for WMD_j ($p < 0.001$ and $p = 0.004$, respectively), but only Z_b was significant for SD_j ($p < 0.001$). The size classes (j = L, M, and S) had significantly different slopes for WMD_j and SD_j as functions of Z_b ($p < 0.001$ for both), whereas slopes were not significantly different between the size classes for WMD_j as a function of K^{-1} (not shown). The table shows parameters with 95% confidence levels (CL), degrees of freedom (df), and variance explained (R^2). Thirteen percentage of the stations lacked Chl a and salinity measurements used to approximate K (hence different df in the two models), and there were missing values for the large, intermediate, and small size fraction in $n = 8$, 2, and 2 samples, respectively.

	a_j (intercept)	b_j (Z_b)	Lower CL	Upper CL	c (K^{-1})	Lower CL	Upper CL	df	R^2
Weighted mean depth ($WMD_j = a_j + b_j Z_b + c K^{-1}$)									
Large (L)	−40.1	0.75	0.70	0.79	n.s.				
Intermediate (M)	−1.8	0.59	0.55	0.63	n.s.				
Small (S)	−2.7	0.40	0.36	0.44	n.s.				
All					1.13	0.38	1.88	1563	0.657
Distribution compactness ($SD_j = a_j + b_j Z_b + c K^{-1}$)									
Large (L)	−4.5	0.23	0.22	0.25	n.s.				
Intermediate (M)	−16.4	0.29	0.28	0.31	n.s.				
Small (S)	−10.9	0.32	0.31	0.34	n.s.				
All					n.s.	n.s.	n.s.	1794	0.663

n.s., not significant.

presence of algae (Morel and Maritorena 2001) and chromophoric dissolved organic matter (CDOM) (Bricaud et al. 1981). Many studies have shown that the CDOM concentration of marine waters is a strong function of the observed freshwater fraction or its salinity (reviewed by Nelson and Siegel 2013). This is particularly true for the Baltic Sea, the North Sea, and the Norwegian Coastal Water (NCW), which contain large amounts of CDOM of terrestrial origin (Højerslev et al. 1996; Stedmon et al. 2000; Kowalczuk et al. 2005; Aksnes 2015). NCW is transported into the Barents Sea with the Norwegian Coastal Current; and here, we have used data on Chl a and salinity from CTD casts at the MOCNESS stations, to approximate the water column light attenuation (K, m^{-1}) where the zooplankton was sampled (note that 13% of the stations lacked Chl a and salinity measurements).

Chl a has regularly been measured down to 100 m depth in the Barents Sea, though some samples had deeper measurements (Supporting Information Fig. S1). We used data from 10 m depth intervals between 0–50 m, 25 m intervals between 50–150 m, and additional 50 m intervals below 150 m when data were available. Chl a and salinity were interpolated between the depth intervals, and light attenuation was approximated down to the maximum depth where we had measurements for both variables. Few Chl a measurements below 100 m might have led to an underestimation of light attenuation at deeper stations.

Light attenuation by algae (K_{chl}) was here approximated for 440 nm wavelength, using the relationship of Morel and Maritorena (2001):

$$K_{Chl}(440) = 0.10963(Chl)^{0.67175} \quad (3)$$

Light attenuation by CDOM (K_{CDOM}) was estimated from the empirical relationship for nonchlorophyll light attenuation in mixtures of North Atlantic Water and NCW given by Aksnes (2015):

$$K_{CDOM}(440) = 1.47 - 0.041S \quad (4)$$

where S is salinity. Total light attenuation (K) is the sum of Eqs. 3 and 4.

It is uncertain how well Eq. 4 relates to absorption by CDOM in the Barents Sea, as the freshwater component in this water also has other origins (melting of sea ice) than the water masses studied by Aksnes (2015). We therefore tested the effect of both total K and K_{chl} as predictors for the zooplankton WMD (see Statistics section below).

