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Winter distribution and size structure of Antarctic krill *Euphausia superba* populations in-shore along the West Antarctic Peninsula

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ABSTRACT: Antarctic krill *Euphausia superba* are a key component of food webs in the maritime West Antarctic Peninsula, and their life history is tied to the seasonal cycles of sea ice and primary production in the region. Previous work has shown a general in-shore migration of krill in winter in this region; however, the very near-shore has not often been sampled as part of these surveys. We investigated distribution, abundance, and size structure of krill in 3 fjordic bays along the peninsula, and in the adjacent Gerlache Strait area using vertically stratified MOCNESS net tows and ADCP acoustic biomass estimates. Krill abundance was high within bays, with net estimated densities exceeding 60 krill m^{-3}, while acoustic estimates were an order of magnitude higher. Krill within bays were larger than krill in the Gerlache Strait. Within bays, krill aggregations were observed near the seafloor during the day with aggregations extending to the sediment interface, and exhibited diel vertical migration higher into the water column at night. We suggest these high winter krill abundances within fjords are indicative of an active seasonal migration by krill in the peninsula region. Potential drivers for such a migration include reduced advective losses and costs, and availability of sediment food resources within fjords. Seasonally near-shore krill may also affect stock and recruitment assessments and may have implications for managing the krill fishery in this area.

KEY WORDS: Euphausiid · Abundance · Diel vertical migration · DVM · WAP · Fjord

INTRODUCTION

Antarctic krill *Euphausia superba* (hereafter 'krill') are key members of Southern Ocean ecosystems. Krill serve as important prey to many megafauna; in the West Antarctic Peninsula (WAP) region krill make up over 90 % of the diet of numerous species of baleen whales and the brush-tailed Adélie, gentoo, and chinstrap penguins, and over a third of the diet of additional species of seals, birds, and fish (Quetin & Ross 1991). These small pelagic crustaceans have a huge global biomass, estimated at over 300 million tons, with 70 % of the stock found in the Atlantic sector from 0° to 90° W, encompassing the WAP (Atkinson et al. 2008).

This huge biomass of krill in the Southern Ocean is not distributed evenly on any spatial scale, with strong patchiness on scales from thousands of kilometers around the continent, to meters within and between aggregations (Hamner & Hamner 2000, Atkinson et al. 2008, Tarling et al. 2009). Krill are at the 'awkward boundary between plankton and nekton' (Atkinson et al. 2008, p. 2); their distribution can be strongly influenced by current flows, but they are

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also strong swimmers, capable of sustained pleiopod swimming speeds of 35 cm s^{-1} and escape velocities in excess of 60 cm s^{-1} (Kils 1981, Hamner 1984).

Much of the research on krill distributions in Antarctica has been focused on the productive and more accessible summer season (Atkinson et al. 2008). A few studies have investigated patterns in the seasonal distributions of krill, both in general and along the WAP. The general paradigm for *E. superba* in the WAP region has been that krill spend the summer feeding in aggregations along the shelf break and in the waters beyond, with females laying eggs into the deep waters beyond the shelf; while in the fall and winter krill migrate to more in-shore areas (Siegel 1988, Lascara et al. 1999, Nicol 2006, Atkinson et al. 2008). The smallest individuals have generally been found closest in-shore, where they may rely on sea ice for refuge from predation or food resources (Siegel 1988, Lascara et al. 1999, Lawson et al. 2004, Atkinson et al. 2008). The ecological reasons for this migration remain unclear, although it has been suggested it may improve feeding or reduce advection out of the favorable WAP region (Siegel 1988).

Many of the studies that have addressed seasonal variations in krill distribution have observed much lower levels of krill in winter as compared to other seasons. This prominent absence of krill in winter, with early studies indicating winter abundances of just 0.086 krill individuals m^{-3}, an order of magnitude fewer krill than summer, has been termed the winter krill 'vacuum' (Siegel 1988). Later work has continued to provide further evidence of this vacuum; Lascara et al. (1999), sampling broadly over the WAP shelf outside the coastal islands, found krill in winter at just one of their 25 acoustic stations, with total biomass estimates an order of magnitude lower than those in the same region in summer. Seasonal sampling in Marguerite Bay also observed much lower biomass in winter than in fall (Lawson et al. 2004).

Unlike for smaller zooplankton, seasonal changes in observed krill abundance cannot be a result of population growth or contraction. Krill are long lived, taking 2 to 3 yr to reach sexual maturity, with lifespans estimated at 5 to 7 yr (Siegel 1987, Lascara et al. 1999). Additionally, the fall/winter reduction in krill abundance, and corresponding spring increase, is evident in krill from a wide range of sizes (Siegel 1988, Atkinson et al. 2008). Given both the multiyear life cycle of krill, and the parallel abundance patterns amongst different age classes, the seasonal decline and increase in observed krill abundance is more likely to be due to krill entering and exiting the

sampled waters. Limited near-shore sampling has suggested this may be where large krill are found in winter (Lawson et al. 2004).

Although krill are thought to move in-shore in winter, the most in-shore regions of the WAP have been poorly sampled, and are missed by the ongoing standardized sampling programs (PalLTER, NOAA AMLR). The coast of the WAP is complex and convoluted, with a series of deep fjordic bays. Vessel and gear safety considerations mean that standardized or randomized transects of the type most often used in broad scale surveys are typically not possible within these areas (Johnston et al. 2012). Sampling within Wilhelmina Bay has shown the presence of krill 'super-aggregations', suggesting this very near-shore region may be important winter habitat for krill (Nowacek et al. 2011).

In this project we used spatially adaptive sampling with nets and acoustics to investigate the distribution, abundance, and size structure of krill within Wilhelmina, Andvord and Flandres Bays and in adjacent comparison areas of the Gerlache Strait in winter. By sampling krill in this poorly known very near-shore region in winter we aimed to refine our understanding of krill seasonal distributions, and the implications of these distributions for the ecology and life history of *E. superba* in the WAP region.

