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Zooplankton diel vertical migration during Antarctic summer

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Abstract

Zooplankton diel vertical migration (DVM) during summer in the polar oceans is presumed to be dampened due to near continuous daylight. We analyzed zooplankton diel vertical distribution patterns in a wide range of taxa along the Western Antarctic Peninsula (WAP) to assess if DVM occurs, and if so, what environmental controls modulate DVM in the austral summer. Zooplankton were collected during January and February in paired day-night, depth-stratified tows through the mesopelagic zone along the WAP from 2009-2017, as well as in day and night epipelagic net tows from 1993-2017. The copepod *Metridia gerlachei*, salp *Salpa thompsoni*, pteropod *Limacina helicina antarctica*, and ostracods consistently conducted DVM between the mesopelagic and epipelagic zones. Migration distance for *M. gerlachei* and ostracods decreased as photoperiod increased from 17 to 22 h daylight. The copepods *Calanoides acutus* and *Rhincalanus gigas*, as well as euphausiids *Thysanoessa macrura* and *Euphausia crystallorophias,* conducted shallow (mostly within the epipelagic zone) DVMs into the upper 50 m at night. *Rhincalanus gigas*, *T. macrura*, and *L. h. antarctica* DVM behavior was modulated by chlorophyll *a* concentration, mixed layer depth, and depth of the subsurface chlorophyll *a* maximum, respectively. Carnivorous and detritivorous taxa – including the calanoid copepod *Paraeuchaeta antarctica*, ostracods, chaetognaths, and *Tomopteris* spp. polychaetes – as well as seasonally migrating copepods, were most abundant in the mesopelagic zone regardless of the diel cycle. *Paraeuchaeta antarctica* underwent reverse DVM within the top 100 m. The impacts of Antarctic zooplankton summer DVM and the resident mesopelagic assemblage on carbon export should be better quantified.

1. Introduction

Many zooplankton and fishes throughout the world's oceans undergo diel vertical migration (DVM), feeding in productive surface waters at night and seeking refuge from visual predators at mesopelagic depths during the daytime (Hays, 2003). A global estimate suggests ~50% of sound-scattering mesopelagic biomass performs DVM (Klevjer et al., 2016). Diverse zooplankton taxa independently evolved DVM behavior, as it optimizes the adaptive balance between feeding and predator evasion (Zaret and Suffern, 1976; Stich and Lampert, 1981; Gliwicz, 1986; Hays, 2003). While predator avoidance is the accepted evolutionary driver for DVM, shifts in downwelling irradiance at sunrise and sunset are the dominant proximate cues for this behavior (Ringelberg and Van Gool, 2003; Cohen and Forward, 2009). Thus, it was assumed that DVM is restricted in polar regions and may cease altogether in mid- winter and summer during 24-h darkness and light, respectively (Blachowiak-Samolyk et al., 2006).

DVM studies in the polar oceans show seasonal variability in behavior, with DVM magnitude changing in relation to photoperiod. During moored Acoustic Doppler Current Profiler deployments in the Ross, Lazarev, and Weddell Seas, DVM continued through Antarctic winter but ceased during the period of extended daylight from November to February (Cisewski et al., 2010; Cisewski and Strass, 2016; Picco et al., 2017). Persistent winter DVM occurs as far north as 77°N (Hobbs et al., 2018), although zooplankton DVM is restricted to small-scale (6 to 8 m) migrations within the upper 30 m during Arctic winter (Ludvigsen et al., 2018). Therefore, the apparent pause of DVM during Antarctic summer may in fact be due to seasonal changes in DVM amplitude as some species undertake shallower migrations during summer that go undetected by conventional sampling (Flores et al., 2014; Daase et al., 2016). Asynchronous migrations throughout the diel cycle may also explain why acoustic records do not detect summer DVM in the Southern Ocean (Cottier et al., 2006).

In addition to photoperiod, other environmental conditions are likely to influence the amplitude of zooplankton DVM during polar summer. Phytoplankton blooms may halt DVM as zooplankton remain in surface waters to feed (Cisewski et al., 2010; Cisewski and Strass, 2016). The depth of the subsurface chlorophyll *a* maximum can also influence zooplankton DVM, as observed with Arctic copepods (La et al., 2015a). Similarly, vertically migrating Arctic zooplankton concentrate just below the mixed layer (Berge et al., 2014). In the southern California Current, increased light attenuation results in a decreased amplitude of copepod DVM (Ohman and Romagnan, 2016). The interaction between light conditions and phytoplankton distribution is thus likely to be a key driver of Antarctic zooplankton vertical distribution.

Few studies address polar mesopelagic zooplankton composition and taxon-specific variability in DVM behavior. Arctic zooplankton demonstrate asynchronous DVM patterns, which are explained by variation in feeding ecology, predation risk, and seasonal migration behavior (Fortier et al., 2001; Cottier et al., 2006; Falk-Petersen et al., 2008). Prior studies assessing zooplankton vertical distribution along the Western Antarctic Peninsula (WAP) have either focused on specific taxonomic groups (e.g., Nordhausen, 1994a; Lopez and Huntley, 1995) or lacked the comparable day and night sampling necessary to assess DVM behavior (Marrari et al., 2011). Additionally, there have not been any comprehensive studies resolving polar DVM variability over interannual timescales.

We analyzed zooplankton diel vertical distribution patterns along the WAP during mid-summer as part of the Palmer Antarctica Long-Term Ecological Research (PAL LTER) program. Zooplankton were sampled at discrete depth intervals through the epi- and mesopelagic zones in paired day and night net tows using a MOCNESS (2009-2017) to assess taxon-specific zooplankton vertical distribution. Day and night epipelagic net tows (1993-2017) throughout the PAL LTER sampling region provided additional information on DVM behavior. We examined environmental controls (e.g., photoperiod, mixed layer depth) on DVM amplitude in taxa showing clear DVM. Our results show diverse zooplankton DVM modes, depth distributions, and responses to phytoplankton biomass and vertical distribution, all of which can affect zooplankton-mediated carbon export during Antarctic summer.

2. Materials and Methods

2.1. Study region

The PAL LTER study region ranges from Anvers Island (64.77ºS, 64.05ºW) in the north to Charcot Island (69.45ºS, 75.15ºW) in the south, extending from the WAP coast to the continental slope (Ducklow et al., 2012) (Fig. 1). The PAL LTER research grid is composed of sampling lines running perpendicular to the Peninsula every 100 km, and standard grid stations within each line are separated by 20 km (Waters and Smith, 1992). From 1993-2008, the sampling plan included all stations on grid lines 600 to 200. In more recent years, the study area has expanded to include lines 100, 000, and -100, with sampling resolution reduced to three stations per line. As in previous studies, three latitudinal sub-regions were designated to represent hydrographic, sea ice, and ecological gradients (Martinson et al., 2008; Stammerjohn et al., 2008; Steinberg et al., 2015) (Fig. 1), with regional boundaries along sampling grid lines as follows: ‘North’ (lines 600 to 400), ‘South’: (lines 300 and 200), and ‘Far South’ (lines 100 to -100).

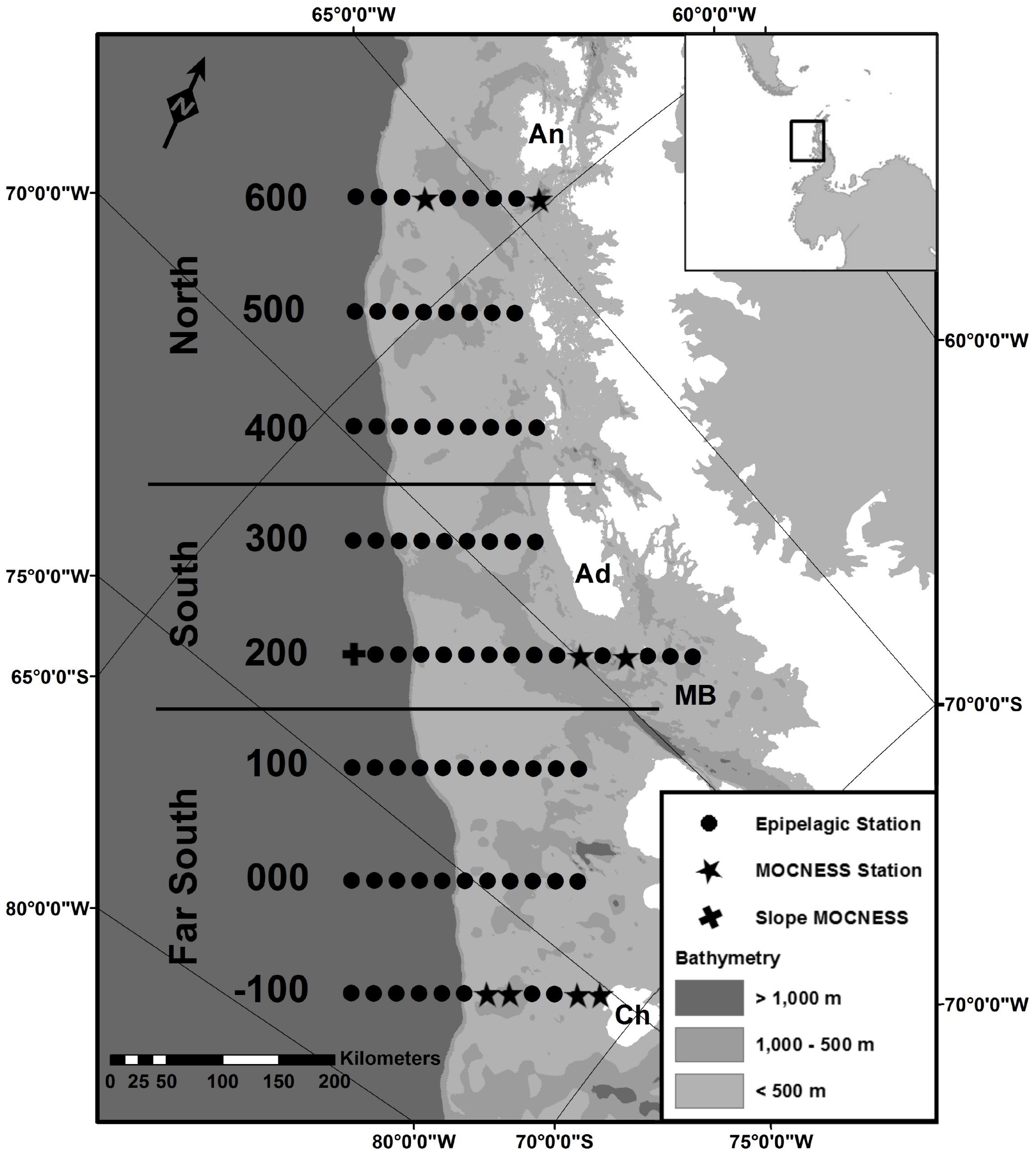

Figure 1. PAL LTER study area along the Western Antarctic Peninsula. 'North,' 'South,' and 'Far South' regions are indicated. Circles indicate epipelagic sampling stations (1993-2017). Stars indicate paired day-night MOCNESS sampling locations on the shelf (2009-2017). Cross indicates paired day-night MOCNESS sampling station on the slope (2017). Shading indicates bathymetry. An: Anvers Island; Ad: Adelaide Island; MB: Marguerite Bay; Ch: Charcot Island.

