Meso- and macro-zooplankton community structure of the Amundsen Sea Polynya, Antarctica (Summer 2010–2011)

Stephanie E. Wilson1* • Rasmus Swalethorp2,3 • Sanne Kjellerup2,3,4 • Megan A. Wolverton1 • Hugh W. Ducklow6 • Patricia L. Yager7

1Bangor University, School of Ocean Sciences, Menai Bridge, United Kingdom
2Department of Biology and Environmental Sciences, University of Gothenburg, Göteborg, Sweden
3DTU Aqua, Technical University of Denmark, Charlottenlund, Denmark
4Greenland Climate and Research Center, Greenland Institute of Natural Resources, Nuuk, Greenland
5Arizona State University, Tempe, Arizona, United States
6Lamont-Doherty Earth Observatory, Columbia University, Palisades, New York, United States
7University of Georgia, Athens, Georgia, United States

*stephanie.wilson@bangor.ac.uk

Abstract

The Amundsen Sea Polynya (ASP) has, on average, the highest productivity per unit area in Antarctic waters. To investigate community structure and the role that zooplankton may play in utilizing this productivity, animals were collected at six stations inside and outside the ASP using paired “day-night” tows with a 1 m² MOCNESS. Stations were selected according to productivity based on satellite imagery, distance from the ice edge, and depth of the water column. Depths sampled were stratified from the surface to ~ 50–100 m above the seafloor. Macrozooplankton were also collected at four stations located in different parts of the ASP using a 2 m² Metro Net for krill surface trawls (0–120 m). The most abundant groups of zooplankton were copepods, ostracods, and euphausiids. Zooplankton biovolume (0.001 to 1.22 ml m⁻³) and abundance (0.21 to 97.5 individuals m⁻³) varied throughout all depth levels, with a midsurface maximum trend at ~ 60–100 m. A segregation of increasing zooplankton trophic position with depth was observed in the MOCNESS tows. In general, zooplankton abundance was low above the mixed layer depth, a result attributed to a thick layer of the unpalatable colonial haptophyte, Phaeocystis antarctica. Abundances of the ice krill, Euphausia crystallarophias, however, were highest near the edge of the ice sheet within the ASP and larvae:adult ratios correlated with temperature above a depth of 60 m. Total zooplankton abundance correlated positively with chlorophyll a above 150 m, but negative correlations observed for biovolume vs. the proportion of P. antarctica in the phytoplankton estimated from pigment ratios (19’hexanoyloxyfucoxanthin:fucoxanthin) again pointed to avoidance of P. antarctica. Quantifying zooplankton community structure, abundance, and biovolume (biomass) in this highly productive polynya helps shed light on how carbon may be transferred to higher trophic levels and to depth in a region undergoing rapid warming.

Introduction

The structure of planktonic communities can play a defining role in the export, retention, and eventual fate of surface-derived organic carbon (Legendre and Rassoulzadegan, 1996; Boyd and Newton, 1999; Wilson et al., 2008). Variations in climate have been shown to affect planktonic communities in regions worldwide and will likely have an effect on export fluxes to the deep sea (Lavaniegos and Ohman, 2007; Richardson, 2008; Steinberg et al., 2012). In Antarctic waters, for instance, the observed shift in abundance from krill to salps as the dominant zooplankton species as a result of decreasing winter sea ice in the Western Antarctic Peninsula region may cause a significant change in carbon export (Atkinson et al., 2004; Gleiber et al., 2012).
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Polynyas, seasonally occurring areas of open water surrounded by sea ice, are important sources of primary productivity along the continental shelf of Antarctica (Arrigo and Van Dijken, 2003; Arrigo and Alderkamp, 2012). Antarctic polynyas are hypothesized to be unusually productive because the additional iron input from melting sea ice can help fuel phytoplankton blooms (Raiswell et al., 2006; Alderkamp et al., 2012; Arrigo et al., 2012). Usually these areas are the earliest to be productive in a season and attract many higher trophic level Antarctic species (Arrigo and Van Dijken, 2003). The numbers of polynyas are expected to increase with global climate change, an increase that, with additional sea ice melting, will impact primary productivity, food web structures, and carbon export (Ainley et al., 2005; Stammerjohn et al., 2008; Alderkamp et al., 2012).