Statistics

Our main focus was samples collected during daylight ($n = 604$), when fish are able to detect their prey by vision. Resembling Dupont and Aksnes (2012), we used linear regression techniques to evaluate the WMD for zooplankton size class j as a function of bottom depth (Z_b) and optical depth (K^{-1}) at the sampling station:

$$WMD_j = a_j + b_j Z_b + c_j K^{-1} \quad (5)$$

We used ANCOVA to estimate the coefficients a_j, b_j, and c_j and ANOVA to test whether the coefficients were significantly different between the size classes. Taking SD_j instead of WMD_j as response variable, we also applied Eq. 5 to assess variation
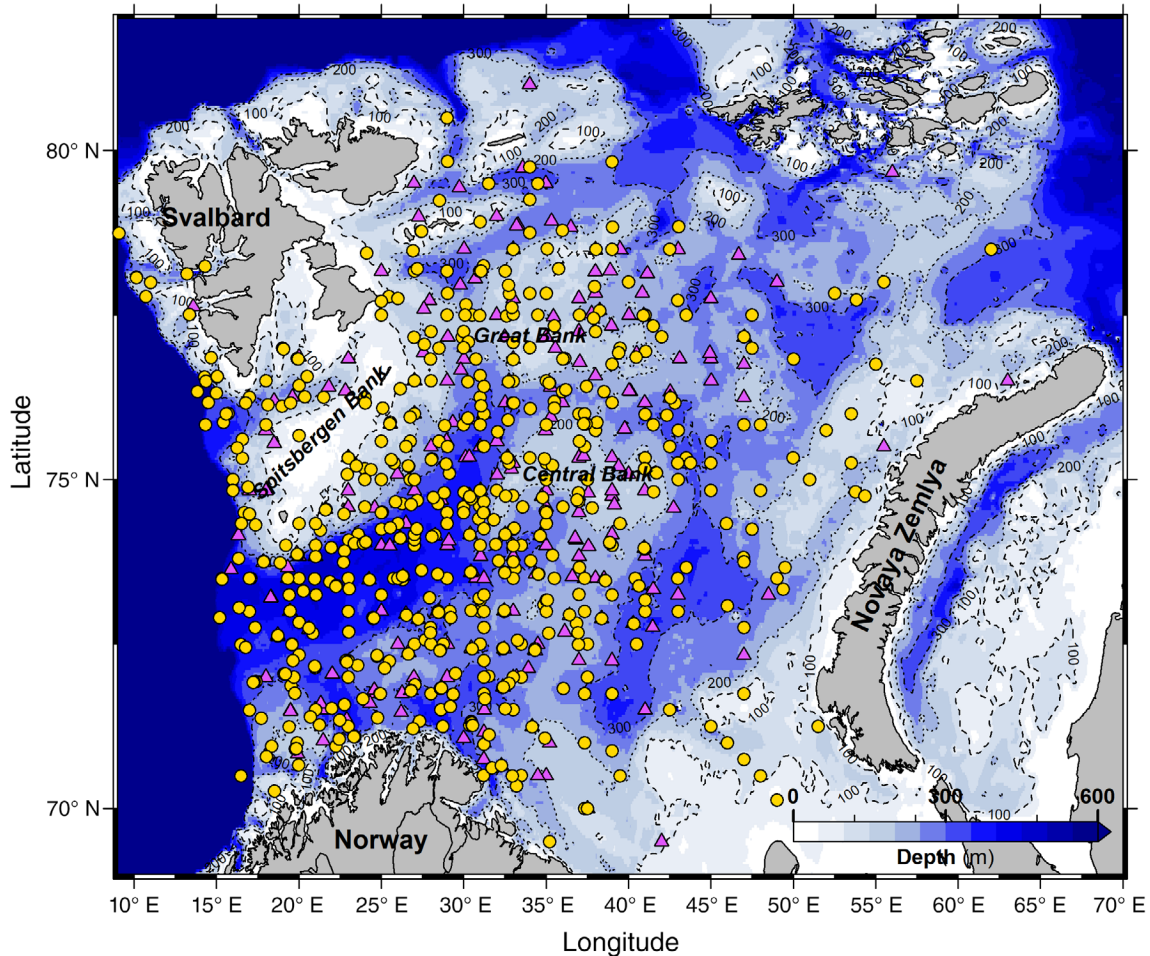
Fig. 1. Barents Sea study area and distribution of samples from MOCNESS sampling gear, providing data on the vertical distribution of zooplankton in the period 1992–2016. The map shows samples collected during daylight (yellow, $n = 604$) and at night (pink, $n = 258$), based on our definition of day vs. night described in Materials and Methods section. Bathymetry data from the ETOPO1 database (1 -min resolution) are plotted on a darkening blue scale for increasing bottom depth. Major banks with depth < 200 m are labeled in the map.