2.2. Zooplankton collection

Zooplankton were sampled during austral summer (02 January to 13 February) on annual PAL LTER research cruises aboard the MV *Polar Duke* (1993-1997) and ARSV *Laurence M. Gould* (1998-2017). Zooplankton sampling was conducted using two types of gear as described below.

2.2.1. Multiple discrete depth sampling through the epi- and mesopelagic zones

A 1.4-m^2 frame, 500-µm mesh Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) (Wiebe et al., 1985) was used to collect meso- and macrozooplankton in discrete depth intervals from 2009-2017. Each year, paired day (10:07-15:15 local start time) and night (23:03-01:46) MOCNESS tows were carried out in coastal or shelf waters in the 'North', and in most years also the 'South' and 'Far South' (Fig. 1). Sampling time and location were used to calculate solar elevation at the start of tows (Meeus, 1998); daytime solar elevation was > 35.51° and nighttime solar elevation < 0.56°. The MOCNESS was towed obliquely at a speed of 2-2.5 knots, with a typical tow duration of 2.25-3 h. On average, 790 m^3 (range 161-1900 m^3) of water was filtered within a single depth interval as measured by a flow meter mounted on the system.

Eight discrete depth intervals were sampled during the upcast as follows: 500-400, 400-300, 300-250, 250-200, 200-150, 150-100, 100-50, and 50-0 m. Occasionally, the deeper intervals were not sampled when towing in waters shallower than the deep target depths. On four occasions, two depth intervals were combined due to net sampling errors. In these cases, the taxon density in each interval was assumed to equal the density calculated for the combined interval. Sea ice conditions occasionally prevented MOCNESS sampling in the South and Far South regions, therefore, the sample size $n = 7$ for paired day/night tows in the North, while $n =$

6 for the South, and $n = 4$ for the Far South from 2009-2015. Data from additional paired MOCNESS tows in 2016 and 2017 are presented for euphausiids and salps only (for these taxa, $n = 10$ for the North, $n = 8$ for the South, and remains $n = 4$ for the Far South).

A pair of day (09:54 local start time) and night (22:03) tows was also carried out over the continental slope in 2017 (Fig. 1). In this case, eight discrete depth intervals were sampled during the upcast as follows: 1000-750, 750-500, 500-400, 400-300, 300-200, 200-100, 100-50, and 50-0 m (100-0 m for day, due to a net sampling error). Salp data from this slope sample are presented independent of the coastal and shelf data.

2.2.2. Epipelagic sampling

Macrozooplankton were also collected from 1993-2017 throughout the PAL LTER study area using a 2 x 2 m square, 700-µm mesh Metro net towed obliquely to 120 m (Ross et al., 2008, Steinberg et al., 2015) (Fig. 1). The net depth and tow profile were monitored with a depth sensor linked to the conducting hydro wire. Average volume filtered was 9023 m^3 (range 1715-71929 m^3), calculated using a General Oceanics flow meter suspended in the net opening. Ship speed was 2–2.5 knots while towing, and typical tow duration was 30–35 minutes.

Epipelagic samples were designated night tows when the sun was below the horizon, accounting for atmospheric refraction (calculated solar elevation $\leq -0.833°$ at the start of the tow) (Atkinson et al., 2008; Steinberg et al., 2015). Sample size varied by taxon (day $n = 966\text{-}1071$ and night $n = 181\text{-}198$), as not all taxa were identified during shipboard processing throughout the time series.

2.3. Taxonomic composition

2.3.1. Discrete depth samples

All euphausiids and salps collected in MOCNESS tows were identified and quantified at sea. Whole samples were then preserved in sodium borate-buffered 4% formaldehyde and shipped to the Virginia Institute of Marine Science (Gloucester Point, VA, USA) for further taxonomic analysis to quantify all non-euphausiid or salp taxa. Samples were size-fractionated using a 5-mm mesh, with all individuals in this larger size fraction identified and counted. This size-fractionation step removed large, abundant taxa (i.e., salps and euphausiids) from the microscopic analysis. At least 1/64 of the < 5-mm size fraction was counted under a stereo dissecting microscope after dividing the sample with a plankton splitter. A minimum of 100 individuals of the most abundant species was enumerated in this smaller size fraction.

Discrete depth analyses focused on abundant taxonomic groups. Five common calanoid copepod species were included: *Metridia gerlachei*, *Calanoides acutus*, *Calanus propinquus*, *Rhincalanus gigas*, and *Paraeuchaeta antarctica*. Identification included adults and conspicuous copepodites. Discrete depth-stratified data were only analyzed for the smaller, but abundant, euphausiids *Thysanoessa macrura* and *Euphausia crystallorophias*, because the larger Antarctic krill *Euphausia superba* was underrepresented due to avoidance of the 1.4-m^2 MOCNESS (Nordhausen, 1994b). The pelagic tunicate *Salpa thompsoni* was included. The thecosome (shelled) pteropod *Limacina helicina antarctica* was analyzed individually while the gymnosome (shell-less) pteropods *Clione antarctica* and *Spongiobranchea australis* were grouped together (as in Thibodeau et al., 2019). *Tomopteris* spp. polychaetes were combined into a single group including *T. carpenteri*. Other groups were analyzed by major taxa, such as ostracods, amphipods (including the hyperiids *Themisto gaudichaudii*, *Cyllopus lucasii*, *Hyperiella macronyx*, *Hyperoche medusarum*, *Primno macropa*, *Vibilia stebbingi*, *Scina* spp., and the gammarid *Eusirus* spp.), and chaetognaths (inclusive of large, conspicuous *Pseudosagitta gazellae* and *P. maxima*).

2.3.2. Epipelagic samples

Grid-wide epipelagic tows were sorted at sea as reported in Steinberg et al. (2015). All above taxa were included in the analysis of epipelagic samples except for the calanoid copepods and ostracods. The Antarctic krill *Euphausia superba* was included in analysis of epipelagic samples.

2.4. Vertical structure

Night to day ratios (N:D) were calculated to identify diel changes in surface abundance of each taxon. For paired day and night MOCNESS samples, abundance was integrated to 150 m and to 50 m (individuals m^{-2}) when a taxon was present in both the day and night tows (Steinberg et al., 2008). These values are referred to as MOCNESS 150 m N:D and MOCNESS 50 m N:D, respectively. MOCNESS N:D data typically ranged across multiple orders of magnitude and were positively skewed. A relatively few large values were influential on the mean MOCNESS N:D values, typically resulting in large mean values compared to the median (Supplemental Tables 1 and 2). Therefore, the median was used to describe the central tendency of MOCNESS N:D data. Additionally, mean day abundance and mean night abundance were calculated from epipelagic (0-120 m) samples to calculate grid-wide N:D ratios for 1993-2017. These values are referred to as grid-wide 120 m N:D.

The vertical distribution of taxa in the MOCNESS discrete depth samples was quantified using weighted mean depth (WMD). WMD (m) is calculated as follows:

$$WMD = \sum (n_i \times z_i \times d_i) \,/ \sum (n_i \times z_i)$$

where for depth interval *i,* d_i is the midpoint (m), z_i is the interval thickness (m), and n_i is abundance (no. m^{-3}) (Andersen et al., 2001). WMD was only calculated for tows reaching 500 m. Night WMD was subtracted from day WMD to determine the amplitude of diel migration (ΔWMD, m). Data used in the analyses are available at: https://pal.lternet.edu/data.

2.5. Environmental controls

The environmental water column data used in this analysis was collected at sampling stations where paired day-night MOCNESS tows were conducted. Discrete chlorophyll *a* (chl-*a*) measurements were made fluorometrically (Parsons et al., 1984). Primary productivity rates were measured with 24-h incubations of ^{14}C uptake at various light levels (Steemann Nielsen, 1952; Schofield et al., 2018). Both chl-*a* and primary production were depth-integrated to 100 m. The depth of the subsurface chl-*a* maximum (Z_{SCM}) and euphotic zone defined by the 1% isolume ($Z_{1\%}$) were determined with a fluorometer and a photosynthetically active radiation (PAR) sensor, respectively, mounted on the CTD rosette. Mixed layer depth (MLD) was calculated as the depth of maximum buoyancy frequency from the same CTD casts (Carvalho et al., 2017). Photoperiod (hours) was calculated for all day-night MOCNESS tow pairs using latitude and day of year (Kirk, 2011).

2.6. Statistical analyses

Single-factor ANOVA was used to test for differences in ΔWMD and log-adjusted MOCNESS N:D ratios among the North, South, and Far South sub-regions. The significance level (α) was set at 0.05. There was no significant difference among latitudinal sub-regions for any taxa for MOCNESS 150 m N:D or MOCNESS 50 m N:D (ANOVA; $p > 0.06$). All statistical tests were conducted with R version 3.3.2 (R Core Team, 2016).

Differences between day and night surface abundance (0-150 m and 0-50 m) from MOCNESS pairs were tested using the Wilcoxon signed-rank test. This non-parametric test does not require transformation of non-normal data and gave comparable results to the paired *t*-test using log-transformed data (Supplemental Tables 1 and 2). Differences between unpaired day and night grid-wide epipelagic abundance (0-120 m) were tested using the Wilcoxon rank-sum test.

Multiple linear regression was used to identify environmental controls on ΔWMD for taxa that made DVMs from the mesopelagic zone into the epipelagic zone. Only *M. gerlachei* and ostracods were included in this analysis; ΔWMD was not a sensitive metric for *L. h. antarctica*, because it was concentrated in the epipelagic zone, and *Salpa thompsoni* was excluded due to an insufficient sample size. ΔWMD did not differ among latitudinal sub-regions for *M. gerlachei* or ostracods (ANOVA; $p > 0.96$). Therefore, data for the analysis were combined across the entire sampling region.

MOCNESS 50 m N:D was a sensitive metric for taxa that were concentrated in the epipelagic zone or conducted DVM within the epipelagic zone. These taxa included *L. h. antarctica*, *C. acutus*, *R. gigas*, *T. macrura*, and *E. crystallorophias*. Generalized linear models with a gamma distribution and log link function were used to identify environmental controls on MOCNESS 50 m N:D. The gamma distribution is appropriate for ratios, because it is constrained to positive, continuous values. The log link function also ensures positive fitted values. Significant model fits were not achieved for the shallow migrators *C. acutus* and *E. crystallorophias*.