Few studies directly consider the impact of Antarctic polynyas on zooplankton, although there are more such studies for the Arctic (e.g., Ashjian et al., 1997; Tagliabue and Arrigo, 2003; Deibel and Daly, 2007; Lee et al., 2012). Factors influencing zooplankton abundance and biomass in polynyas include advection from local waters, diatom productivity, and the presence or absence of the colonial haptophyte, Phaeocystis antarctica (Ashjian et al., 1997; Tagliabue and Arrigo, 2003; Deibel and Daly, 2007). Of particular interest is the Amundsen Sea Polynya, which has the highest phytoplankton biomass and rates of primary productivity per unit area in Antarctic waters (Arrigo and Van Dijken, 2003; Alderkamp et al., 2012). P. antarctica dominates the phytoplankton assemblage in the ASP, with diatoms more prevalent closer to the ice edges (Arrigo and McClain, 1994; Lee et al., 2012). From Ross Sea studies, there is little evidence that P. antarctica is grazed frequently by zooplankton (Caron et al., 2000; Tagliabue and Arrigo, 2003).

There is little information available about the zooplankton biomass and community structure within the ASP itself, especially below 200 m. Lee et al. (2013) sampled Amundsen Sea zooplankton above 200 m in the Austral summer of 2010–2011 and observed high abundances of copepods outside the ASP and of the euphausiid E. crystallorophias, the major ASP grazer, inside the ASP. Further investigating depth-specific trends in zooplankton distribution from the surface to the seafloor is of interest as a prerequisite for understanding the fate of ASP primary production and potential implications of warming seas.

The objective of the Amundsen Sea Polynya International Research Expedition (ASPIRE) was to investigate factors as to why the Amundsen Sea Polynya has such high rates of primary productivity per unit area compared to other Antarctic polynyas (Yager et al., 2012). The ASPIRE team also desired to understand the fate of this productivity. The aims of this study were to describe and quantify depth-specific zooplankton community structure and biovolume within the ASP as part of ASPIRE during the austral summer of 2010–2011. The results of this study were compared to other biological-physical parameters; e.g., chlorophyll a, pigments ratios indicative of diatoms vs. Phaeocystis measured via high performance liquid chromatography (HPLC) and mixed layer depth (MLD), as measured during the cruise and presented in this and other papers (e.g., Yager et al., 2014) of this Special Feature. The main objectives of this study were to determine which factors are structuring the zooplankton community and begin to assess how this community may utilize the unusually high primary productivity of the polynya and the potential effects on particulate organic carbon (POC) flux out of the system.

Methods

Zooplankton sampling and processing were carried out onboard the RV Nathaniel B. Palmer NBP 10–05 as part of the multidisciplinary Amundsen Sea Polynya International Research Expedition (ASPIRE), and in collaboration with the Swedish Antarctic Research Programme (SWEDARP), between 19 December 2010 and 8 January 2011 (Yager et al., 2012). For a more in-depth description of the study area, see other papers in this special feature.

Twelve oblique plankton tows using the Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS) with a 1 m² opening (333 µm mesh) were executed within and around the ASP region at noon and midnight as “day/night” pairs (green labels, Figure 1). Day/night pairs were utilized at each station, as the intensity of the diel periodicity of zooplankton in the ASP is unknown. Zooplankton in the ASP had not been sampled prior to this study. The tow speed was 15 m min⁻¹ and ship speed was 2 knots. The tow locations and depth intervals were selected according to bathymetry, depth of the water column, productivity, and distance from the ice edge. Three shallow “MOC” tow locations were conducted on the shelf below the ASP (ASPIRE “long daily” stations 13, 25 and 35, respectively), two within a deep trough region on the shelf (Yager et al., 2012), where potential warmer and nutrient-rich Circumpolar Deep Water (CDW) may be intruding (ASPIRE stations 50 and 57), and one on the shelf slope outside the polynya (ASPIRE station 68), where CDW may be entering the shelf into the trough (e.g., Wahlin et al., 2010; Randall- Goodwin et al., 2014). Station 57 was also located near a large iceberg (Randall-Goodwin et al., 2014). Depths sampled were stratified at eight intervals from the surface to approximately 50–100 m above the seafloor.