MATERIALS AND METHODS

Field collections

Sampling was carried out on the Research Vessel Ice Breaker Nathaniel B. Palmer between May 16 and June 15, 2013, in Wilhelmina, Andvord and Flandres Bays, in Gerlache Strait outside the bays, and at Palmer Deep further off-shore (Fig. 1, Table 1). Actual sampling locations were fairly tightly constrained based on bathymetry as observed with multibeam sonar, and the need to maintain safe distances from coastlines and large icebergs over a straight line run of 3 km for MOCNESS towing. At each site, stations consisting of a CTD deployment for hydrography and water collection, a 1 m^2 Multiple Opening Closing Net Environmental Sensing System (MOCNESS) (Wiebe et al. 1976, 1985) deployment for krill and larger zooplankton, a vertical tow with a 0.5 m 64 μm mesh ring net for mesozooplankton and fecal pellets, and a camera deployment for krill observations, were conducted during both day and night. Palmer Deep was sampled only at night due to time and weather limitations.
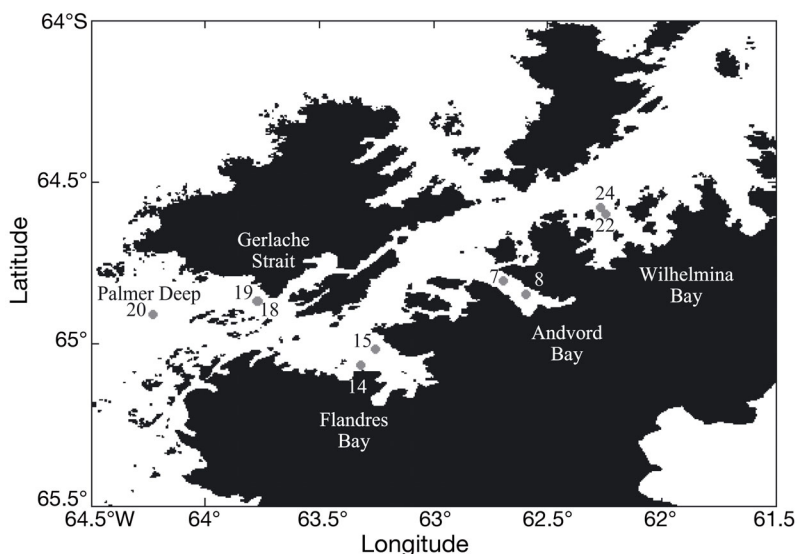
Fig. 1. MOCNESS tow locations. Tows 18 and 19 occurred at the same location at different times

Table 1. MOCNESS station information: dates are in 2013; time is local 24 h time (GMT − 4 h)

MOC tow	Location	Latitude, longitude	Date	Time (local)
22	Wilhelmina Bay	64° 36.01' S, 62° 14.55' W	June 3	16:18
24	Wilhelmina Bay	64° 34.86' S, 62° 15.93' W	June 4	11:38
7	Andvord Bay	64° 48.23' S, 62° 41.56' W	May 23	22:13
8	Andvord Bay	64° 50.89' S, 62° 35.82' W	May 24	09:41
14	Flandres Bay	65° 03.88' S, 63° 19.11' W	May 29	21:47
15	Flandres Bay	65° 00.92' S, 63° 15.28' W	May 30	09:16
19	Gerlache Strait	64° 51.94' S, 63° 46.12' W	May 31	20:35
18	Gerlache Strait	64° 51.93' S, 63° 46.30' W	May 31	11:28
20	Palmer Deep	64° 54.62' S, 64° 13.78' W	June 1	05:46

CTD profiles were collecting using an SBE 911+ (SeaBird) CTD unit with dual salinity and temperature sensors, an *in situ* fluorescence unit, and a carousel of 22×12-l Niskin bottles. Chlorophyll was measured from Niskin collected water at 5 m depth with extracted pigments in triplicate on a TD-700 fluorometer (Turner Designs) (Jespersen & Christoffersen 1987).

Mesozooplankton were sampled with a 64 µm mesh 0.5 m diameter ring net towed vertically at 15 m min^{-1} from 200 m to the surface. This fine-mesh net was used to sample the previously seldom sampled smaller zooplankton, including copepod nauplii. Cod end contents were preserved in 4% final concentration solution of sodium borate-buffered formalin in seawater. No clogging was evident because of the very low phytoplankton concentrations and volume filtered was calculated from the net mouth open area and depth of the tow.

Vertically stratified samples of krill were collected with a 1 m^2 MOCNESS equipped with nine 333 µm mesh black nets. Two LED strobe lights (Brightwaters Instruments) were attached to the frame above the net mouth, and flashed continuously throughout all tows at approximately 2 flashes per second with a nominal light output of 3 W, in order to reduce net avoidance behavior by krill (Sameoto et al. 1993, Wiebe et al. 2004, Lawson et al. 2004). However, despite the presence of bright strobes, black nets, and no bridle or other obstructions in front of the net opening, some krill individuals may still successfully avoid capture, and thus these net catch densities must be considered as a minimum estimate of the true krill abundance in the environment. The net was towed obliquely at a 45° angle at 1.5 to 2 knots from 50 m above the seafloor to the surface. Net opening and closing depths varied between tows and were determined based on real-time information on the vertical distribution of krill from the Acoustic Doppler Current Profiler (ADCP) data in order to maximize vertical resolution of aggregation structure. Such acoustic guided net interval sampling allowed for separate samples above, within, and below krill aggregations, and provides more accurate information about *in situ* density than fixed depth intervals that may sample both aggregation and empty water within a single net. Each net filtered between 53 and 900 m^3 of water, with larger volumes necessary in depth intervals and locations where krill were less abundant.