A suite of nine models was fitted for each individual taxon included in ΔWMD analysis (multiple linear regression) and in MOCNESS 50 m N:D analysis (generalized linear model with gamma distribution and log link function). The water column properties investigated in this study were correlated with one another and therefore were not included in the same models to avoid problematic collinearity. For example, as MLD deepened so did Z_{SCM} (Pearson's $r = 0.69$; $p = 0.0004$). $Z_{1\%}$ deepened as depth-integrated chl-*a* decreased (Pearson's $r = -0.60$; $p = 0.004$) and as Z_{SCM} deepened (Pearson's $r = 0.44$; $p = 0.044$). None of the water column properties were correlated with photoperiod. Therefore, the nine models included each explanatory variable individually (i.e., photoperiod, chl-*a*, Z_{SCM}, $Z_{1\%}$, and MLD) as well as photoperiod paired with each of the water column properties. Model selection statistics are presented in Supplemental Tables 3-7. Final models were selected according to the lowest Akaike Information Criterion value corrected for small sample size (AICc) (Hurvich and Tsai, 1989) using the model.sel function in the MuMIn package (Bartoń, 2016). Presented models satisfied assumptions as verified by plotting residuals versus fitted values and explanatory variables.

3. Results

3.1. Environmental conditions

Mean photoperiod during MOCNESS sampling was 20 h 11 min (range: 17 h 41 min to 21 h 47 min), and mean $Z_{1\%}$, was 47 m (range: 16-81 m). Mean depth-integrated chl-*a* was 126 mg m^{-2} (range: 13-517 mg m^{-2}), and mean depth-integrated primary production was 2489 mg C m^{-2} d^{-1} (range: 605-5354 mg C m^{-2} d^{-1}). Mean MLD was 28 m (range: 5-79 m), and mean Z_{SCM} was 20 m (range: 4-60 m).

3.2. Diel vertical depth distributions by taxon

3.2.1. Calanoid copepods

The calanoid copepod *Metridia gerlachei* was the most abundant taxon in MOCNESS tows and a strong diel vertical migrator (Fig. 2), with a median MOCNESS 150 m N:D of 8.0

(Wilcoxon signed-rank test $p = 0.002$) (Table 1). Much of the *M. gerlachei* population did not migrate and resided between 300-500 m, particularly in the North (Fig. 2a). The *M. gerlachei* depth distribution was more even in the South and Far South (Fig. 2b-c). *Calanoides acutus* was the second-most abundant calanoid and although its abundance from 0-150 m did not differ significantly between day and night (Wilcoxon signed-rank test $p = 0.64$) (Table 1), it was more abundant during night tows from 0-50 m with a median MOCNESS 50 m N:D of 2.3 (Fig. 3d; Table 2) (Wilcoxon signed-rank test $p = 0.001$). Like *M. gerlachei*, *C. acutus* vertical distribution also varied with latitudinal sub-region. *Calanoides acutus* was distributed relatively evenly with depth in the North and South (Fig. 3a-b) but was concentrated between 250-400 m in the Far South (Fig. 3c), where it was also an order of magnitude more abundant at this depth zone compared to the other sub-regions.

In contrast to *M. gerlachei* and *C. acutus, Calanus propinquus*, *Rhincalanus gigas*, and *Paraeuchaeta antarctica* were an order of magnitude less abundant and did not vary appreciably with latitudinal sub-region. *Calanus propinquus* was most abundant in the surface 50 m (Fig. 4a) unlike other calanoid copepods, which had peak abundances in the mesopelagic zone (day and night). Epipelagic *C. propinquus* abundance did not differ between day and night (Tables 1 and 2). *Rhincalanus gigas* was most abundant from 250-300 m during the day and from 200-250 m at night (Fig. 4b), and abundance in the surface 50 m was significantly greater at night than during the day (Wilcoxon signed-rank test $p = 0.004$). Median *R. gigas* MOCNESS 50 m N:D was 36.6 (Table 2). *Paraeuchaeta antarctica* was most abundant from 300-500 m and mostly remained resident in the mesopelagic zone during day and night (Fig 4c). Although scarce in the epipelagic zone, *P. antarctica* was significantly more abundant from 0-50 m during the day (Wilcoxon signed-rank test $p = 0.012$) (Table 2), which suggests this species conducted reverse DVM.

Table 1. Diel, depth-integrated zooplankton abundance (0-150 m) from MOCNESS tows along the WAP continental shelf. For euphausiids and *Salpa thompsoni*, Day and Night *n* = 22 (samples from 2009-2017). For all other taxa, Day and Night *n* = 17 (samples from 2009-2015). Night:Day *n* varies because taxa were not always present in both day and night paired tows. *p*-values are for the Wilcoxon signed-rank test comparing paired day-night abundance values when a taxon was present in both tows.

	Day (individuals m^{-2})		**Night (individuals m^{-2})**		**Night:Day**			
Taxon	**Median**	**Range**	**Median**	**Range**	**Median**	**25% - 75% Quantiles**	***p***	***n***
Calanoid copepods								
Metridia gerlachei	32.7	0.1 - 1975.0	249.5	3.1 - 2860.8	8.0	6.2 - 32.0	0.002	17
Calanoides acutus	37.1	4.2 - 230.6	51.6	7.3 - 269.1	1.0	0.8 - 1.5	0.64	17
Calanus propinquus	4.8	0.0 - 165.4	7.3	1.0 - 75.7	1.7	0.4 - 4.4	0.67	16
Rhincalanus gigas	4.2	0.3 - 20.3	3.9	0.0 - 14.8	1.2	0.5 - 2.3	0.82	16
Paraeuchaeta antarctica	0.9	0.0 - 4.5	1.4	0.0 - 7.1	1.1	0.6 - 2.3	0.68	12
Euphausiids								
Thysanoessa macrura	5.0	0.2 - 60.4	9.9	0.1 - 74.9	1.4	1.1 - 2.5	0.003	22
Euphausia crystallorophias	0.2	0.0 - 18.3	0.1	0.0 - 61.6	0.7	0.5 - 5.6	0.58	11
Other crustaceans								
Ostracoda	3.8	0.0 - 38.2	20.1	1.2 - 219.1	2.9	1.7 – 7.4	0.0003	16
Amphipoda	1.9	0.0 - 8.5	1.3	0.0 - 16.4	0.9	0.6 – 2.1	0.56	15
Gelatinous zooplankton								
Salpa thompsoni [†]	0.0	0.0 - 19.4	0.0	0.0 - 174.4	9.0	4.5 - 9.0	0.75	3
Limacina helicina antarctica	1.2	0.0 - 53.2	3.4	0.0 - 56.1	1.7	1.2 - 3.6	0.021	13
Gymnosomata	0.5	0.0 - 25.3	0.6	0.0 - 3.3	0.8	0.5 - 1.3	0.34	12
Chaetognatha	24.0	0.7 - 118.6	21.8	1.7 - 84.1	1.0	0.6 - 1.6	0.75	17
***Tomopteris* spp.**	0.04	0.0 - 1.1	0.4	0.0 - 1.6	1.2	1.1 - 6.7	0.30	9

[†] See Figure 7b for *Salpa thompsoni* data from the continental slope.

Table 2. Diel, depth-integrated zooplankton abundance (0-50 m) from MOCNESS tows along the WAP continental shelf. For euphausiids and *Salpa thompsoni*, Day and Night *n* = 22 (samples from 2009-2017). For all other taxa, Day and Night *n* = 17 (samples from 2009-2015). Night:Day *n* varies because taxa were not always present in both day and night paired tows. *p*-values are for the Wilcoxon signed-rank test comparing paired day-night abundance values when a taxon was present in both tows.

	Day (individuals m^{-2})		**Night (individuals m^{-2})**		**Night:Day**			
Taxon	**Median**	**Range**	**Median**	**Range**	**Median**	**25% - 75% Quantiles**	***p***	***n***
Calanoid copepods								
Metridia gerlachei	4.0	0.0 - 153.8	7.6	0.0 - 948.6	1.8	1.4 - 7.0	0.013	13
Calanoides acutus	9.0	0.0 - 76.0	13.8	0.0 - 155.5	2.3	1.6 - 2.9	0.001	12
Calanus propinquus	0.2	0.0 - 159.5	4.0	0.0 - 62.0	2.1	0.9 - 4.2	0.38	8
Rhincalanus gigas	0.3	0.0 - 4.9	13.8	0.0 - 155.5	36.6	18.2 – 112.4	0.004	9
Paraeuchaeta antarctica	4.0	0.0 - 62.0	0.1	0.0 - 1.6	0.2	0.1 - 0.4	0.012	9
Euphausiids								
Thysanoessa macrura	0.2	0.0 - 54.8	3.1	0.1 - 47.1	11.7	3.6 - 19.4	0.006	16
Euphausia crystallorophias	0.0	0.0 - 4.7	0.1	0.0 - 56.3	8.8	4.3 - 13.1	0.047	7
Other crustaceans								
Ostracoda	1.0	0.0 - 23.3	0.9	0.0 - 24.0	1.3	1.0 - 2.1	0.24	11
Amphipoda	0.3	0.0 - 8.0	0.3	0.0 - 3.2	0.7	0.5 - 2.4	0.85	10
Gelatinous zooplankton								
Salpa thompsoni	0.0	0.0 - 5.4	0.0	0.0 - 63.0	1.2	0.6 - 6.5	0.75	3
Limacina helicina antarctica	0.6	0.0 - 28.4	0.9	0.0 - 31.7	2.8	1.7 – 3.6	0.13	9
Gymnosomata	0.0	0.0 - 25.0	0.1	0.0 - 2.5	1.2	0.4 - 1.3	1.00	6
Chaetognatha	1.9	0.0 - 14.2	1.6	0.0 - 10.4	0.9	0.7 - 1.5	0.68	13
***Tomopteris* spp.**	0.0	0.0 - 1.1	0.0	0.0 - 0.8	0.5	NA	NA	1

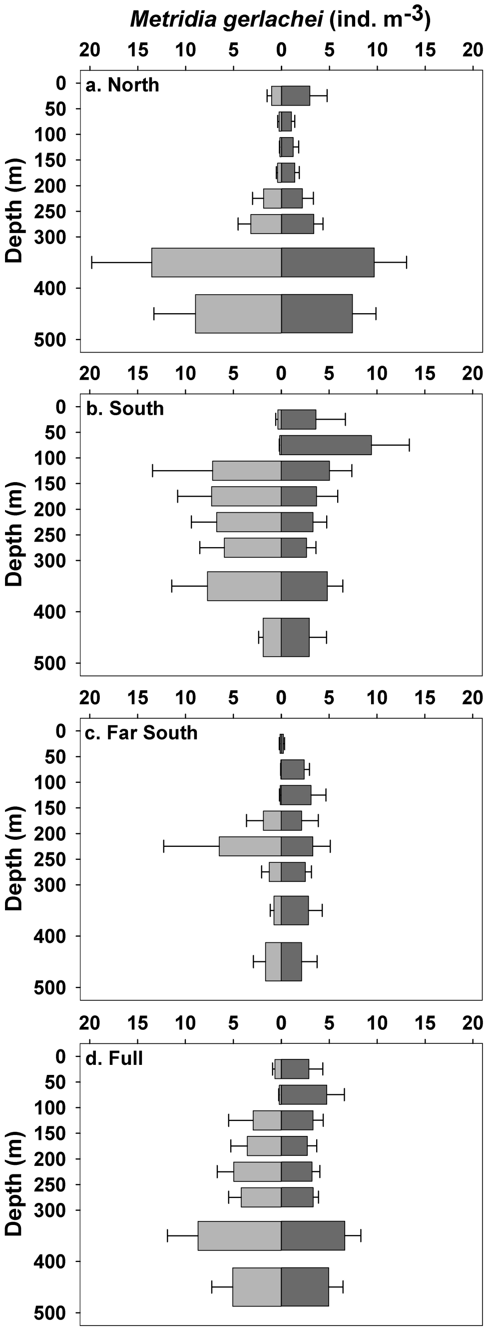

Figure 2. Mean day (light gray, left) and night (dark gray, right) abundance of the calanoid copepod *Metridia gerlachei* in the North (a), South (b), Far South (c) sub-regions, and full shelf sampling region (d) at discrete depth intervals from 0-500 m. Error bars indicate one standard error. North n = 5-7; South n = 5-6; Far South n = 2-4; Full n = 12-17.