In addition, four 2 m² Metro net (700 µm mesh) krill surface trawls (0–120 m) were also taken throughout the ASP (blue labels, Figure 1), with two tow stations selected due to close proximity to the ice margin (ASPIRE stations 57 and 66) and two selected in open water regions (ASPIRE stations 29 and 35). The 2 m² 700 µm mesh Metro net was used in addition to the MOCNESS to focus on collecting larger krill
species that can avoid smaller nets and also to have results comparable to other studies in the region (e.g., Ross et al., 1988; Ross et al., 2008). Due to potential damage of the nets by brash ice accumulation around the edges of the polynya, no net sampling was initiated at the ice edge itself.

Immediately following collection, zooplankton > 5 mm were live-processed and quantified onboard the NB Palmer for species abundance and biovolume (as a proxy for biomass) measured as displacement volume. The large, > 5 mm fraction of zooplankton were counted and identified onboard. The biovolumes were measured individually for each species or group identified; total biovolume was measured for each tow. In cases where there was a visible (thick green mats) presence of the colonial haptophyte *Phaeocystis antarctica* in the cod-end buckets, all of the individual zooplankton species biovolumes were summed for that depth to measure a total *Phaeocystis*-free biovolume (generally in the top three or four depth intervals). The remaining individuals in the samples were split using a Folsom plankton splitter as follows: 1/2 of each tow was split and preserved in alcohol and archived, 1/4 was preserved in 10% buffered formalin for further taxonomic identification of the smaller individuals, and 1/4 was frozen in -80°C for separate analyses. Krill species collected from the Metro tows were also enumerated onboard, 50–100 were randomly selected and measured for total length, and total biovolume was measured. All tows were counted and preserved in entirety except MET 66, which was split 1/15. Laboratory analysis consisted of zooplankton taxonomic identification with size-fractionated aliquots of 5 mm–500 µm and 500–333 µm samples from the MOCNESS tows.

Depth-integrated zooplankton biovolume and abundance (ml m⁻² and ind m⁻³, respectively) were also calculated to compare with independent sampling results, including chlorophyll *a* and pigment ratios associated with diatoms and *Phaeocystis* (Alderkamp et al., 2014). Chlorophyll *a* and pigments were normalized to the same depths as the MOCNESS tows; trapezoidal integration was utilized to calculate depth-integrated concentrations (mg m⁻³). These results will help to determine if primary productivity or phytoplankton community structure play a role in zooplankton distribution and biomass within the ASP. Weighted mean depths (WMD) were calculated for taxa found in several depth intervals on every day-night sampling event using the following equation:

\[
WMD = \frac{\sum n_i d_i}{\sum n_i},
\]

where *d* is the mean depth of the sampled depth interval *s* and *n* is the abundance (ind m⁻³) (Bollens and Frost, 1989).
Statistical testing was conducted using the software packages Minitab 16 and Primer 6. Biomass and abundance data for each station and depth were assumed nonparametric (Kolmogorov-Smirnov test for normal distribution); therefore, Mann-Whitney U tests were used to compare data between stations. When pooled across all depths and stations, and for individual species, a Mann-Whitney U test was also used to compare day to night values. The Pearson’s R correlation coefficient was calculated for pooled data to compare abundance and biomass with salinity, chlorophyll $a$, and HPLC pigments. A Bray-Curtis similarity index was plotted with 2D Multidimensional Scaling (MDS) to compare grouped species abundances (ind m$^{-3}$) between stations and depths. A further ANOSIM test on 4th root-transformed abundances was used to determine significance.