in the compactness of zooplankton distributions with bottom depth and optical depth.

In addition, we analyzed the complete dataset (i.e., including samples collected at night, $n = 258$) to check for a diel migration pattern in the data, or if *WMD* changed between day and night. These analyses were run individually for each size class, using day/night (l) as categorical covariate:

$$WMD_{j,l} = a_{j,l} + b_{j,l} Z_b \qquad (6)$$

All analyses and figures were made in the statistical software package R version 3.4.0 (R Core Team 2016).

Expectations from topographic constraints of daytime occurrences

We hypothesized that zooplankton have deep daytime distributions to avoid depths where planktivorous fish can forage efficiently by sight and that the bathymetry limits

their preferred depth distribution without a bottom constraint. This implies the expectation of a positive statistical effect of bottom depth on the weighted mean zooplankton depth. Given that larger zooplankton need to go deeper than smaller zooplankton to reduce their visibility to fish, we expected a significant interaction between Z_b and j and that $b_L > b_M > b_S$. Note that if all zooplankton biomass is caught in the deepest stratum, WMD_j is equal to the mean depth Z_m of that stratum (Eq. 1) rather than to the bottom depth Z_b, so the coefficient b_j of Eq. 5 becomes less than 1. Therefore, the closer b_j is to 1, the stronger the effect of Z_b on WMD_j. Less transparent water (high K) allow zooplankton to remain closer to the surface at the same light exposure (Ohman and Romagnan 2016). We therefore expected the *WMD* to be deeper in clear water and to find a positive effect of optical depth (K^{-1}) on WMD_j (c_j of Eq. 5 larger than 0). Yet, if distributions are limited by the bathymetry, the effect of K should be small in areas where

Table 2. Results from linear regressions evaluating WMD_j and SD_j as functions of Z_b in day and night samples (l = day or night), j indicates size class (L, M, and S). The table shows parameters with 95% confidence levels (CL), degrees of freedom (df), and variance explained (R^2).

		a_j (intercept)	b_j (Z_b)	Lower CL	Upper CL	df	R^2
Weighted mean depth: $WMD_{j,l} = a_{j,l} + b_{j,l}Z_b$							
Large (L)	Day	−29.8	0.73	0.69	0.77	850*	0.69
	Night	−40.5	0.75	0.68	0.80		
Intermediate (M)[†]	Day	20.9	0.55	0.51	0.59	856[‡]	0.56
	Night	−13.7	0.66	0.60	0.73		
Small (S)[†]	Day	18.8	0.36	0.32	0.40	856[‡]	0.41
	Night	−17.1	0.52	0.45	0.58		
Distribution compactness: $SD_{j,l} = a_{j,l} + b_{j,l}Z_b$							
Large (L)[§]	Day	−4.5	0.23	0.21	0.25	850*	0.53
	Night	−7.7	0.27	0.24	0.3		
Intermediate (M)	Day	−16.4	0.29	0.28	0.31	856[‡]	0.63
	Night	−15.1	0.31	0.28	0.34		
Small (S)	Day	−10.9	0.32	0.31	0.34	856[‡]	0.77
	Night	−15.1	0.35	0.33	0.37		

[*] Missing values in eight samples.
[†] Significant difference in slopes for day and night ($p < 0.01$).
[‡] Missing values in two samples.
[§] Significant difference in slopes for day and night ($p = 0.02$).

the zooplankton are forced to occupy depths with unfavorable light levels despite low water clarity.