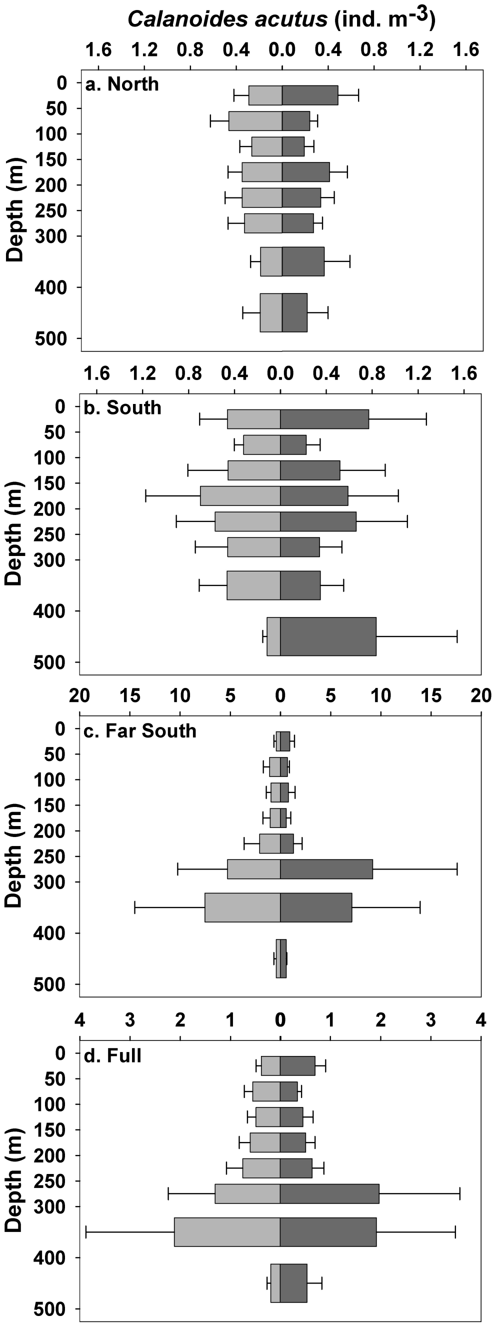

Figure 3. Mean day (light gray, left) and night (dark gray, right) abundance of the calanoid copepod *Calanoides acutus* in the North (a), South (b), Far South (c) sub-regions, and full shelf sampling region (d) at discrete depth intervals from 0-500 m. Error bars indicate one standard error. North *n* = 5-7; South *n* = 5-6; Far South *n* = 2-4; Full *n* = 12-17. Note different scaling on x-axes.

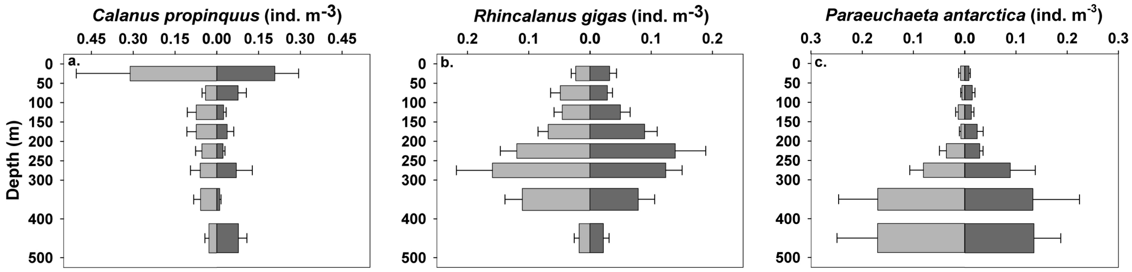

Figure 4. Mean day (light gray, left) and night (dark gray, right) abundance of the calanoid copepods *Calanus propinquus* (a), *Rhincalanus gigas* (b), and *Paraeuchaeta antarctica* (c) sampled at discrete depth intervals from 0-500 m for the full shelf sampling region. Error bars indicate one standard error. Full *n* = 12-17. Note different scaling on x-axes.

3.2.2. Euphausiids

The abundant krill species *Thysanoessa macrura* was concentrated in the epipelagic zone during day and night, but ascended at night, especially into the upper 50 m (Fig. 5a). Some degree of DVM by *T. macrura* was supported by all metrics tested. This species was significantly more abundant in 0-50 m depths at night compared to day (Wilcoxon signed-rank test $p = 0.006$) (Table 2), and *T. macrura* median MOCNESS 50 m N:D was 11.7. *Thysanoessa macrura* was also more abundant at night vs. day in the upper 0-150 m (MOCNESS tows; Wilcoxon signed-rank test $p = 0.003$; median MOCNESS 150 m N:D = 1.4) (Table 1) and from 0-120 m during nighttime grid-wide epipelagic tows (Wilcoxon rank-sum test $p = 0.0003$; grid-wide 120 m N:D = 1.6) (Table 3). *Euphausia crystallorophias* was less abundant than *T. macrura*, but similarly was concentrated in the upper 100 m (Fig. 5b) and migrated into the top 50 m at night, as indicated by higher abundance from 0-50 m at night than day (Wilcoxon signed-rank test $p = 0.047$) and a median MOCNESS 50 m N:D of 8.8 (Table 2). *Euphausia superba* remained in the epipelagic zone through the diel cycle with a grid-wide 120 m N:D of 0.93 (Table 3).

3.2.3. Other crustaceans

Ostracods migrated nightly into the upper 200 m (Fig. 6a), with significantly higher abundance from 0-150 m at night vs. day (Wilcoxon signed-rank test $p = 0.0003$) and a median MOCNESS 150 m N:D of 2.9 (Table 1). Mean ostracod abundance peaked in the 200-250 m layer, where they were about 50% more abundant during day than night (Fig. 6a). Most of the ostracod community did not migrate and resided between 200-500 m throughout the diel cycle. Amphipods were an order of magnitude less abundant than ostracods, with two distinct abundance peaks in the mesopelagic zone during day, and highest abundance from 100-200 m at night (Fig. 6b). Amphipods were significantly more abundant in nighttime epipelagic tows and had a grid-wide 120 m N:D of 2.1 (Wilcoxon rank-sum test $p = 2.6 \times 10^{-12}$) (Table 3).

Table 3. Diel, depth-integrated zooplankton abundance (0-120 m) from grid-wide epipelagic tows across the PAL LTER sampling region from 1993-2017. *n* varies because not all taxa were identified consistently throughout the time series. *p*-values are for the Wilcoxon rank-sum test.

	Day (individuals m^{-2})			**Night (individuals m^{-2})**				
Taxon	**Mean**	**SE**	***n***	**Mean**	**SE**	***n***	**Night:Day**	***p***
Euphausiids								
Thysanoessa macrura	22.9	2.0	1063	36.9	6.8	197	1.6	0.0003
Euphausia crystallorophias	2.9	0.38	1067	6.2	2.3	196	2.1	0.77
Euphausia superba	13.7	2.0	1071	12.7	6.1	198	0.9	0.001
Other crustaceans								
Amphipoda	0.36	0.025	1026	0.75	0.13	185	2.1	2.6×10^{-12}
Gelatinous zooplankton								
Salpa thompsoni	4.9	1.4	1069	12.5	3.0	197	2.6	7.7×10^{-17}
Limacina helicina antarctica	7.3	0.62	1056	9.9	1.1	195	1.4	0.004
Gymnosomata	0.22	0.014	1050	0.31	0.039	193	1.4	0.0002
Chaetognatha	1.5	0.16	994	0.88	0.20	183	0.6	0.088
***Tomopteris* spp.**	0.051	0.0049	966	0.095	0.014	181	1.9	0.0002

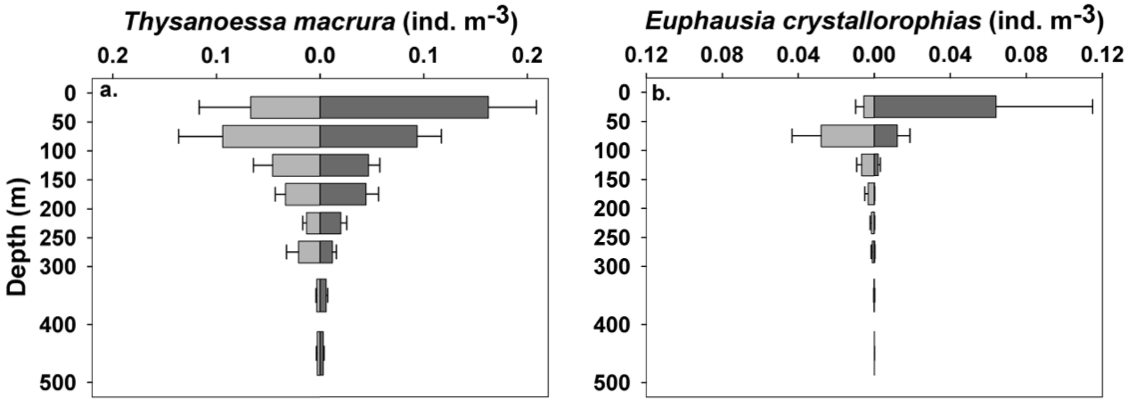

Figure 5. Mean day (light gray, left) and night (dark gray, right) abundance of the euphausiids *Thysanoessa macrura* (a) and *Euphausia crystallorophias* (b) sampled at discrete depth intervals from 0-500 m for the full shelf sampling region. Error bars indicate one standard error. Full *n* = 17-22. Note different scaling on x-axes.