Results

**Mesozooplankton distribution and community structure – MOCNESS**

Zooplankton MOCNESS biomass in the form of biovolume density ranged from 0.001 ml m$^{-3}$ at 10–30 m depth at MOC 57 to 1.22 ml m$^{-3}$ at 0–10 m depth at MOC 13 (Figure 2). Abundance values ranged from 0.21 ind m$^{-3}$ at 0–10 m depth at MOC 25 to 97.5 ind m$^{-3}$ at 60–100 m depth at MOC 13, (Figure 3). Biovolume and abundance were significantly correlated (Pearson correlation, R$_p$ = 0.27, p = 0.01). Low zooplankton values were measured above 60 m (biovolume) and 30 m (abundance), with the exception of the value for 0–10 m at MOC 13 which was high due to the biovolumes of several individuals of the ice krill, *Euphausia crystallorophias*, at this depth. *E. crystallorophias* was the species with the largest total biovolume within the ASP (maximum MOCNESS biovolume of 0.85 ml m$^{-3}$). The subsurface maximum biovolume and abundance of zooplankton was generally between 30 or 60 and 150 m depth and below the mixed layer depth (MLD; Alderkamp et al., 2014). This subsurface maximum was also immediately below the depth where thick aggregates of the haptophyte, *Phaeocystis antarctica*, were observed in the tows along with the zooplankton (Lee et al., 2012; Alderkamp et al., 2014).
Despite 24 h of sunlight, an apparent (not statistically significant) diel periodicity of varying intensity was observed in zooplankton density. Mann-Whitney U tests of pooled MOCNESS abundance and biovolume densities showed insignificant differences between night and day samples (Mann-Whitney, biovolume: $p = 0.14$; abundance: $p = 0.83$). Although not significant, at most stations zooplankton abundance and biovolume were slightly higher during the night. The results of weighted mean depth analyses (WMD) show that zooplankton were distributed shallower in the water column (Table 1). Upon further investigations of the individual species observed in all tows at several depths, WMD calculation results for day and night of individual species were not significantly different (Mann-Whitney, $p > 0.05$), though at five of the six MOC stations *E. crystallarophias* (15 ± 24 m, night-day WDM difference ± SD), amphipods of the genus *Orchomene* (35 ± 70 m), and the calanoid copepods *Metridia gerlachei* (57 ± 59 m) and *Paraeuchaeta antarctica* (25 ± 38 m) were distributed at shallower depths (data not shown).

Crustacean zooplankton comprised the bulk of the zooplankton samples with >90% of the total biomass and abundance. The majority of these zooplankton were calanoid copepods (maximum density of 93 ind m$^{-3}$ at 60–100 m depth at MOC 13), followed by euphausiids and ostracods (Figure 4). Euphausiids dominated in the shallower nets for most stations; copepods, the middle nets; and ostracods, the deeper nets. Proportionally, ostracods were the dominant zooplankton species at the shallower stations: at MOC 13–35 below 250 m and at MOC 68 at 350–500 m (Figure 4). Chaetognaths were observed in all tows and all stations but were present predominately below 100 m. Results of the Bray-Curtis MDS on the MOCNESS species abundance data show similarities between depths (above and below 60 m), but no pattern was apparent between stations (Figure S1). Results of the ANOSIM test show these depth similarities to be significantly different (Global R = 0.44, P = 0.001).

Figure 3 Mesozooplankton abundances (ind m$^{-3}$) of MOCNESS (MOC) tows within and near the ASP. Dashed line indicates mixed layer depth. Note different y axis.

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The most abundant of the euphausiids was *E. crystallarophias* (maximum MOCNESS density of 3.1 ind m$^{-3}$ at 0–10 m depth at MOC 13). Other less common species of krill observed in the polynya were *Thysanoessa macrura*, *E. tricantha*, and *E. frigida*. There were few, if any, salps or *E. superba* observed within the polynya; however, two *E. superba* gravid adult females were found outside the polynya along the shelf edge at MOC 68 at depth intervals 300–500 and 500–800 m. The majority of the calanoid copepods were largely *Calanoides acutus* (maximum density of 62.3 ind m$^{-3}$ at 60–100 m depth at MOC 13) followed by *M. gerlachei*, and *Paraeuchaeta antarctica* (Figure 5). Copepods smaller than 500 µm (e.g., *Oithona* sp.) also comprised a significant proportion of the copepod abundance, especially above 150 m (Figure 4). The majority of *C. acutus* and *M. gerlachei* were distributed between 30 and 150 m at most stations, although *M. gerlachei* also displayed shallow diel vertical migration behavior. *P. antarctica* was the largest in size of the copepods and generally remained below 100 m, with their numbers increasing with depth.