Net catches were processed immediately. Catches were split on board the ship using a bucket splitter (a 20 l cylinder with a 5 cm diameter tube extending from the bottom to a T-junction with identical 5 cm outflow tubes pouring into 2 separate 20 l cylinders), as many times as required to produce a sample of roughly 150 to 200 ml biovolume. Split samples were preserved in a 4% final concentration solution of sodium borate buffered formalin in seawater.

The ship-mounted ADCP, a narrow band 153 kHz system mounted in a seawater-filled acoustic window, was configured for both current and volume

backscattering measurements. Both the pulse and bin lengths were set at 8 m, and the blank-after-transmission was set to 4 m. Volume backscattering measurements were acquired at approximately 1 Hz throughout the entire cruise. Because of technical difficulties in calibrating a ship-mounted ADCP, the absolute estimates of biomass from backscattering measurements were reached empirically by comparison with estimates from other calibrated methods (Flagg & Smith 1989, Zhou et al. 1994, Brierley et al. 1998, Nowacek et al. 2011). During ADCP data processing, corrections for absorption and range were made based on the standard sonar equation (Flagg & Smith 1989, Zhou et al. 1994). Automatic Gain Control (K_c) in the ADCP sonar equation was corrected using the equation developed from least squares fitting, minimizing the difference between a calibrated SIM-RAD EK-60 and ADCP biomass estimates (Nowacek et al. 2011, Espinasse et al. 2012). Power into water (K_2) was based on the manufacturer's value. To convert volume backscattering measurements to biomass, krill target strengths were estimated based on the mean and standard deviation of krill length analyzed from MOCNESS samples, literature values on the orientation and material properties of krill, and the deformed cylinder model (Chu et al. 1993, Chu & Wiebe 2004, Lawson et al. 2006). ADCP backscattering data in dB were converted to biomass wet weight (WW) concentrations of krill in g m^{-3} using a prolate spheroid model and the density of an individual krill approximately 1 g WW cm^{-3}. Because the real K_2 and K_c are unknown, the measurements of backscattering and estimates of krill biomass should be treated as a relative metric, which can be used for analysing spatial variability rather than being an absolute measure of krill biomass.

Laboratory processing

In the laboratory, subsamples of 64 μm net catches were taken with a 5 or 10 ml Stempel pipet, for a target sample size of 200 individuals and all zooplankters, including any early life stage euphausiids, were identified and enumerated. Krill fecal pellet length and diameter were measured from photographs of Stempel samples in ImageJ (Schneider et al. 2012).

MOCNESS catches were further split if necessary in the lab for a final target sample size of 100 *Euphausia superba* individuals using a box splitter. The final counted sample ranged from the full net catch to a 128th split. All krill which could be visually identified without magnification were counted from these splits, setting an operational lower size limit of 5 mm Standard Length, thus including adult and furcillia stages. Krill of >5 mm in length will be quantitatively retained by the 333 μm MOCNESS mesh (maximum mesh opening along diagonal = 471 μm; minimum diameter of a 5 mm long krill, given a 1:8 aspect ratio = 625 μm; Zhou & Dorland 2004). For each krill individual, Standard 1 Length (anterior tip of telson to posterior end of uropods) was measured to the nearest 0.5 mm (as per Everson 2000), and individual krill were dried at 60°C for ≥24 h and weighed on a BP310S microbalance (Sartorius).

Data processing

Krill fecal pellet volume was calculated assuming a cylindrical shape and carbon estimated from the volume measurements using a factor of 0.058 mg C mm^{-3} (Gonzalez 1994, as cited in Dubischar & Bathmann 2002), and an 80% carbon assimilation efficiency, a mid-range estimate from a rather wide range reported in the literature (Atkinson et al. 2012b). With fecal pellet sinking rates of around 300 m d^{-1} (Atkinson et al. 2012a) and the strong diel vertical migration observed, these fecal pellets most likely represent krill feeding over somewhere between 12 and 24 h. To calculate the feeding rate necessary to produce the observed fecal pellets, highest and lowest fjord krill abundances were combined with lowest and highest fjord fecal pellet concentrations, respectively, to determine a range of feeding rates.

MOCNESS net catch data were used to calculate numbers and biomass of krill in each 2.5 and 5 mm length increment size fraction per m^3 of water filtered in each depth interval and per m^2 of integrated water column. Water column biomass estimate calculations used the conservative approach of assuming no krill were present in the unsampled, deepest part of the water column. Length−weight analysis was conducted as quality control on the data with MatLab's curve-fitting toolbox, and extreme outliers (n = 4) were removed as potentially erroneous. Differences in the length frequency distributions between tows were investigated by analyzing individual length data from each tow. Because some tows exhibited multiple peaks and were thus not normally distributed, we used both parametric and non-parametric ANOVA (Kruskal-Wallis) tests, followed by pairwise Tukey test comparisons between tows.
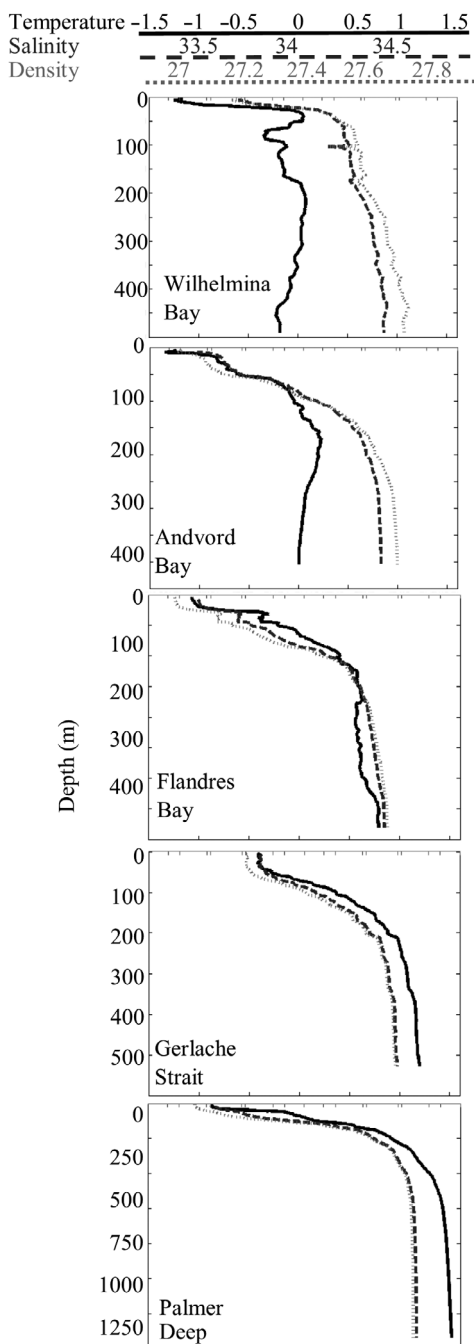
Temperature -1.5 -1 -0.5   0   0.5   1   1.5
Salinity   33.5   34   34.5
Density   27 27.2 27.4 27.6 27.8