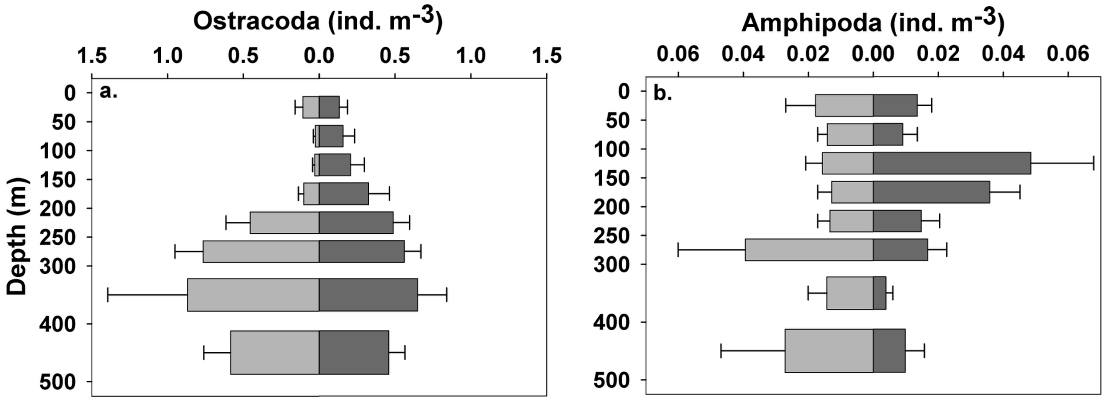

Figure 6. Mean day (light gray, left) and night (dark gray, right) abundance of ostracods (a) and amphipods (b) sampled at discrete depth intervals from 0-500 m for the full shelf sampling region. Error bars indicate one standard error. Full *n* = 12-17. Note different scaling on x-axes.

3.2.4. Salps

Salpa thompsoni was a strong diel vertical migrator. Mean abundance over the continental shelf was highest from 200-400 m during the day, and from 0-200 m at night (Fig. 7a). *Salpa thompsoni* median MOCNESS 150 m N:D was 9.0, although salps were only present in three day-night MOCNESS tow pairs along the continental shelf (Table 1). Salps were also significantly more abundant at night in epipelagic tows, with a grid-wide 120 m N:D of 2.6 (Wilcoxon rank-sum test $p = 7.7 \times 10^{-17}$) (Table 3). Over the continental slope, *S. thompsoni* migrated mostly from daytime residence depths in the 200-300 m layer into the surface 100 m at night (Fig. 7b), with MOCNESS 100 m N:D = 94.6 and MOCNESS 200 m N:D = 6.3. Salps were relatively scarce below 300 m, although a small, deep peak occurred from 750-1000 m on the slope.

3.2.5. Pteropods

The thecosome (shelled) pteropod *Limacina helicina antarctica* was concentrated in surface waters but also migrated from 150-250 m during the day into the upper epipelagic zone at night (Fig. 8a). This result is supported by their higher abundance in the upper 150 m at night from MOCNESS tows (Wilcoxon signed-rank test $p = 0.021$) (Table 1) and from 0-120 m at night in epipelagic tows (Wilcoxon rank-sum test $p = 0.004$) (Table 3). Median *L. h. antarctica* MOCNESS 150 m N:D was 1.7 (Table 1), and grid-wide 120 m N:D was 1.4 (Table 3). Gymnosome (shell-less) pteropods were less abundant than *L. h. antarctica* in the epipelagic zone and were distributed relatively evenly with depth, with highest mean gymnosome abundance from 0-50 m during the day (Fig. 8b). However, DVM by gymnosomes is indicated grid-wide, with significantly higher abundance at night in the epipelagic zone and a grid-wide 120 m N:D of 1.4 (Wilcoxon rank-sum test $p = 0.0002$) (Table 3).

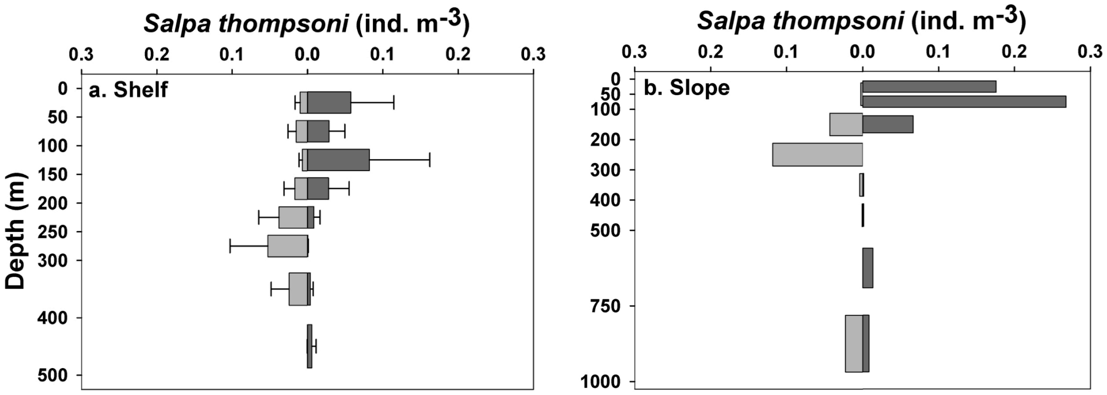

Figure 7. Mean day (light gray, left) and night (dark gray, right) abundance of *Salpa thompsoni* from the full continental shelf sampling region (a) and a single pair of tows on the continental slope (b) sampled at discrete depth intervals from 0-500 m and 0-1000 m, respectively. Error bars indicate one standard error. Full Shelf *n* = 17-22; Slope *n* = 1. Note different scaling on y-axes.

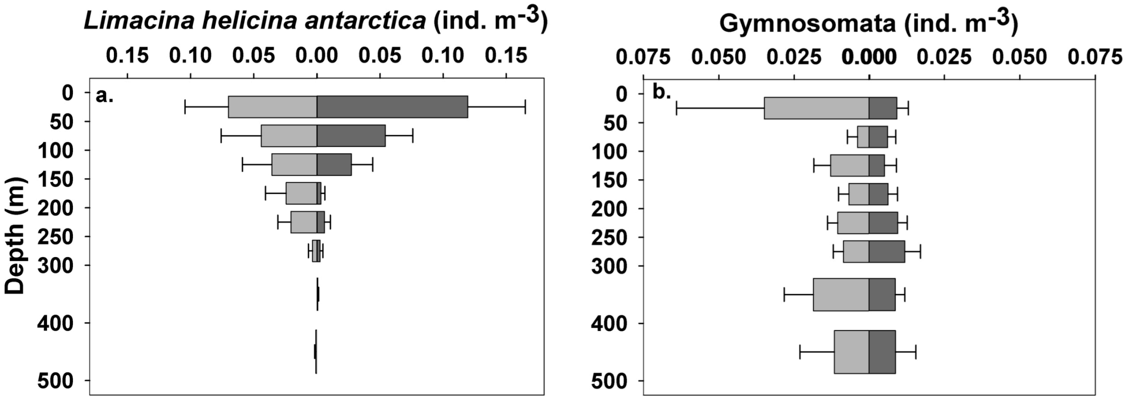

Figure 8. Mean day (light gray, left) and night (dark gray, right) abundance of the pteropod *Limacina helicina antarctica* (a) and gymnosome pteropods (b) sampled at discrete depth intervals from 0-500 m for the full shelf sampling region. Error bars indicate one standard error. Full *n* = 12-17. Note different scaling on x-axes.

3.2.6. Gelatinous carnivores

Chaetognaths and *Tomopteris* spp. polychaetes were mostly resident in the mesopelagic zone and relatively scarce from 0-100 m (Fig. 9). Mean abundance of both taxa was highest from 200-250 m during the day and from 150-200 m at night (*Tomopteris* spp. also had a second night peak at 300-400 m) (Fig. 9). Median chaetognath MOCNESS 150 m N:D was 1.0 (Table 1) and although grid-wide 120 m N:D was 0.6, epipelagic abundance did not differ between day and night (Tables 1-3), suggesting chaetognaths did not undergo DVM. However, *Tomopteris* spp. polychaetes did appear to undergo DVM as they were significantly more abundant during night epipelagic tows and had a grid-wide 120 m N:D of 1.9 (Wilcoxon rank-sum test $p = 0.0002$) (Table 3).

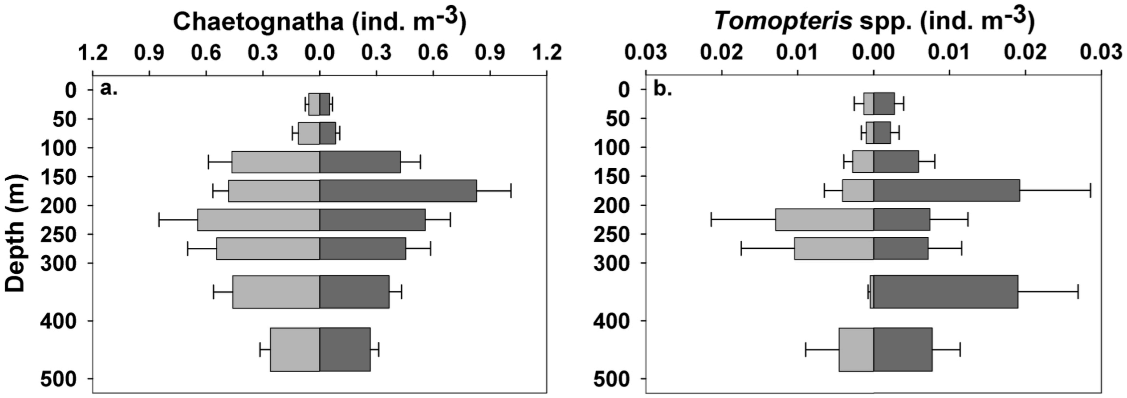

Figure 9. Mean day (light gray, left) and night (dark gray, right) abundance of chaetognaths (a) and *Tomopteris* spp. polychaetes (b) sampled at discrete depth intervals from 0-500 m for the full shelf sampling region. Error bars indicate one standard error. Full $n = 12$-17. Note different scaling on x-axes.

3.3. Environmental controls on DVM

For strong migrators traveling between the mesopelagic and epipelagic zones, migration distance (i.e., ΔWMD) was sensitive to photoperiod and vertical water column structure. For the copepod *M. gerlachei*, photoperiod and Z_{SCM} best explained ΔWMD (Table 4), with *M. gerlachei* making shorter vertical migrations as photoperiod grew longer and when Z_{SCM} was shallower (Fig. 10a). Similarly, photoperiod and MLD best explained ostracod ΔWMD (Table 4). Ostracods made shorter DVMs as photoperiod grew longer and when MLD was deeper (Fig. 10b; note– an outlier that was excluded prior to model selection for ostracods is included for visualization in this figure).

For taxa making shorter-distance DVMs mostly within the epipelagic zone, the magnitude of DVM into the surface layer (i.e., MOCNESS 50 m N:D) was best explained by phytoplankton abundance and distribution. The final models each included a different, single explanatory variable for the copepod *R. gigas*, euphausiid *T. macrura*, and pteropod *L. h. antarctica*. *Rhincalanus gigas* DVM into the surface 50 m decreased as depth-integrated chl-*a* increased (Fig. 11a; Table 5). *Thysanoessa macrura* DVM decreased when MLD was deeper (Fig. 11b), and similarly *L. h. antarctica* DVM decreased when Z_{SCM} was deeper (Fig. 11c – a finding robust to the inclusion of an outlier value – see inset) (Table 5).

Table 4. Statistics from multiple linear regression models assessing the impact of environmental variables on zooplankton ΔWMD from MOCNESS tows (0-500 m) along the WAP continental shelf from 2009-2015.