Results

Bottom constrains zooplankton daytime depth distributions

Bottom depth had a significant effect on the zooplankton WMD ($p < 0.001$), and slopes (b_j) were different between the size classes ($p < 0.001$). The slopes confirmed our prior expectation of $b_L > b_M > b_S$ (Table 1), that is, that larger zooplankton are more constrained by topography than smaller zooplankton. Large zooplankton resided primarily close to the bottom, with a strong effect of bottom depth on WMD_L ($b_L = 0.75$; *see* Table 1; Fig. 2a). Including only samples collected after the change in sampling procedures in 2008 (see *Data* above) did not change this finding. Intermediate-sized zooplankton (j = M) also had the weight of their distribution close to the bottom in a large fraction of the observations (Fig. 2a) and a strong effect of bottom depth on WMD_M ($b_M = 0.59$). The small size class (j = S) had the weight of their distribution closer to the surface (Fig. 2a), although distributions were deeper in deeper areas also for this size class ($b_S = 0.40$). The vertical extension of the zooplankton distributions (as given by SD_j) increased with bottom depth ($p < 0.001$), that is, distributions were more compact in areas where the bathymetry was limiting the depth distributions. Slopes were significantly different between the size classes ($p < 0.001$), and the small size class had the strongest statistical effect of bottom depth on SD (Table 1).

Large, intermediate, and small zooplankton above deep topographies experienced several orders of magnitude reduction in light exposure compared to zooplankton at shallow banks (Fig. 2b). In deep regions, large zooplankton had about 10,000 times lower light exposure than small zooplankton. The ecological consequence of this difference in light exposure is that a hypothetical fish can visually detect a large prey at about 20 cm distance at 100 m, but hardly at all below 300 m (Fig. 2c). The prey detection distance is the radius of the visual sphere and consequently scales to the power of two in terms of how much water a fish can scan for prey per time unit (*see* Supporting Information) (Eggers 1977). The prey encounter rate for the fish is therefore about 25 (proportional to 5^2) and 400 (proportional to 20^2) times larger for the small and large zooplankton, respectively, above (100 m) and off a bank edge (300 m) for any given prey concentration at the WMD of the zooplankton distributions.