Fig. 2. CTD profiles of the areas sampled for krill. Temp: temperature (°C), Salinity is in psu; density is sigma-t in kg m^{-3}

processed ADCP data (8 m depth bins from 32 to 400 m depth, and 6 min time bins) were used for quantitative analyses. ADCP backscatter was analyzed to investigate patterns in the depth of krill aggregations. For each time interval the depth of maximum biomass was found in the ADCP record. These calculations excluded the 4 m immediately above the seafloor, as determined by Knudsen echosounder, due to potential noise from side-lobes of the ADCP beams, and excluded any time interval in which the maximum biomass did not exceed 50 g m^{-3}, as such time intervals may indicate areas without krill or bad data due to bow-thruster noise. An ANOVA was used to investigate spatial differences in peak biomass density and diel variations in the depth of the biomass peak.

RESULTS

Hydrography and chlorophyll

The surface mixed layer ranged from 5 to 50 m in depth, with temperatures in the mixed layer ranging from −1.7°C to +0.5°C over the course of sampling, and mixed layer salinities between 33.4 and 34.4 psu (Fig. 2). Mixed layer water column properties were consistent with Antarctic Surface Water, while below the pycnocline warmer and saltier waters were observed, consistent with modified Circumpolar Deep Water (Lawson et al. 2004). This layer of Antarctic surface water was much more distinct within fjords than offshore, where pycnoclines were less sharp in the Gerlache and Palmer Deep Stations. Mixed layer chlorophyll was uniformly low throughout the study, with all values below 0.4 µg l^{-1} as determined from fluorometric measurements of extracted pigments (Table 2), and no clear chlorophyll maxima were observed from *in situ* fluorescence measurements.

ADCP backscatter data were observed qualitatively in real-time at sea, and were further examined in the laboratory by qualitatively examining profiles of 2–4 h blocks of time throughout the cruise. Broad-scale spatial patterns were observed from water-column integrated acoustic backscatter. Binned and

Table 2. Water column chlorophyll *a* (mean ± SD) from the different sampling locations (n = number of stations per location) for cruise NBP1304. Four depths were sampled at each station, with all samples in triplicate

Location	n	Chl *a* (µg l^{-1})
Wilhelmina	2	0.33 ± 0.02
Andvord	4	0.33 ± 0.02
Flandres	3	0.24 ± 0.01
Gerlache	6	0.27 ± 0.02
Palmer Deep	1	0.20 ± 0.04

Mesozooplankton

Almost no larger copepods were captured with the MOCNESS net. No early life stages of euphausiids were observed in the ring net samples. Zooplankton abundance is shown from the vertical net tows with 64 µm ring net: abundances in the bays were very low, with between 45 and 226 ind. m^{-3} (Table 3), while in Gerlache Strait abundances were higher (1122 ind. m^{-3}). The sample from Palmer Deep was lost. Zooplankton samples were dominated by the small cyclopoid *Oithona* and the poecilostomatoid *Oncaea*. Other copepods present, but at very low abundances (<4 ind. m^{-3}), included *Microcalanus pygmaeus*, *Scolocithricella*, *Metridia* and *Euchaeta*, and unidentified calanoid and cyclopoid nauplii. *Metridia* were predominantly *M. gerlachii*, but also included the smaller *M. lucens*, as confirmed by 18S rDNA sequencing (methods as per Durbin & Casas 2014). At the Gerlache Strait stations the same taxa were observed but in abundances higher than those observed within the bays (Table 3).

Table 3. Zooplankton abundance (no. m^{-3}, mean ± SD) for sampling locations during cruise NBP1304. Samples were collected with vertical hauls of a 0.064 µm mesh 0.5 m diameter net. In Wilhelmina Bay and Flandres Bay 7 and 4 samples were collected, respectively, while Andvord Bay and Gerlache Strait results represent a single tow each. C1−C5, C6F/M: Copepodite stages 1−5, copepod adult stage 6 female/male, respectively