Variable	***n***	**Coefficient**	**SE**	***t***	***p***	**Partial R^2**
Metridia gerlachei **ΔWMD (adjusted R^2 = 0.76; p = 0.001)**	11					
Photoperiod		-19.8	4.6	-4.3	0.003	0.70
Depth of chl-*a* maximum		2.27	0.47	4.8	0.001	0.75
Intercept		400.0	92.5	4.3	0.003	
Ostracoda ΔWMD (adjusted R^2 = 0.79; p = 0.002)	10					
Photoperiod		-12.1	3.0	-4.1	0.005	0.70
Mixed layer depth		-0.666	0.23	-2.9	0.022	0.55
Intercept		283.8	59.7	4.8	0.002	

Table 5. Statistics from generalized linear models (with a gamma distribution and log link function) assessing the impact of environmental variables on zooplankton 50m N:D from MOCNESS tows along the WAP continental shelf from 2009-2015 (for *Rhincalanus gigas* and *Limacina helicina antarctica*) and 2009-2017 (for *Thysanoessa macrura*).

Variable	*n*	Coefficient	SE	*t*	*p*
***Rhincalanus gigas* 50m N:D (deviance explained = 35%)**	8				
Chl-*a* concentration		-0.0088	0.0031	-2.8	0.031
Intercept		5.15	0.41	12.6	1.5×10^{-5}
***Thysanoessa macrura* 50m N:D (deviance explained = 27%)**	15				
Mixed layer depth		-0.035	0.011	-3.1	0.008
Intercept		3.67	0.42	8.7	8.8×10^{-7}
***Limacina helicina antarctica* 50m N:D (deviance explained = 40%)**	8				
Depth of chl-*a* maximum		-0.055	0.020	-2.7	0.035
Intercept		2.06	0.61	3.4	0.015

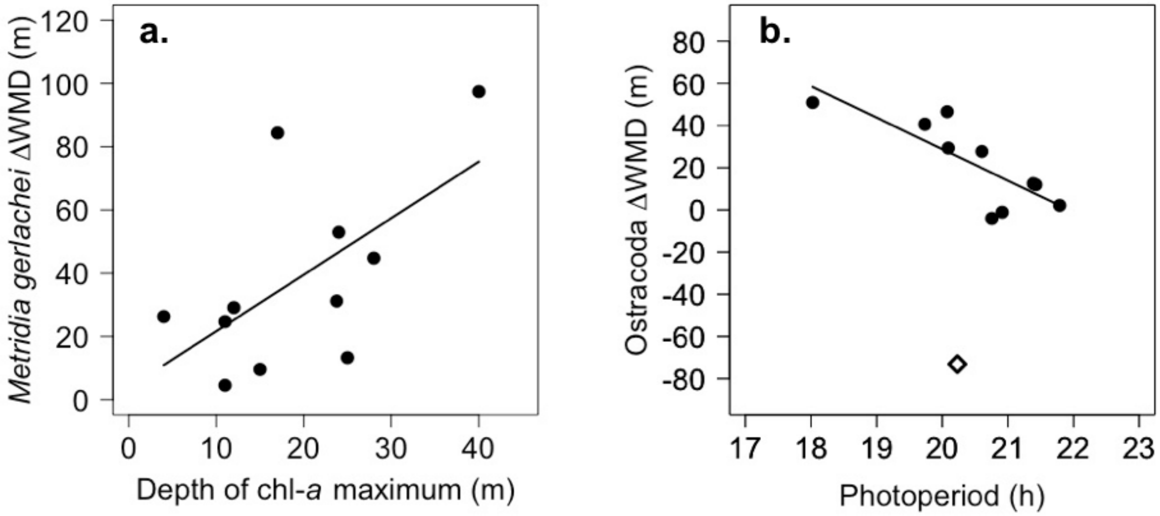

Figure 10. Environmental controls on ΔWMD. (a) Depth of chlorophyll *a* maximum versus *Metridia gerlachei* ΔWMD. (b) Photoperiod versus Ostracod ΔWMD. Solid lines indicate the linear regression with all *M. gerlachei* data points and without the ostracod outlier value, indicated by an open diamond. *M. gerlachei*: $n = 11$, $p = 0.048$, $R^2 = 0.30$; Ostracod (without outlier): $n = 10$, $p = 0.005$, $R^2 = 0.60$.

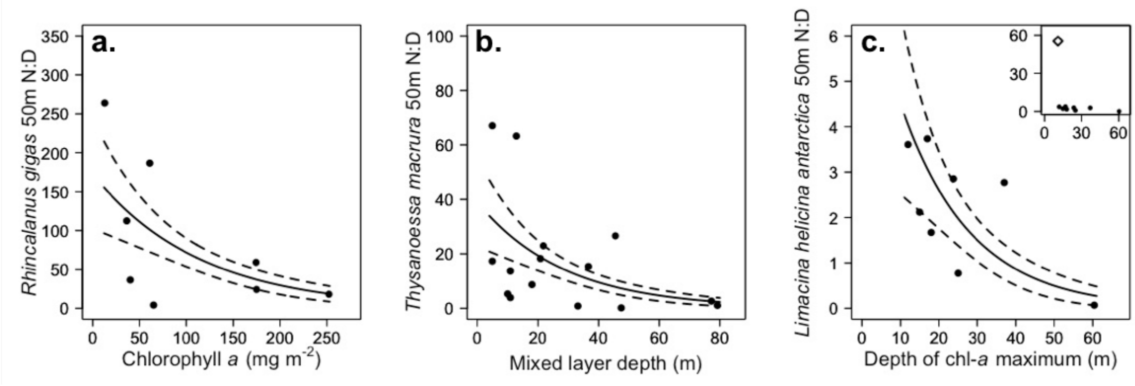

Figure 11. Environmental controls on 50 m N:D. (a) Depth-integrated chlorophyll *a* concentration versus *Rhincalanus gigas* 50 m N:D. (b) Mixed layer depth versus *Thysanoessa macrura* 50 m N:D. (c) Depth of chlorophyll *a* maximum versus *Limacina helicina antarctica* 50 m N:D. Inset includes an outlier *L. h. antarctica* 50 m N:D value indicated by an open diamond. Solid line indicates generalized linear model fit. Dashed lines indicate one standard error. *R. gigas*: $n = 8$, $p = 0.031$, deviance explained = 35%; *T. macrura*: $n = 15$, $p = 0.008$, deviance explained = 27%; *L. h. antarctica* (without outlier): $n = 8$, $p = 0.035$, deviance explained = 40%.

4. Discussion

4.1. Zooplankton DVM modes

4.1.1. DVM between epipelagic and mesopelagic zones

Four taxa performed consistent DVM between the mesopelagic zone during day and epipelagic zone at night. The copepod *Metridia gerlachei* migrated into the upper 100 m at night, consistent with results from prior studies in the northern WAP (Hopkins, 1985; Lopez and Huntley, 1995; King and LaCasella, 2003). Similarly, a portion of the ostracod community made relatively extensive (~100 m) DVMs resulting in a 21% decrease in abundance from 200-300 m and a 3.5-fold increase in abundance from 0-200 m at night. Ostracod DVM is well-documented in the Atlantic and Pacific Oceans (Angel, 1979; Steinberg et al., 2008). Population-wide DVM by *Salpa thompsoni* from 300 m into surface waters supports previous observations throughout the Southern Ocean during summer (Piatkowski, 1985; Casareto and Nemoto, 1986; Perissinotto and Pakhomov, 1998; Pakhomov et al., 2011). Although rarely encountered deeper than 300 m during summer, the pteropod *Limacina helicina antarctica* underwent DVM between the epipelagic and upper mesopelagic zones. In the Lazarev Sea, *L. h. antarctica* also conducted DVM from November to February (Hunt et al., 2008). Collectively, *M. gerlachei*, ostracods, *S. thompsoni*, and *L. h. antarctica* constitute an assemblage of strong vertical migrators along the WAP during summer.

Evidence for amphipod, gymnosome pteropod, and *Tomopteris* spp. polychaete DVM was less consistent than for the above species, but these taxa were each more abundant at night compared to day in grid-wide epipelagic tows. All amphipod species were grouped together, but DVM is likely species-specific. For example, the hyperiid amphipod *Cyllopus lucasii* was more abundant through the upper 200 m at night during summer, autumn, and winter in the Lazarev

Sea where there was no evidence for DVM by the hyperiids *Hyperiella dilatata* and *Primno macropa* (Flores et al., 2014). *Themisto gaudichaudii* (synonym *Parathemisto gaudichaudii*) is abundant along the WAP (Steinberg et al., 2015), and this amphipod made DVMs from ~200 m to the surface 50 m in the Atlantic Ocean (Williams and Robins, 1981). Prior evidence for *Clione antarctica* and *Spongiobranchia australis* DVM is inconsistent (Hunt et al., 2008), but our epipelagic day-night abundance data suggest these gymnosome pteropods conduct DVM, likely to feed on their primary prey *L. h. antarctica* (Lalli and Gilmer, 1989; Van der Spoel and Dadon, 1999) in the epipelagic zone at night. At night, *Tomopteris* spp. polychaete abundance decreased 37% from 200-300 m and increased 3-fold in the surface 0-200 m. We suggest a portion of the amphipod, gymnosome, and *Tomopteris* spp. assemblage conducted DVM to feed in the upper 200 m while other individuals remained at depth.

4.1.2. DVM within epipelagic zone

The copepods *Calanoides acutus* and *Rhincalanus gigas* made shallow DVMs from the 50-100 m layer into the upper 50 m at night. Shallow DVMs within the upper 70 m for *C. acutus* and upper 90 m for *R. gigas* were also reported in January near South Georgia (Atkinson et al., 1992a, 1992b). A study in the Drake Passage and northern Antarctic Peninsula found no *C. acutus* DVM during December to March (Huntley and Escritor, 1991), but was limited to vertical resolution of 0-100 and 100-200 m, making it unlikely to detect shallow DVM.

The krill species *Thysanoessa macrura* and *Euphausia crystallorophias* performed shallow DVM. DVM within the epipelagic zone was reported during spring and autumn further north of our study site for *T. macrura* (Loeb and Shulenberger, 1987; Nordhausen, 1994a) and *E. crystallorophias* (using acoustics; Everson, 1987). Summer surveys in the northern WAP (Nordhausen, 1992) and Amundsen Sea (La et al., 2015b) did not detect DVM by *T. macrura* and *E. crystallorophias*, respectively, possibly due to limitations of sampling methods in detecting shallow DVM. Net avoidance by the larger, faster *E. crystallorophias* was not apparent in the northern WAP during winter (Nordhausen et al. 1994b) but was during autumn (Everson, 1987), which could exaggerate the shallow DVM signal and contribute to higher nighttime abundance depicted in Figure 5b.