Water clarity is a second-order factor in the Barents Sea

The optical depth, given as the reciprocal water column light attenuation (K^{-1}), had a significant, positive effect on the zooplankton WMD ($p = 0.004$), that is, the zooplankton had deeper distributions in clear water, but it did not significantly affect distribution compactness (SD) (Table 1). The effect of K^{-1} (c) was not significantly different between the size classes (j), although only the small size class had in fact a confidence interval for c excluding zero. We therefore ran individual analyses for the WMD of each size class (Eq. 5) and
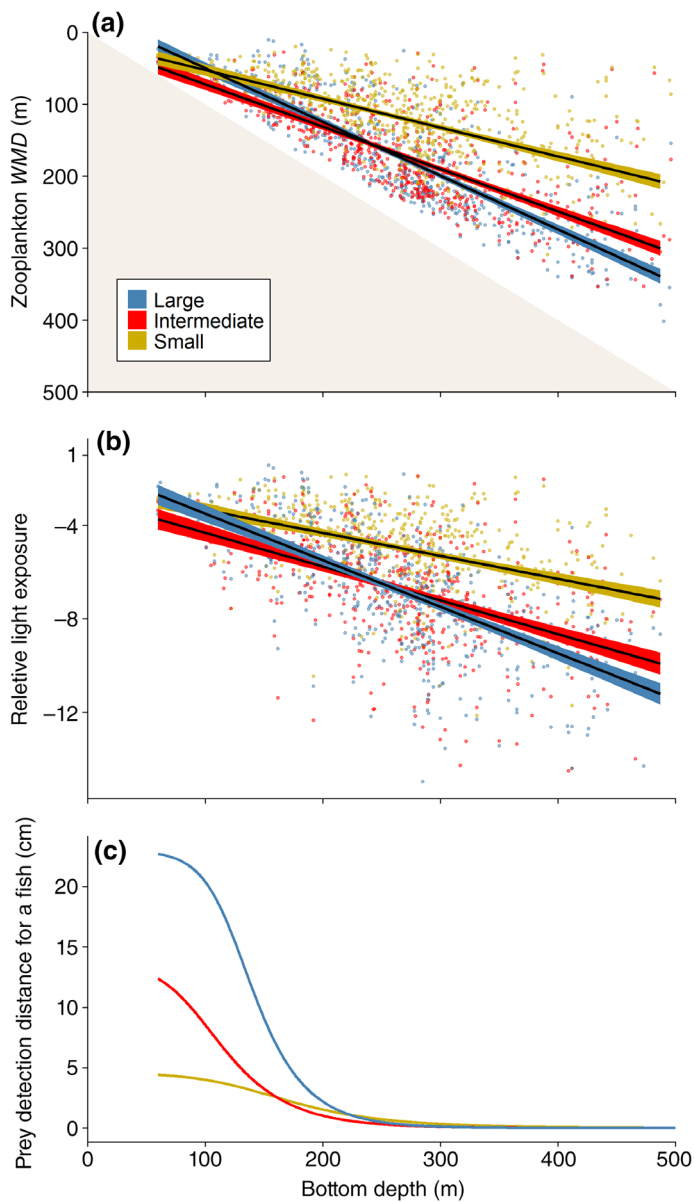
Fig. 2. (a) Estimated WMD (WMD_j) for daytime occurrences of large (> 2000 μm), intermediate (1000–2000 μm), and small (180–1000 μm) zooplankton in the Barents Sea, and linear models with 95% confidence bands of WMD_j as a function of bottom depth and light attenuation (K^{-1}) (Table 1), j indicates size class. Predictions have been plotted using the mean K of all samples (0.08 m^{-1}). Beige area illustrates the bottom depth. **(b)** Deeper distributed zooplankton achieve several orders of magnitude reduction in light exposure relative to the surface irradiance. Relative light exposure was here estimated for the WMD_j based on mean K at the sampling station: $Exp(-K \times WMD_j)$. Note that light exposure is plotted on a $\log_{10}$ scale. Lines are linear regressions with 95% confidence bands. **(c)** Approximated prey detection distance for a fish at the predicted depth of the zooplankton size class from the linear models described in **(a)**. Reaction distance has here been approximated for a 13 cm fish foraging on prey with body lengths of 5, 3, and 1 mm, based on Aksnes and Utne (1997). We used a light attenuation coefficient of 0.08 m^{-1} (mean K for the Barents Sea dataset). All parameters and equations are provided in the Supporting Information ("Elaboration on fish reaction distance" and Table S1).

discovered that while K^{-1} had a significant effect on the *WMD* for the small size class in all areas ($p < 0.001$), it only affected the *WMD* for the large size class in areas > 300 m ($p = 0.03$). Moreover, we found no significant effect of water clarity on the *WMD* for the intermediate size class, both in the total dataset and in samples from deeper areas, when examined individually. The effect of water clarity on WMD_L only in deeper areas implies that large zooplankton are forced to occupy depths with suboptimal light levels regardless of water clarity in areas < 300 m, in line with our prior expectations. Using only K_{chl}^{-1} instead of K^{-1} ($K_{chl}^{-1} + K_{CDOM}^{-1}$), we found a significant effect of water clarity on the *WMD* (all sizes) only in areas > 300 m.

Overall, light attenuation had a second-order effect on the *WMD* of the zooplankton distributions, which we believe is partly due to low variation in the approximated K from our data on Chl *a* and salinity (Supporting Information Fig. S2). Including K did, however, improve the explanatory power (R^2) of the statistical model compared to a simpler model with only bottom depth and size as predictors (models compared with ANOVA, $p = 0.003$).