Tow MOC 68, outside the polynya, did not show any significant difference with stations within the polynya in terms of biomass (Figure 3), including depth-integrated cumulative biomass and abundance (Table 1), due to the higher abundances and biovolumes of gelatinous zooplankton within the nets as well as the greater depths involved (Mann-Whitney, p > 0.05). However, total abundance densities at MOC 68 were significantly less than within the ASP (Mann-Whitney, p = 0.046; Figure 2). MOC 68 also showed a difference in species distribution from the stations within the polynya (Figure 4). Fewer euphausiids were observed at MOC 68 in proportion to other species along with higher proportions of appendicularians

Table 1. Zooplankton depth-integrated cumulative abundance, biovolume, and weighted mean depth (WMD) at day and night from each MOCNESS station

<table>
<thead>
<tr>
<th>Station</th>
<th>Day (ind m$^{-3}$)</th>
<th>Night (ind m$^{-3}$)</th>
<th>Day WMD (m)</th>
<th>Night WMD (m)</th>
<th>Day (ind m$^{-3}$)</th>
<th>Night (ind m$^{-3}$)</th>
<th>Day WMD (m)</th>
<th>Night WMD (m)</th>
</tr>
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<tbody>
<tr>
<td>MOC 13</td>
<td>8816</td>
<td>7262</td>
<td>105</td>
<td>52</td>
<td>35.7</td>
<td>62.2</td>
<td>96</td>
<td>108</td>
</tr>
<tr>
<td>MOC 25</td>
<td>2396</td>
<td>2609</td>
<td>83</td>
<td>95</td>
<td>8.5</td>
<td>15.6</td>
<td>86</td>
<td>65</td>
</tr>
<tr>
<td>MOC 35</td>
<td>3571</td>
<td>5047</td>
<td>151</td>
<td>103</td>
<td>16.1</td>
<td>18.2</td>
<td>89</td>
<td>79</td>
</tr>
<tr>
<td>MOC 50</td>
<td>9244</td>
<td>15585</td>
<td>167</td>
<td>146</td>
<td>55.2</td>
<td>72.1</td>
<td>151</td>
<td>122</td>
</tr>
<tr>
<td>MOC 57</td>
<td>18854</td>
<td>15121</td>
<td>303</td>
<td>261</td>
<td>89.6</td>
<td>60.0</td>
<td>145</td>
<td>185</td>
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<tr>
<td>MOC 68</td>
<td>4315</td>
<td>4186</td>
<td>231</td>
<td>213</td>
<td>40.3</td>
<td>59.0</td>
<td>256</td>
<td>229</td>
</tr>
<tr>
<td>Mean ± SE</td>
<td>7866 ± 2480</td>
<td>8301 ± 2313</td>
<td>173 ± 33</td>
<td>145 ±32</td>
<td>40.9 ± 11.9</td>
<td>47.8 ± 10</td>
<td>137 ± 26</td>
<td>131 ± 26</td>
</tr>
</tbody>
</table>

*SE = standard error of the mean*

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Figure 4

Mesozooplankton functional group numerical proportional abundance.

Abundance is mean of day and night tows for each depth interval. Note different y axis.

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and gelatinous zooplankton (Mann-Whitney: euphausiids, p = 0.07; appendicularians, p = 0.06; gelatinous, p = 0.001). Appendicularians were observed at most depths at MOC 68 although rarely inside the polynya.

**Euphausiid distribution and community structure - Metro net**

Net avoidance can be an issue with larger euphausiids (Wiebe et al., 1982). In this case euphausiid species densities were comparable in range to MOCNESS euphausiid densities with the exception of MET 66, where we encountered a super swarm of *Euphausia crystallarophias*. The highest biovolume of *E. crystallarophias* was observed at MET 66, near the ice margin, where we collected a swarm of approximately 25,000 adults and juveniles (1.8 ml m$^{-3}$, 11.1 ind m$^{-3}$). In comparison, the highest biovolume and abundance of *E. crystallarophias* in the MOCNESS tows was observed at MOC 13 with 0.85 ml m$^{-3}$ and 3.13 ind m$^{-3}$, respectively. MET 29–57 had much lower abundance and biovolume of all species compared to MET 66 (Figure 6A). The dominant krill species collected in the Metro net tows were *E. crystallarophias* and *Thysanoessa macrura* with few, if any, *E. frigida* or *E. superba* (Figure 6B).