4.1.3. DVM within mesopelagic zone

Chaetognaths and the copepod *R. gigas* both undertook a modest DVM within the mesopelagic zone between 150 and 300 m, possibly indicating predator-prey coupling. The chaetognaths *Eukronia hamata* and *Sagitta gazellae* predominately fed on the copepods *C. acutus*, *C. propinquus*, and *M. gerlachei* in the upper 200 m of the Weddell Sea in autumn (Hopkins and Torres, 1989). Chaetognaths along the WAP mainly remained in deeper layers during summer to feed on abundant copepod prey. Although less numerous, *R. gigas* is a larger (Gleiber, 2014), and perhaps preferable, copepod prey item compared to *M. gerlachei* or *C. acutus*.

4.1.4. Reverse DVM

The copepod *Paraeuchaeta antarctica* made relatively short reverse DVMs, from 0-50 m during the day to 50-100 m at night. The primarily carnivorous *P. antarctica* is the largest copepod in this study (mean adult prosome length 7 mm; Gleiber, 2014), making it particularly vulnerable to visual predators in surface waters (Aksnes and Giske, 1993; Ohman and Romagnan, 2016). Reverse DVM is adaptive for species susceptible to predators that undertake normal DVM (Ohman et al., 1983). The reverse DVM of *P. antarctica* is likely used to avoid vertically migrating visual predators.

4.2. Non-migrating zooplankton

4.2.1. Epipelagic non-migrators

The copepod *Calanus propinquus* was concentrated in the upper 50 m and did not consistently undertake DVM. *Calanus propinquus* feeds omnivorously (Atkinson, 1998; Pasternak and Schnack-Schiel, 2001) and was concentrated in the upper 100 m year-round in the Scotia Sea (Atkinson and Sinclair, 2000). Therefore, it appears *C. propinquus* typically remains resident in surface waters on both seasonal and diel time scales.

The negligible difference between night and day *E. superba* abundance in our 120 m tows was expected since this depth was selected to collect Antarctic krill across its main summer depth range (Ross et al., 1996). Acoustic studies have documented sporadic DVM within the upper 100 m during summer while DVM is more pronounced during spring and autumn (Everson, 1983; Godlewska and Klusek, 1987; Demer and Hewitt, 1995; Ross et al., 1996). The daytime formation of larger schools and nighttime dispersal into smaller schools may be a more consistent predator avoidance behavior for *E. superba* in the summer (Everson, 1983; Zhou and Dorland, 2004; Tarling et al., 2018).

4.2.2. Mesopelagic carnivores and detritivores

The copepod *P. antarctica*, ostracods, chaetognaths, and *Tomopteris* spp. polychaetes were concentrated in the mesopelagic zone regardless of the diel cycle, and together compose a deep carnivorous and detritivorous assemblage. The carnivorous *P. antarctica* (synonym *Euchaeta antarctica*) preyed mainly on other copepods in the Weddell Sea (Hopkins and Torres, 1989) and near South Georgia where feeding continued through winter (Øresland and Ward, 1993). Thus, *P. antarctica* likely remains resident in the mesopelagic zone where metazoan prey is sufficiently abundant throughout the year. While vertically migrating ostracods feed in productive surface waters, the more numerous mesopelagic residents feed as carnivores or detritivores (Angel, 1972; Lampitt et al., 1993; Vannier et al., 1998). Elevated ostracod abundance from 200-500 m was also observed in the northern WAP during summer (Blachowiak-Samolyk and Żmijewska, 1997) and in Marguerite Bay during autumn (Marrari et al., 2011). Chaetognaths along the WAP likely remained in deeper layers during summer to feed on abundant copepod prey as previously discussed. Chaetognaths were the numerically dominant macrozooplankton in the mesopelagic zone throughout the year in the Lazarev Sea (Flores et al., 2014) and are similarly important in the WAP mesopelagic zone. Small *Tomopteris* spp. polychaetes in the epipelagic zone fed on phytoplankton in the northern WAP during summer (Phleger et al., 1998) and during autumn in the Weddell Sea (Hopkins and Torres, 1989). However, *Tomopteris spp*. polychaetes in the mesopelagic zone are carnivores or detritivores (Steinberg et al., 1994; Jumars et al., 2015). In particular, individuals larger than 20 mm are primarily carnivorous (Jumars et al. 2015), and large *Tomopteris* spp. individuals in our study exceeded 60 mm, further supporting their role as carnivores in the mesopelagic zone.

Amphipods and gymnosome pteropods were distributed throughout the water column, with a substantial portion of the population residing in the mesopelagic zone during day and night. A diet study in the Weddell Sea during March found multiple amphipod species were feeding mainly on copepods, larval euphausiids, and gelatinous zooplankton (Hopkins and Torres, 1989). Therefore, carnivory explains increased amphipod density below 100 m where metazoan prey is abundant. Although the highest gymnosome abundance was in surface waters, their consistent mesopelagic presence suggests gymnosomes consume other prey in addition to the shelled pteropod *L. h. antarctica.* A genetic diet analysis of the Arctic *Clione limacina* found this species fed on amphipods and calanoid copepods in addition to shelled pteropods (Kallevik, 2013). Similar to other mesopelagic zooplankton, amphipods and gymnosome pteropods likely have multiple feeding modes.

4.2.3. Seasonal vertical migrators

The copepods *M. gerlachei*, *R. gigas*, and *C. acutus* all make seasonal vertical migrations, although *M. gerlachei* and *R. gigas* feed through winter while *C. acutus* enters diapause at depth once it has acquired sufficient lipid reserves (Atkinson, 1998; Pasternak and Schnack-Schiel, 2001; Schnack-Schiel, 2001). Elevated mesopelagic concentrations for these species in our study are more similar to autumn or winter depth distributions farther north in the Scotia Sea (Atkinson and Sinclair, 2000; Ward et al., 2012). High *M. gerlachei* and *R. gigas* concentrations from 200-500 m are likely indicative of carnivorous and detritivorous feeding, which may be more important along the WAP where the productive season is shorter vs. lower latitudes. High mesopelagic abundance indicates *C. acutus* adults were likely in diapause and had not yet fully begun their ascent (Atkinson and Shreeve, 1995) in the Far South where we sampled pre-bloom conditions and mean depth-integrated chl-*a* was only 38 mg m^{-2}. Reduced seasonal sea ice coverage coincident with increasing phytoplankton biomass in the PAL LTER study area (Stammerjohn et al., 2008; Montes-Hugo et al., 2009) may result in earlier ascents for seasonally migrating copepods.

Indications that the pteropod *L. h. antarctica* conducts a seasonal vertical migration to feed in WAP surface waters during summer and overwinter at depth include that this species was concentrated from 0-100 m during our sampling but was most abundant from 100-200 m during autumn in Marguerite Bay (Marrari et al., 2011). Furthermore, *L. h. antarctica* is typically absent from a moored sediment trap sampling at 170 m on the WAP shelf during summer but commonly collected from June to October (Thibodeau et al., in review). A seasonal vertical migration for the closely related *Limacina helicina helicina* is also suggested in the Arctic Ocean (Kobayashi, 1974).

4.3. Environmental controls on DVM

4.3.1. DVM between epipelagic and mesopelagic zones

The copepod *M. gerlachei* and ostracods made shorter DVMs as photoperiod increased from 17 to 22 h, consistent with previous work demonstrating the sensitivity of polar zooplankton to seasonal irradiance cycles. Acoustic studies throughout the Southern Ocean (64°S to 74°S) suggest that DVM ceases during summer (Cisewski et al., 2010; Cisewski and Strass, 2016; Picco et al., 2017). In these studies, sound scattering layers remained in surface waters around-the-clock rather than descending during the day. However, our results show some taxa continue to migrate between the epipelagic and mesopelagic zones, responding to relatively small changes in photoperiod during Antarctic summer from 64°S to 70°S.

Metridia gerlachei made DVMs over a greater depth range when Z_{SCM} was deeper, likely due to changing phytoplankton availability and predation risk. Deeper Z_{SCM} was associated with reduced light attenuation. With a deep Z_{SCM}, *M. gerlachei* encountered maximum phytoplankton concentrations farther from the surface at night, but DVM distance increased as *M. gerlachei* migrated deeper to avoid visual predators during day. This finding is consistent with previous work in the southern California Current, where reduced light attenuation was associated with longer DVM distances – particularly deeper daytime depths – for migrating copepods (Ohman and Romagnan, 2016). *Metridia gerlachei* (mean prosome length 3 mm; Gleiber, 2014) is within the size range of the strongest vertical migrators in that study, and therefore may be similarly susceptible to visual predators. Z_{SCM} thus influences *M. gerlachei* DVM distance directly by concentrating prey distribution and indirectly by modulating predation threat (i.e., via light attenuation).

Ostracods made shorter DVMs when MLD was deeper, likely because migrating ostracods ascended from the mesopelagic zone at night until reaching elevated phytoplankton concentrations in the mixed layer. A shallow mixed layer results in a longer nighttime feeding ascent and a longer return to mesopelagic daytime residence depth. In an acoustic study during Arctic autumn, migrating zooplankton sound scattering layers were coincident with, or just below, the MLD at midnight (Berge et al., 2014). Deeper MLD is associated with reduced sea ice coverage along the WAP (Schofield et al., 2018), which may result in shorter ostracod DVMs under future regional climate conditions.

4.3.2. DVM within epipelagic zone

Depth-integrated chlorophyll *a* concentration influenced DVM by the copepod *R. gigas* within the epipelagic zone. *Rhincalanus gigas* remained in the surface 0-50 m during day and night to feed on elevated phytoplankton biomass, as indicated by decreasing N:D with increasing chl-*a*. Gut content analysis showed *R. gigas* feeds primarily on phytoplankton during summer (Pasternak and Schnack-Schiel, 2001). Elevated chl-*a* was also associated with increased light attenuation, reducing the susceptibility of *R. gigas* to visual predators in surface waters and limiting any benefit gained by daytime migration out of the upper 50 m. Future long-term declines in regional sea ice coverage, upper ocean stability, and chl-*a* concentration in the PAL LTER study region (Montes-Hugo et al., 2009; Brown et al., 2019) may increase the amplitude of *R. gigas* DVM.

The 0-50 m N:D ratio for the euphausiid *T. macrura* and for the pteropod *L. h. antarctica* increased with shallower MLD and Z_{SCM}, respectively, as these taxa appeared to cue on vertical phytoplankton distribution. MLD and Z_{SCM} were positively correlated in our study. We suggest increased 0-50 m N:D indicates a larger portion of the population migrated into the upper 50 m at night when phytoplankton was concentrated near the surface. When MLD and Z_{SCM} were deeper, *T. macrura* and *L. h. antarctica* DVM into the upper 50 m likely decreased because phytoplankton availability and predator avoidance were both maximized below the 50 m threshold of our sampling resolution. During autumn, Arctic zooplankton sound scattering layers migrated to the MLD at midnight (Berge et al., 2014). Migrating pteropods and copepods ascended to the Z_{SCM} at night during Arctic summer (Daase et al., 2016). Deeper MLD under reduced sea ice conditions along the WAP (Schofield et al., 2018) may result in deeper nighttime distributions for *T. macrura* euphausiids and *L. h. antarctica* pteropods.