Zooplankton biomass depth profiles

Vertical profiles of mean zooplankton biomass (g dw m^{-3}) by depth confirmed that large zooplankton had the bulk of their biomass close to the bottom, particularly in areas > 200 m (Fig. 3). Intermediate sizes also had a large part of their biomass close to the bottom, although in areas > 200 m, they displayed a bimodal distribution pattern with more biomass in surface waters and low biomass between 50 and 200 m. This bimodality was most pronounced in areas with 400–500 m depth, which covers the western entrance where Atlantic water flows into the Barents Sea (Fig. 1). The intermediate size class had the largest variation in sampled biomass, both in the surface and deeper waters (shown as 95% confidence intervals in Fig. 3). Small zooplankton had greater biomass in surface waters (0–50 m), also showing tendencies of a bimodal vertical distribution in areas > 200 m. Zooplankton appeared to be more evenly spread throughout the water column in areas < 200 m.

Night-time occurrences indicate overwintering and inverse DVM

For large zooplankton, we found a similar, strong effect of bottom depth on WMD_L during both day and night (Table 2), and b_L was not significantly different in day vs. night samples. This indicates that the majority in this size class had ceased feeding in surface waters and migrated downward for overwintering (samples were from mid-August to mid-October). Bottom depth had a stronger effect on the spread in distributions (SD_L) in night-time samples ($b_{L,day} = 0.23$ vs. $b_{L,night} = 0.27$, $p = 0.02$), that is, distributions were more compact (closer to the bottom) during the day.
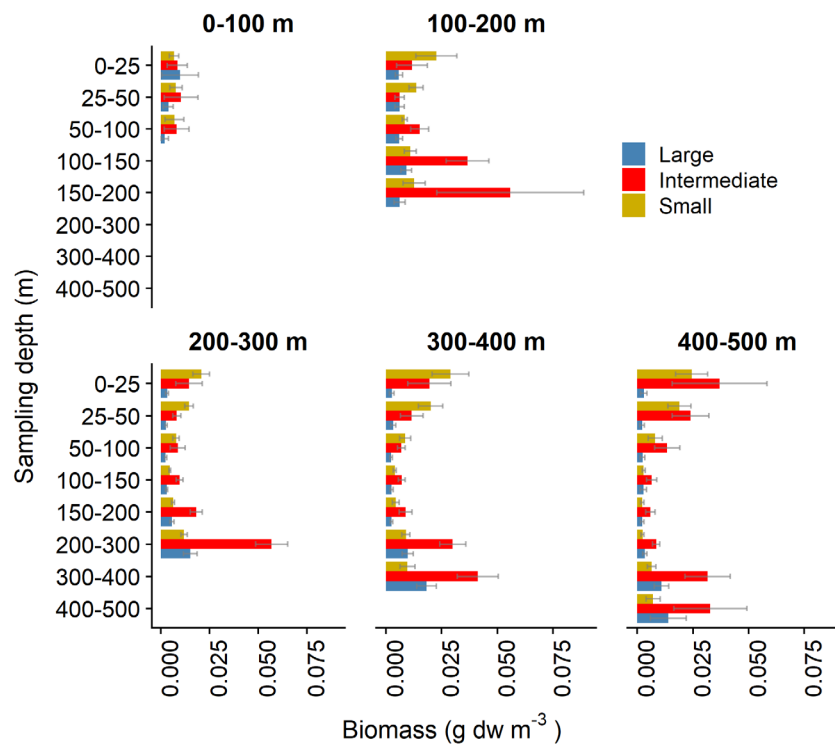
Fig. 3. Vertical biomass profiles (average of all stations, samples collected by day) for the three sizes of zooplankton, panel titles specifies bottom depth at the sampling station. Samples have been sorted according to the mean strata depth (*y*-axis, $Z_{m,i}$), and the figure shows mean biomass (g dw m^{-3}) with 95% confidence intervals ($\pm 1.96 \times$ SEM). Small zooplankton were largely caught in the surface waters in all areas, whereas the intermediate and large size fraction had greater biomass closer to the bottom. Intermediate zooplankton constituted the largest biomass of the three and showed a bimodal distribution pattern in deeper areas (> 200 m).