**Chlorophyll, pigments, and other parameters**

Log-transforming the data did not change the homoscedasticity of the data set. Zooplankton abundance at all stations and depths was negatively correlated with salinity with high variability (Pearson's R, R$_p$ = –0.26, p = 0.01; Figure 7A), although biovolume was not. Temperature, however, did not correlate with zooplankton abundance or biovolume. A correlation was observed between depth-integrated zooplankton abundance and integrated chlorophyll $a$ in MOCNESS samples collected above 150 m (Pearson's R, R$_p$ = 0.32, p = 0.02; Figure 7B), but not with biovolume. With the ratio of 19'hexanoyloxyfucoxanthin to fucoxanthin (19-hex:fuco) measured from HPLC analysis (Alderkamp et al., 2014), indicative of the prevalence of *Phaeocystis*, the potentially less palatable phytoplankton than diatoms (Smith et al., 2010), a negative correlation was observed with both depth-integrated zooplankton abundance (marginal significance) and biovolume at polynya stations above 150 m (Pearson's R, abundance R$_p$ = –0.26, p = 0.07; biovolume Rp = –0.35, p = 0.01; Figure 7C). Euphausiid nauplii abundance and the calypotopis:adult ratio increased with increasing surface temperature (top 60 m of the water column where nauplii and calyptopis were located; Figure 8), peaking at the warm MOC 57 which also had the highest levels of chl $a$ (916 mg chl $a$ m$^{-3}$).
Zooplankton abundance and biovolumes in the ASP

The results of high resolution (finer depth scale) sampling using the MOCNESS demonstrate that there was a distinct zooplankton biovolume and abundance depth distribution trend within this region during the sampling period. Within the polynya, a subsurface maximum of zooplankton was often observed at approximately 60–100 m, below the mixed layer depth (MLD, Figure 2 and 3). Directly outside of the polynya along the shelf slope at MOC68, where abundance was significantly lower, this depth-distribution trend was not nearly as well resolved. Further north, zooplankton sampling associated with the Swedish Antarctic Research Programme (SWEDARP) in Marguerite Bay during the same cruise (P. Moksness, unpublished data), showed that the highest biovolume was at the surface (0–10 m), nearly double the biovolume of the highest ASP values, and that it decreased step-wise with depth.

In other coastal regions such as the lower Antarctic Peninsula, the overall Metro net zooplankton biovolume was comparable. Zooplankton abundance and biovolume in January 2011 at the Charcot Island process station of the Palmer Long-term Ecological Research (LTER) study (the furthest south and furthest inshore of the LTER sampling grid) were slightly lower than the comparable Metro net tows during ASPIRE (data are available at the LTER DataZoo, http://oceaninformatics.ucsd.edu/datazoo/data/pallter/datasets, dataset number 199). Euphausia crystallarophias was also the dominant krill species at both locations.

Discussion

Zooplankton abundance and biovolumes in the ASP

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Figure 7
Zooplankton distribution correlated to environmental parameters.

A) Zooplankton abundance correlated to salinity (all stations and depths). B) Depth-integrated abundance correlated to depth-integrated chlorophyll $a$ (all stations and depths above 150 m). C) Zooplankton depth-integrated biovolume correlated to hex:fuco (19'-hex :fucoxanthin) a ratio which compares prevalence of *Phaeocystis* to diatoms (all stations and depths above 150 m).

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(Charcot maximum, 2.65 ind m$^{-3}$; ASPIRE maximum, 10.24 ind m$^{-3}$); however, more *E. superba* were present at Charcot than ASP (Charcot maximum, 0.0211 ind m$^{-3}$; ASPIRE maximum, 0.0041 ind m$^{-3}$). Pakhomov and Perissinotto (1996) presented abundance data that led to their conclusion that polynyas provide favorable conditions for spawning and growth of *E. crystallarophias*, which may account for the higher maximum values observed within the ASP.