Zooplankter	Wilhelmina	Andvord	Flandres	Gerlache
Ctenocalanus citer, C1−C5	0.29 ± 0.58	0.00	0.45 ± 0.60	0.00
Euchaeta sp., C1−C5	0.15 ± 0.38	0.00	0.16 ± 0.19	0.00
Metridia spp., nauplii	0.07 ± 0.19	0.00	2.96 ± 1.58	57.30
Metridia spp., C1−C5	0.87 ± 1.16	0.00	2.10 ± 1.63	6.37
Metridia spp., C6F	0.00 ± 0.00	0.00	0.51 ± 0.30	0.00
Microcalanus pygmaeus, C1−C5	0.55 ± 0.78	2.04	4.01 ± 1.11	12.73
Microcalanus pygmaeus, C6F	0.07 ± 0.19	0.00	1.05 ± 1.07	0.00
Microcalanus pygmaeus, C6M	0.00 ± 0.00	0.00	0.00 ± 0.00	1.27
Scolecithricella sp., C1−C5	2.29 ± 2.68	0.00	3.60 ± 2.35	15.28
Scolecithricella sp., C6F	0.25 ± 0.39	0.00	0.64 ± 0.76	0.00
Scolecithricella sp., C6M	0.00 ± 0.00	0.00	0.06 ± 0.13	0.00
Calanoid spp., nauplii	2.51 ± 4.05	0.51	12.16 ± 7.27	324.68
Calanoid spp., C1−C5	0.04 ± 0.10	0.00	4.90 ± 2.57	39.47
Oncaea sp., C1−C5	33.88 ± 19.78	19.35	34.63 ± 10.1	229.18
Oncaea sp., C6F	4.15 ± 3.70	0.51	15.53 ± 4.61	1.27
Oncaea sp., C6M	17.21 ± 24.84	1.02	19.03 ± 8.59	8.91
Oithona sp., C1−C5	32.91 ± 19.78	21.90	84.57 ± 35.2	351.41
Oithona sp., C6F	5.34 ± 1.94	2.04	6.11 ± 2.54	3.82
Oithona sp., C6M	0.04 ± 0.10	0.00	0.06 ± 0.13	0.00
Cyclopoid spp., nauplii	11.59 ± 12.38	5.09	33.65 ± 18.4	71.30
Harpacticoid copepod spp.	0.47 ± 0.43	0.00	0.73 ± 0.92	0.00
Total	112.68 ± 45.18	52.46	226.54 ± 66.8	1122.99

Krill fecal pellets

Krill fecal pellets were observed in all of the bay samples, but not in Gerlache Strait. Estimated fecal pellet carbon was 27.5, 81, and 29.7 mg C m^{-2}, in Wilhelmina, Andvord and Flandres Bays, respectively. Thus the observed fecal pellets correspond to an estimated consumption rate of 0.035−1.21% of the krill biomass approximately daily.

Krill from net sampling

In total, 4047 krill were counted and measured from 56 discrete depth interval nets in 9 tows encompassing 3 bays and the more off-shore Gerlache Strait and Palmer Deep regions. Krill collected in MOCNESS tows were almost exclusively *E. superba*, with less than 5 individuals of *Euphausia crystallorophias* and *Thysanoessa macrura* encountered over the entire cruise. These other species of krill were not included in any analysis, and 'krill' is used throughout the remaining results and discussion to mean exclusively *E. superba*. Krill ranged in length from 9 to 51 mm and in dry weight from 0.001 to 0.217 g.

The distribution of krill lengths showed a strong peak at sizes of 27.5 to 32.5 mm, with a smaller secondary peak at 12.5 to 15 mm (Fig. 3). Krill from the larger size peak were found mainly within the bays, but were present in all tows, while the smallest size classes, representing young-of-the-year (YOY) individuals, were mainly observed in the Gerlache Strait and Palmer Deep stations (Fig. 3). Not only did these more off-shore Gerlache and Palmer Deep tows have the highest relative abundances of krill in the smallest size fractions, they also had the highest total abundances of krill less than 20 mm in length (Fig. 3). Mean krill lengths were significantly different (p < 0.01) between all of the in-shore tows and the Palmer Deep and Gerlache Strait Day tows and these differences were robust to the choice of statistic (ANOVA/
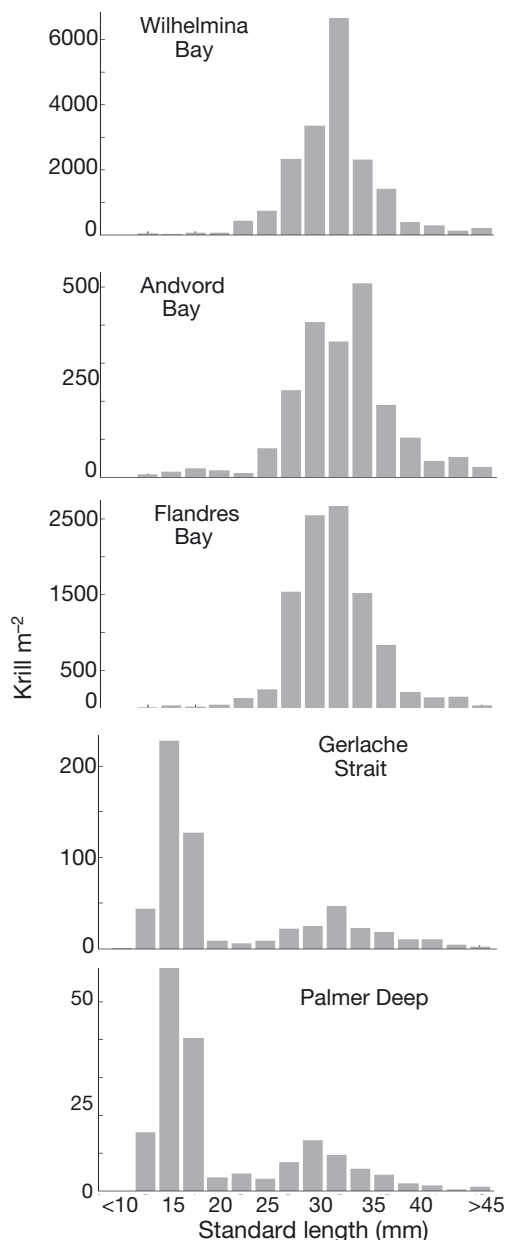
Fig. 3. Length–frequency histograms by location, showing the similar distributions observed in the 3 bays and the high contribution of young-of-the-year in the more off-shore Gerlache Strait and Palmer Deep samplings

observed in length distributions, with most tows not significantly different from each other under either analysis.