Both intermediate and small sizes had significantly different slopes (b_j) for day and night ($p < 0.01$), with deeper distributions at night than during the day (Table 2). This suggests an inverse diel vertical migration (DVM) behavior; however, the difference was not very pronounced ($b_M = 0.55$ for day vs. 0.66 for night, and $b_S = 0.36$ for day vs. 0.52 for night), making it difficult to draw any firm conclusions. It can also suggest that distributions are more spread out through the water column at night, yet the spread in the distributions (SD_j) was not significantly different between day and night samples (Table 2; see also Supporting Information Fig. S3). We cannot exclude that this is also due to a sampling bias, with more night-time samples collected later in the period when there is fewer hours of daylight and when more zooplankton likely have migrated out of the surface for overwintering.

Note that coefficients for $b_{j,day}$ in Table 2 are slightly different than b_j in Table 1, as analyses shown in Table 1 include the effect of *K* and were run on a smaller dataset (13% of the samples lacked data for approximating *K*).

Discussion

The Barents Sea is a continental shelf with a varied topography consisting of banks with trenches in between. It is also an important fishery area supporting some of the world's largest fish stocks (Eriksen et al. 2017a). Our results provide observational evidence for topographic constraints of zooplankton vertical distributions in this fish-rich continental shelf ecosystem. The uniqueness of our dataset stems from the magnitude of samples, covering the large and varied bathymetry of the Barents Sea seascape (Fig. 1). Topographic constraints limit the depth distribution for large and intermediate-sized zooplankton in particular, resulting in increased light exposure at the banks. Consequently, planktivores presumably have higher probability of detecting zooplankton prey in areas with bottom depth < 200 m (Fig. 2).

The blockage mechanism has previously been shown for seamounts (e.g., Isaacs and Schwartzlose 1965; Genin et al. 1994) and shelf breaks (Simard and Mackas 1989; Robinson and Goómez-Gutieérrez 1998), and parallels can be drawn with depth constraints on *Daphnia* populations by hypolimnetic anoxia in freshwater lakes (Sakwińska and Dawidowicz 2005). Advection is key in the blockage mechanism; with no replenishment of zooplankton by advection, it is likely that the zooplankton standing stocks over banks are quickly predated due to lack of refuge from visual foraging. Genin et al. (1994) observed patches devoid of zooplankton (gaps) formed on a daily basis over a seamount in California and attributed this to predation by planktivores on topographically blocked zooplankton. Lower biomass of zooplankton in

areas shallower than 100 m in our study may have been an effect of predation (Fig. 3). The strength of the blockage mechanism in terms of providing foraging opportunities for visually feeding fish would in general depend on the topographic configuration and the exchange of water and plankton between deep and shallow waters (Genin 2004). Variation in advection of zooplankton over shallow topographies will create additional variation in the food availability and foraging success for the fish. The major banks in the Barents Sea, for example, the Central Bank, Great Bank, and Spitsbergen Bank (*see* Fig. 1), are large structures (100–200 km) with complex hydrography and circulation features associated with the topographically steered oceanographic polar front (Ingvaldsen and Loeng 2009). We have merged data from a large ecosystem with both Arctic and Atlantic characteristics (e.g., Johannesen et al. 2012*b*), and there can be spatial variation that we have not unveiled. Studies combining hydrodynamic and particle-tracking models (e.g., Harms et al. 2000) will be useful to further identify important feeding grounds where there is both topographic blockage and zooplankton replenishment by advection.