Within the nearby Ross Sea, where primary productivity is both high and dominated by *Phaeocystis antarctica*, zooplankton biomass was also low compared to other areas within the Southern Ocean such as the Western Antarctic Peninsula (Tagliabue and Arrigo, 2003; Ducklow et al., 2006). The low zooplankton biomass in the Ross Sea, Terra Nova Bay and potentially the ASP, may result from an inability to match the high growth rates of the phytoplankton blooms in the early spring (Tagliabue and Arrigo, 2003). The increase in phytoplankton biomass is due to the presence of *P. antarctica*, which is not necessarily grazed by zooplankton at the same rate due to its colony size and potential chemical deterrents (Bautista et al., 1992; Ducklow et al., 2006).

With high variability, there was a relationship between zooplankton abundance and salinity but not temperature. Similar results were also observed earlier by Lee et al. (2013) in the upper 200 m of the polynya. The relationship to salinity but not temperature may be due to mixing processes in the polynya that include melting glacier and sea ice (Randall-Goodwin et al., 2014). The positive correlation between the ratio of euphausiid nauplii and calyptopis to adults may indicate, however, that temperature was affecting euphausiid reproduction rates at the time of sampling. Euphausiid development rate increases with temperature (Ross et al., 1988; Pinchuk and Hopcroft, 2006) which may also reduce oocyte maturation time and affect when spawning is initiated during the productive season, as has been observed in the North Atlantic copepod *Calanus finmarchicus* (e.g., Niehoff, 2007). Furthermore, the highest chl $a$ concentration found at MOC 57 is also likely to have shortened oocyte maturation time and maximized nutrient assimilation fueling the reproduction (Schmidt et al., 2012).

**Vertical and spatial distribution of species**

We found some differences in community composition within the ASP compared to the outside station. Most notably were the low abundances of gelatinous zooplankton and rarity of appendicularians and salps within the ASP. Salps and appendicularians produce large, dense fecal pellets that can quickly transport small-particle biomass to the seafloor (Anderson, 1998; Phillips et al., 2009); their absence would have an effect on zooplankton-derived POC flux out of the system (Pakhomov et al., 2002; Ducklow et al., 2006). Salps are more common offshore, away from ice regions, and may have thermo-physiological limitations at higher latitudes (Pakhomov et al., 2002; Ward et al., 2004; Ross et al., 2008), which could explain their rarity in the ASP. Appendicularians are less well studied in Antarctic waters but are important producers of sinking carbon flux in Arctic polynyas (Deibel et al., 2007). Lindsey and Williams (2010) observed the highest abundances of larvaeans away from the shelf break and that numbers correlated with latitude in the southwest Indian Ocean region of East Antarctica between 30 and 80° East. Low abundances of appendicularians and salps, both filter feeders, in the ASP may also be due to the presence of *Phaeocystis antarctica*, which are able to alter colony size as a defense strategy against grazers (Tang 2003; Tang et al., 2008) and potentially clog feeding filters (Harbison et al., 1986; Acuña et al., 1989; Kawaguchi et al., 2004).
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Along with biovolume and abundance, we also found that species differed in their vertical distribution (Figures 4 and 5). For example, large carnivorous copepods (e.g., 

Paraeuchaeta antarctica

) and chaetognaths were observed deeper than many of the more herbivorous/ omnivorous species (e.g., Calanoides acutus and Metridia gerlachii). Vertical position in the water column in the ASP may be a trade-off between light levels, feeding, competition, and predator avoidance (Fledgum et al., 2001; Coyle and Pincuk, 2005; Marrari et al., 2011; Rabindranath et al., 2011) resulting in the observed segregation of increasing trophic position with depth.