Krill abundances were much higher in the in-shore stations than in the Gerlache and Palmer Deep stations (Fig. 4, Table 4). Highest krill biomass was observed in Wilhelmina and Flandres Bays at night, with 506 and 308 g DW m^{-2}, respectively. Lowest abundances and biomass were observed at Palmer Deep and the Gerlache Strait at night.

Vertical patterns of krill abundance showed both diel and spatial differences (Fig. 5). Within Wilhelmina, Andvord, and Flandres Bays a diel pattern was observed with krill more concentrated and deeper during the day, and relatively more dispersed and shallower at night (Fig. 5, Table 4). In the Gerlache Strait krill were concentrated in the upper 200 m of the water column during both day and night. No data are presented for Palmer Deep depth intervals 100–150 or 500–700 m as the cod-ends were lost at sea.

Acoustic sampling of krill

General observations from the acoustic data were similar to patterns observed in MOCNESS tow catches. Although acoustic data are not able to sample the uppermost (<24 m) or lowermost (>424 m) parts of the water column, MOCNESS catches indicated that the shallowest depths contained relatively few krill individuals, and where seafloor depths exceeded ADCP sampling depths few krill were caught in these deepest layers, suggesting acoustic observations sampled the majority of the krill bio-

Kruskal-Wallis). Palmer Deep and Gerlache Strait Day were significantly different from each other with ANOVA, but not with Kruskal-Wallis. The one other off-shore tow, Gerlache Strait Night (tow 18) was significantly different from all in-shore stations under ANOVA, but not significantly different from Andvord Bay night (tow 7) under Kruskal-Wallis (while still significantly different from all other bay tows). Within the bay stations, no clear patterns were
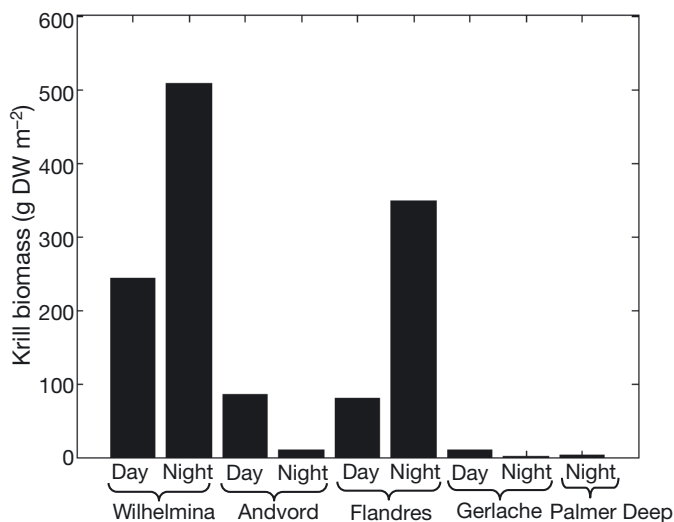

Fig. 4. Water column krill biomass (dry weight) in each tow

Table 4. Krill length and weight (mean ± SD), for each tow, number of krill analyzed and overall abundance for each tow. Total DW: water column total dry weight biomass of krill; weighted mean depth: index of the depth at which krill were located, calculated as the sum over all nets in a tow of [(net krill m^{-2})/(water column krill m^{-2})] × (mean depth of net)

Tow	No. of krill analysed	Length (mm)	DW (g)	Total DW (g m^{-2})	Weighted mean depth (m)
Wilhelmina					
Night	513	30.24 ± 0.439	0.039 ± 0.019	506.843	182
Day	491	28.33 ± 0.606	0.035 ± 0.02	242.128	293.5
Andvord					
Night	265	26.37 ± 1.012	0.037 ± 0.035	10.399	100.3
Day	286	30.82 ± 0.705	0.045 ± 0.029	84.558	231.7
Flandres					
Night	443	29.30 ± 0.433	0.038 ± 0.02	348.138	161.3
Day	453	28.63 ± 0.701	0.036 ± 0.023	80.059	182.4
Gerlache					
Night	645	14.56 ± 0.302	0.006 ± 0.008	1.73	133.4
Day	578	24.68 ± 1.002	0.034 ± 0.033	9.114	95.5
Palmer Deep					
Night	373	16.55 ± 0.64	0.010 ± 0.014	2.41	248.3

mass throughout the cruise. No mesozooplankton were present in high enough abundances to have a significant impact on ADCP estimates of krill biomass, and we therefore consider all backscatter to have come from *E. superba*.

Krill abundance was higher within bays than in the Gerlache Strait and off-shore regions (Fig. 6). Peak krill abundance was statistically significantly differ-