4.4. Zooplankton-mediated carbon export

Zooplankton vertical structure and behavior play key roles in mediating carbon export (Steinberg and Landry, 2017; Cavan et al., 2019), and regional, taxon-specific data are needed to accurately model the contribution of zooplankton DVM to the global biological carbon pump (e.g., Aumont et al., 2018; Archibald et al., 2019). DVM between the epipelagic and mesopelagic zones by WAP zooplankton through Antarctic summer likely results in substantial active carbon transport out of the euphotic zone, which may help resolve surprisingly low regional particle export to primary production ratios (Stukel et al., 2015; Ducklow et al., 2018). Zooplankton DVM is an important control on POC export in the Scotia Sea (Cavan et al., 2015; Liszka et al., 2019), and likely plays a similar role along the WAP where zooplankton fecal pellets constitute 67% of summer POC flux at 170 m (Gleiber et al., 2012). Future work also should estimate active transport of dissolved carbon (i.e., respiration of CO_2 and excretion of DOC at depth). Additionally, seasonal vertical migrators (e.g., *C. acutus* copepods and *L. h. antarctica* pteropods) transfer carbon to the ocean interior as they respire and die in the mesopelagic zone, but this “lipid pump” (for copepods) is yet to be quantified in the Southern Ocean (Kobari et al., 2008; Jónasdóttir et al., 2015). Abundant mesopelagic zooplankton also consume sinking detritus and produce fecal pellets, which regulates POC availability to mesopelagic and benthic food webs (Wilson et al., 2008; Belcher et al., 2017). Our findings show it will be essential to consider species feeding ecology and variable DVM amplitudes when assessing zooplankton roles in Southern Ocean carbon cycling. Finally, documented long-term changes in WAP zooplankton composition (e.g., Steinberg et al., 2015; Thibodeau et al., 2019) as well as phytoplankton biomass and vertical distribution (e.g., Brown et al., 2019) will alter zooplankton-mediated export pathways.

Author contributions

John A. Conroy: Conceptualization, Investigation, Formal analysis, Visualization, Writing – original draft. **Deborah K. Steinberg:** Conceptualization, Methodology, Investigation, Writing – review & editing, Funding acquisition. **Patricia S. Thibodeau:** Conceptualization, Investigation, Writing – review & editing. **Oscar Schofield:** Conceptualization, Investigation, Writing – review & editing.

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Supplemental Table 1. Diel, depth-integrated zooplankton abundance (0-150 m) from MOCNESS tows along the WAP continental shelf. For euphausiids and *Salpa thompsoni*, Day and Night n = 22 (samples from 2009-2017). For all other taxa, Day and Night n = 17 (samples from 2009-2015). Night:Day n varies because taxa were not always present in both day and night paired tows. p-values are for the paired t-test comparing log-transformed day-night abundance values when a taxon was present in both tows.

	Day (individuals m^{-2})		**Night (individuals m^{-2})**		**Night:Day**			
Taxon	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	***p t*-test**	***n***
Calanoid copepods								
Metridia gerlachei	168.7	114.0	494.0	169.3	80.2	45.1	0.00004	17
Calanoides acutus	71.8	17.1	74.5	17.5	1.5	0.5	0.64	17
Calanus propinquus	21.2	9.9	15.5	5.0	3.0	0.9	0.47	16
Rhincalanus gigas	5.9	1.4	5.5	1.1	2.9	1.2	0.68	16
Paraeuchaeta antarctica	1.3	0.3	1.8	0.4	4.0	2.1	0.39	12
Euphausiids								
Thysanoessa macrura	10.3	3.3	15.1	3.5	5.0	2.2	0.024	22
Euphausia crystallorophias	2.0	1.0	3.9	2.8	3.5	1.4	0.56	11
Other crustaceans								
Ostracoda	9.3	2.9	38.4	13.0	7.5	2.7	0.0002	16
Amphipoda	2.4	0.5	3.6	1.1	2.5	1.2	0.78	15
Gelatinous zooplankton								
Salpa thompsoni	1.6	1.1	8.4	7.9	6.0	3.0	0.76	3
Limacina helicina antarctica	7.5	3.6	10.1	3.5	3.5	1.1	0.008	13
Gymnosomata	2.6	1.5	1.0	0.3	1.4	0.5	0.40	12
Chaetognatha	31.7	7.5	28.1	5.4	1.6	0.4	0.90	17
***Tomopteris* spp.**	0.25	0.1	0.5	0.1	5.1	2.7	0.14	9

Supplemental Table 2. Diel, depth-integrated zooplankton abundance (0-50 m) from MOCNESS tows along the WAP continental shelf. For euphausiids and *Salpa thompsoni*, Day and Night *n* = 22 (samples from 2009-2017). For all other taxa, Day and Night *n* = 17 (samples from 2009-2015). Night:Day *n* varies because taxa were not always present in both day and night paired tows. *p*-values are for the paired *t*-test comparing log-transformed day-night abundance values when a taxon was present in both tows.

	Day (individuals m^{-2})		**Night (individuals m^{-2})**		**Night:Day**			
Taxon	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	***p t*-test**	***n***
Calanoid copepods								
Metridia gerlachei	29.2	10.9	127.4	64.4	889.5	884.0	0.044	13
Calanoides acutus	19.2	5.4	34.7	10.6	2.4	0.3	0.000	12
Calanus propinquus	15.6	9.6	10.4	4.2	14.7	12.6	0.25	8
Rhincalanus gigas	1.2	0.4	1.6	0.6	79.4	30.3	0.000	9
Paraeuchaeta antarctica	10.4	4.2	0.4	0.1	0.3	0.1	0.004	9
Euphausiids								
Thysanoessa macrura	3.4	2.5	8.1	2.3	17.3	5.1	0.000	16
Euphausia crystallorophias	0.3	0.2	3.2	2.5	9.9	3.2	0.034	7
Other crustaceans								
Ostracoda	4.1	1.7	5.0	1.8	2.3	0.9	0.53	11
Amphipoda	0.9	0.5	0.7	0.2	1.5	0.4	0.66	10
Gelatinous zooplankton								
Salpa thompsoni	0.5	0.3	2.9	2.9	4.3	3.7	0.80	3
Limacina helicina antarctica	3.5	1.7	6.0	2.3	8.1	5.9	0.21	9
Gymnosomata	1.7	1.5	0.5	0.2	0.9	0.3	0.35	6
Chaetognatha	2.9	0.9	2.6	0.8	1.8	0.6	0.44	13
***Tomopteris* spp.**	0.06	0.1	0.1	0.1	0.5	NA	NA	1

Supplemental Table 3. Summary of model selection statistics from multiple linear regression models assessing the impact of environmental variables on *Metridia gerlachei* ΔWMD from MOCNESS tows (0-500 m) along the WAP continental shelf from 2009-2015. Statistics – AICc: corrected Akaike Information Criterion; ΔAICc: difference from lowest AICc; AICc weight – relative model support or probability. Explanatory variables – Photoperiod: day length; Z_{SCM}: depth of subsurface chlorophyll *a* maximum; MLD: mixed layer depth; Chl: chlorophyll *a* concentration depth-integrated to 100 m; $Z_{1\%}$: depth of 1% surface irradiance.

Explanatory variables	**AICc**	**ΔAICc**	**AICc weight**
Photoperiod + Z_{SCM}	101.3	0.00	0.967
Z_{SCM}	109.3	7.95	0.018
Photoperiod	111.2	9.83	0.007
MLD	113.9	12.60	0.002
Chl	114.1	12.72	0.002
Photoperiod + MLD	114.2	12.85	0.002
$Z_{1\%}$	114.3	12.99	0.001
Photoperiod + $Z_{1\%}$	116.4	15.05	0.001
Photoperiod + Chl	116.4	15.07	0.001

Supplemental Table 4. Summary of model selection statistics from multiple linear regression models assessing the impact of environmental variables on Ostracoda ΔWMD from MOCNESS tows (0-500 m) along the WAP continental shelf from 2009-2015. Statistics and explanatory variables as defined for Supplementary Table 3.

Explanatory variables	**AICc**	**ΔAICc**	**AICc weight**
Photoperiod + MLD	85.2	0.00	0.666
Photoperiod	87.1	1.96	0.250
MLD	91.3	6.13	0.031
Photoperiod + Chl	92.1	6.91	0.021
Photoperiod + $\mathbf{Z_{SCM}}$	92.8	7.69	0.014
Photoperiod + $\mathbf{Z_{1\%}}$	93.0	7.84	0.013
$\mathbf{Z_{1\%}}$	97.2	12.09	0.002
$\mathbf{Z_{SCM}}$	97.3	12.18	0.002
Chl	97.4	12.22	0.001

Supplemental Table 5. Summary of model selection statistics from generalized linear models (with a gamma error distribution and log link function) assessing the impact of environmental variables on *Rhincalanus gigas* MOCNESS 50 m N:D along the WAP continental shelf from 2009-2015. Statistics and explanatory variables as defined for Supplementary Table 3.

Explanatory variables	AICc	ΔAICc	AICc weight
Chl	95.7	0.00	0.386
Z_{SCM}	96.6	0.88	0.248
$Z_{1\%}$	97.3	1.56	0.177
MLD	97.9	2.22	0.127
Photoperiod	99.7	3.99	0.052
Photoperiod + Chl	105.0	9.29	0.004
Photoperiod + Z_{SCM}	105.8	10.10	0.002
Photoperiod + $Z_{1\%}$	106.0	10.32	0.002
Photoperiod + MLD	106.7	11.00	0.002

Supplemental Table 6. Summary of model selection statistics from generalized linear models (with a gamma error distribution and log link function) assessing the impact of environmental variables on *Thysanoessa macrura* MOCNESS 50 m N:D along the WAP continental shelf from 2009-2017. Statistics and explanatory variables as defined for Supplementary Table 3.

Explanatory variables	**AICc**	**ΔAICc**	**AICc weight**
MLD	117.8	0.00	0.449
Photoperiod + MLD	119.2	1.44	0.218
$Z_{1\%}$	120.7	2.95	0.103
Chl	121.7	3.96	0.062
Photoperiod	122.0	4.19	0.055
Z_{SCM}	122.4	4.64	0.044
Photoperiod + Chl	123.0	5.19	0.033
Photoperiod + Z_{SCM}	124.0	6.24	0.020
Photoperiod + $Z_{1\%}$	124.0	6.59	0.017

Supplemental Table 7. Summary of model selection statistics from generalized linear models (with a gamma error distribution and log link function) assessing the impact of environmental variables on *Limacina helicina antarctica* MOCNESS 50 m N:D along the WAP continental shelf from 2009-2015. Statistics and explanatory variables as defined for Supplementary Table 3.

Explanatory variables	AICc	ΔAICc	AICc weight
Z_{SCM}	35.8	0.00	0.627
Photoperiod	39.4	3.55	0.106
Chl	39.7	3.87	0.091
MLD	39.8	3.96	0.087
$Z_{1\%}$	40.0	4.19	0.077
Photoperiod + Z_{SCM}	44.2	8.41	0.009
Photoperiod + MLD	48.4	12.57	0.001
Photoperiod + Chl	48.5	12.70	0.001
Photoperiod + $Z_{1\%}$	48.7	12.86	0.001