Diel periodicity was small and night/day biovolume and abundance ratios tended to be larger at night (though not statistically significant; Table 1). Diel vertical migration (DVM) behavior in polar regions generally changes seasonally, with complete cessation during early summer (e.g., Cisewski et al., 2010). With some exceptions, the observed variations in general vertical distribution are not likely due to DVM given the time of year; however, specific organisms M. gerlachii, 

Paraeuchaeta antarctica

, E. crystallarophias, and Orchohene spp. displayed weak DVM behavior. Although the sun was above the horizon around-the-clock during the ASPIRE cruise, irradiation levels were substantially lower at night, a difference that may be detectable by polar zooplankton (Berge et al., 2010). Engaging in minimal diaz vertical migration may at least reduce the risk of predation while maintaining the ability to feed on the high productivity of the seasonal bloom (e.g., Dale and Kaartvedt, 2000; Berge et al., 2009; Cisewski et al., 2010).

Station MOC 57, in close proximity to a drifting iceberg, had some of the highest proportions of diatoms to 

Phaeocystis

compared to other stations within the ASP (Figure 7C, Alderkamp et al., 2014), a pattern also reflected in zooplankton community structure, abundance and biovolume, and in euphausiid larvae ratio data. These results support earlier conclusions that proximity to an iceberg affects zooplankton distribution and abundance (e.g., Smith et al., 2007). Two studies investigating Weddel Sea iceberg-macrozooplankton interactions showed higher zooplankton biomasses within close proximity of two large icebergs potentially due to aggregation via turbulent flows (Sherlock et al., 2011) and enhanced food availability (Kaufmann et al., 2011; Smith et al., 2007). Our results showed a slightly higher proportion of euphausiid nauplii and calyptopis at MOC 57, compared to the other stations, as well as slightly elevated abundance levels of 

C. acutus

(at 30–60 m) and a second mid-depth maximum abundance (at 250–350 m). Although not statistically significant in this case (Kruskal–Wallis ANOVA, p > 0.05), higher proportions of euphausiid nauplii and calyptopis near icebergs may be due to ice being an essential stage in their developmental life history (Brinton and Townsend, 1991; Pakhomov and Perissinotto, 1996). The higher availability of diatoms would also increase the amount of energy allocated for reproduction (Schmidt et al., 2012).

The strongest biological correlations measured in this study were for zooplankton abundance with chl a and for zooplankton biovolume and abundance with the ratio of 19-hex to fucoxanthin. These results suggest that, despite a positive relationship between overall abundance and chl a, a negative relationship exists with 

Phaeocystis antarctica

. Negative correlations with 

Phaeocystis

spp. suggest selective feeding, which Bautista et al. (1992) speculate "might indirectly contribute to the development of 

Phaeocystis

spp. blooms because of the reduced grazing pressure and decrease in copepod abundances." Our current hypothesis for low surface-water biomass is that zooplankton are generally avoiding areas of high 

P. antarctica

due to limited palatability and other defense mechanisms of these phytoplankton. We thus assume that, during the period sampled, phytodetritus and bacterial remineralization rather than zooplankton grazing and fecal pellet production are driving carbon flux in the ASP (Ducklow et al. 2006; Smetacek et al., 2004; Ducklow et al., 2014 et al., 2014; Yager et al., 2014). However, sediment trap data for this area do show a contribution by zooplankton to POC flux (as evidenced by the presence of fecal pellets in trap samples) as the bloom progressed (Ducklow et al., 2014). With the region around the ASP changing dramatically due to increased warming (Stammerjohn et al., 2014), we suggest that evaluating effects of these changes on the structure and biomass of the zooplankton on an expanded seasonal basis will be of further importance to determining carbon flux to both higher trophic levels and the benthos (Yager et al., 2012; Ducklow et al., 2014; Yager et al., 2014).

References


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Contributions

- Contributed to conception and design: SW, PY, RS, HD
- Contributed to acquisition of data: SW, RS, SK, PY, HD
- Contributed to analysis and interpretation of data: SW, MW, RS
- Drafted and/or revised the article: SW, RS
- Approved the submitted version for publication: SW, RS, HD, PY
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Competing interests
None of the authors declare a competing interest for the work reported in this publication.

Data accessibility statement
All data will be publically available from BCO-DMO: http://www.bco-dmo.org/project/2132.

Supplemental material
- Figure S1. Multidimensional scaling (MDS) plot using a Bray-Curtis dissimilarity matrix on species abundance and depth. Numbers in plot indicate ASPIRE station, colors indicate depth of tow, and closed vs. open circles indicate time of tow (night or day).

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