ent between each of the bays and the off-shore region (p < 0.01), with abundances decreasing from Andvord to Wilhelmina, and then Flandres Bays, with lowest peak abundances in the Gerlache Strait and Palmer Deep off-shore region. During the day within bays, krill were typically concentrated in dense layers 50 to 100 m thick in the deepest part of the water column. Acoustically estimated biomass
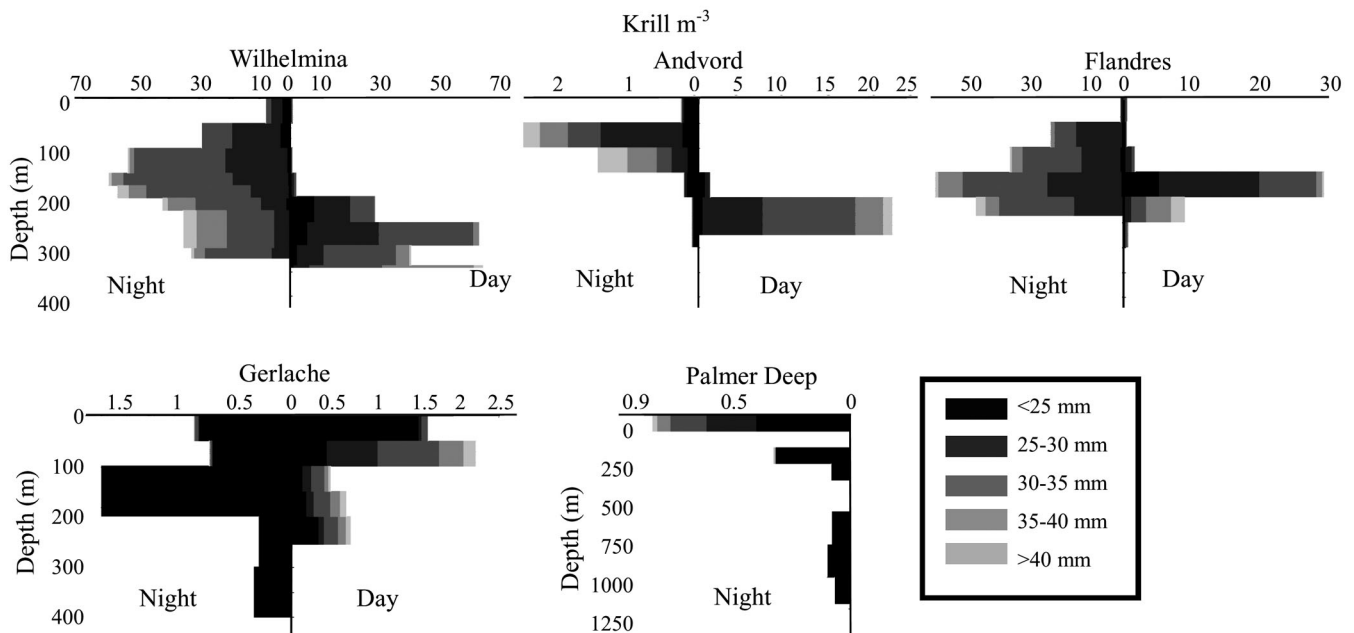

Fig. 5. Vertical profiles of size fractions of krill. Please note that the abundance scale is different in each plot to show details. Shade indicates the standard length of krill individuals, with the larger krill in the fjords (Wilhelmina, Andvord, Flandres), the small krill off-shore (Palmer Deep, Gerlache), and no consistent vertical partitioning by size
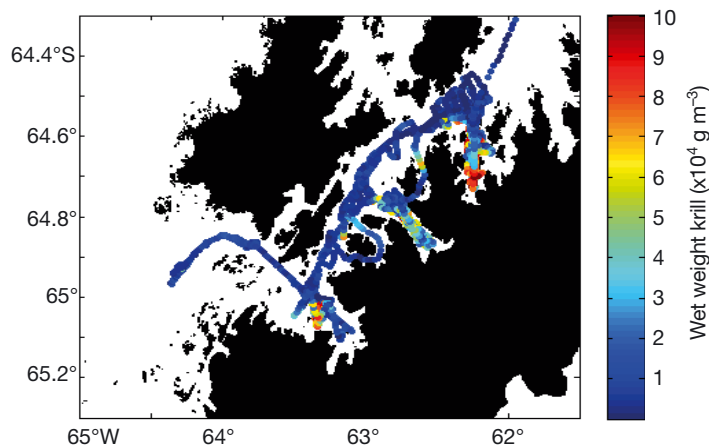
Fig. 6. Spatial distribution of krill in the West Antarctic Peninsula in winter (May–June) from acoustic estimates. Each point indicates the vertically integrated biomass from the surface to 400 m (or 10 m above the seafloor) in g wet weight m^{-3} averaged over a 6 min time interval

concentrations within these layers were at times in excess of 1000 g WW m^{-3}. Where the seafloor was shallower than 300 m, these aggregations were extended down to the sediment interface; where the seafloor was deeper, the aggregations tended to separate from the sediment but stay deep in the water column, typically between 200 and 300 m. At night the krill tended to come up in the water column

and form less dense aggregations. These night-time aggregations were typically most abundant between 100 and 200 m depth (Fig. 7) The depth of peak krill abundance was significantly different (ANOVA p < 0.001) between day, night, and twilight periods, with deepest mean peak depths in the day (10:00 to 14:00 h, 239.5 m), shallowest mean peak depths at night (16:00 to 08:00 h, 162.6 m), and intermediate depths at twilight (08:00 to 10:00 h and 14:00 to 16:00 h, 207.5 m) (Fig. 7). Outside of the bays in the Gerlache Strait area acoustic krill biomass estimates were generally very low, with the few observations of higher biomass close to the coasts (Fig. 6).