Results from our study are likely transferrable to other regions with a rugged bathymetry. The topographic blockage mechanism has been suggested to sustain fish populations above steep oceanic topographies like seamounts and shelf breaks (Isaacs and Schwartzlose 1965; Mauchline and Gordon 1991; Genin et al. 1994; Seki and Somerton 1994; Fock et al. 2002), and large remains of dead copepods (carcasses) indicate elevated predation over these topographies (Haury et al. 1995). Topographic blockage of zooplankton may also have contributed to denser capelin concentrations at banks than over deeper troughs in the central Gulf of Alaska (McGowan et al. 2018). In the North Sea, predation from herring has been identified as a major driver of *Calanus finmarchicus* mortality (Papworth et al. 2016), and topographic blockage resulting in increased visibility is a likely explanation for the low abundance of *C. finmarchicus* during winter. The stock is replenished in spring by *C. finmarchicus* advected with Norwegian Sea deep water through the Faroe-Shetland Channel (Heath et al. 1999). Reduced deep-water inflow is thus suggested to explain the long-term (1950–present) decline in abundance (Heath et al. 1999), with a negative effect on the recruitment of cod (Beaugrand and Kirby 2010) and also potentially on the growth rate of planktivorous fish (van Deurs et al. 2015).

The type of migration pattern exhibited by zooplankton will determine if their depth distribution limits fish in its search for prey. Shallow topographies may, for instance, be more important for fish during autumn and winter, if their prey here is unable to seek deeper waters for overwintering. Transport of *Calanus* from the deep basins of the Norwegian Sea onto the Barents Sea shelf as well as the Norwegian Shelf (Samuelsen et al. 2009; Opdal and Vikebø 2015) is in some respects a part of the topographic blockage mechanism on a seasonal basis (although it is rarely called so in the literature). In our autumn dataset from the Barents Sea, *C. finmarchicus*

has for the most part entered the overwintering dormant state (Hirche 1996) or is descending to overwintering depths which in the adjacent Norwegian Sea is below 500 m (Edvardsen et al. 2006). Our data suggest that *C. finmarchicus* and other overwintering species are seeking the deeper part of the water column in concert with the deepening water depth. Zooplankton can also display daily migration patterns, although it is debated whether DVM is present in Arctic zooplankton during summer (e.g., Blachowiak-Samolyk et al. 2006; Berge et al. 2009).

Capelin (*Mallotus villosus*) is a key planktivore in the Barents Sea ecosystem (Gjøsæter et al. 2009) and exerts a significant top–down control on zooplankton in the central and northern areas where the major banks are found (Fig. 1) (Stige et al. 2014). Capelin can possibly consume all the zooplankton biomass in the upper, illuminated part of the water column in a matter of days when the seasonally migrating "capelin front" moves into a new and previously unpredated area (Hassel et al. 1991). Baleen whales (minke whale *Balaenoptera acutorostrata*, fin whale *Balaenoptera physalus*, and humpback whale *Megaptera novaeangliae*), which forage on both zooplankton and pelagic fish, were found to remain at banks in the northern Barents Sea even in years with low capelin abundance, instead of migrating southward to feed on abundant herring (*Clupea harengus*) (Skern-Mauritzen et al. 2011). Atlantic cod (*Gadus morhua*), a key predator on capelin, is also largely associated with shallow areas of the Barents Sea (Johannesen et al. 2012*aa*). For capelin, these areas therefore represent not only potentially increased prey availability but also higher risk of predation for capelin itself. Due to this trade-off, it is not evident that there is more planktivorous fish in shallow areas in the Barents Sea although their prey are more visible there.

Conclusion

Exponential decay of light in water means that zooplankton can reduce their light exposure considerably by shifting their vertical position by only tens of meters (Fig. 2b). Over a seascape varying in bottom depth from 100 to 500 m, the shallower bathymetry force zooplankton into more illuminated habitats and increase the feeding potential for planktivorous fish. For fish feeding on *Calanus* and other seasonal migrators, the bathymetry effectively prevents prey from deep descends for safer overwintering. This is likely to affect fish distributions and an important factor for pelagic predator–prey interactions and seascape ecology.

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Conflict of Interest

None declared.