DISCUSSION

Very high densities of *Euphausia superba*, in excess of 8000 individuals and 1700 g WW biomass m^{-2}, were observed in the coastal fjords of the WAP in winter. Previous work in these coastal embayments has also suggested their importance as winter habitat for krill (Zhou et al. 1994, Zhou & Dorland 2004, Lawson et al. 2004, 2008, Friedlaender et al. 2013). As early as 1938 the importance of these areas as krill habitat were noted, with '*E. superba* in millions a yard or two from the shore near Andvord Bay' (Bagshawe 1938, as cited in Marr 1962). In adjacent
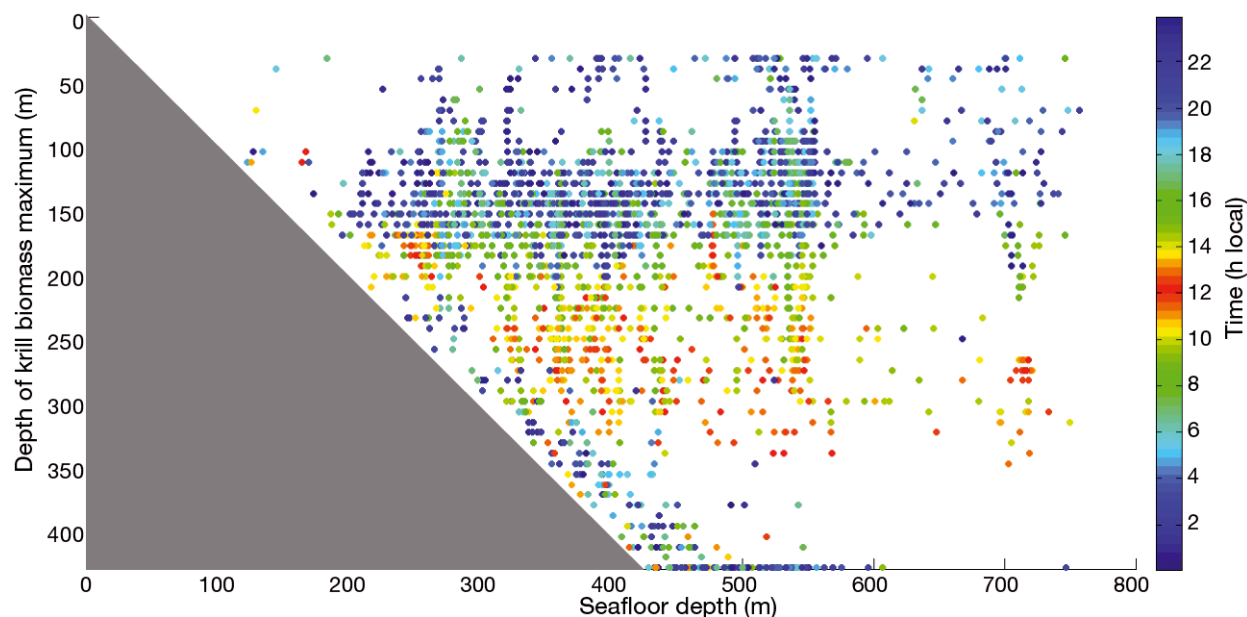

Fig. 7. Krill peak abundance depth over the range of bottom depths. Each point indicates the depth of maximum krill biomass, as compared to the seafloor depth, averaged over 6 min, with color indicating local time of sampling (GMT – 4 h). Points are in order of bottom depth, regardless of order of sampling. Krill tended to either occur close to the seafloor (points along the triangle hypotenuse) or in a layer at 100–200 m depth (points in the horizontal layer). ADCP provides reliable data between 24 and 424 m depth; uppermost and lowermost areas of the water column are not quantitatively sampled

more open water areas in the Gerlache Strait and Palmer Deep krill abundances were orders of magnitude lower (1–9 g WW m^{-2}). This relative lack of krill in winter in the more commonly sampled Gerlache Strait and off-shore areas has also been previously observed, with shelf-wide density estimates of only 2 g WW m^{-2} (Siegel et al. 2013) and 8 g WW m^{-2} (Lascara et al. 1999). Our abundance estimates are based on 2 independent methods (nets and acoustics) indicating that the high values observed within fjords very likely show true areas of high krill concentrations.

If we consider the average values of the more off-shore areas from our MOCNESS sampling (Palmer Deep and Gerlache Strait) to be representative of krill densities over the shelf as a whole, and the densities observed within the 3 sampled fjords (Wilhelmina, Andvord, and Flandres) to be representative of the fjordic bays along the WAP overall, we estimate that close to 90 % of the total krill biomass in the WAP region may be present within fjords in winter. This is despite the shelf region being an order of magnitude larger in extent (~200 km wide vs. 20 km wide) than the fjords, and containing well over an order of magnitude more potential habitat due to greater depth. This concentration of krill within WAP fjordic bays in winter is in stark contrast to summer and fall, when krill are abundant over the shelf, and are more typically concentrated into small schools with large areas of empty water between schools (Lascara et al. 1999, Lawson et al. 2008), while within fjords only small aggregations are observed (E. G. Durbin & M. Zhou unpubl. data). In the remainder of the discussion we consider potential reasons and mechanisms for the observed high winter densities in fjords.

Advection into fjords

Krill are often modeled as passive drifters, and their presence in fjords and canyons may be driven by advection (Schofield et al. 2013, Bernard & Steinberg 2013). Canyons can interrupt the along-shelf flow, serving as conduits for cross-shelf exchange (Allen & Durrieu de Madron 2009). Such cross shelf flow can transport krill into canyons, and retain them in those areas (She & Klinck 2000). High concentrations of euphausiids have been observed in canyons and shelf break regions globally (e.g. Gulf of St. Lawrence: Simmard et al. 1986, Sourisseau et al. 2006, 2008; Georges Bank: Greene et al. 1988, Jech & Michaels 2006; Bering Sea: Coyle & Cooney 1993;

WAP: Lawson et al. 2004). Along the WAP, concentrations of krill in canyons have been particularly noted at the head of Palmer Deep Canyon (Bernard & Steinberg 2013), and at the head of the canyon north of Livingstone Island (Warren et al. 2009). This concentration of krill in canyons is not however universal, with low krill backscatter observed near Marguerite trench, as compared to the surrounding areas (Lawson et al. 2004, 2008).

While advection certainly plays a role in *E. superba* distributions, it does not appear that cross-shelf advection in fjordic canyons is the most plausible explanation for the high winter abundance observed within the WAP fjords. The along-shelf coastal current and the canyon bathymetry are present year round, yet krill are abundant in fjords only in winter. Additionally, the biomass of krill present in the fjords, and the very low abundances observed across the shelf, both in the present work and in more extensive surveys (Siegel 1988, Lascara et al. 1999), suggest krill from across the shelf are moving into fjords in winter, whereas advective flows in canyons would likely impact only those krill closest to the fjord mouths. Thus, an alternative factor must be at least partially responsible for the observed high winter densities within fjords.

Active in-shore seasonal migration

We suggest that rather than a purely physical aggregating mechanism, the most likely process leading to krill aggregation in fjords in winter is active migration as part of an overwintering strategy. Active migration has previously been suggested as a mechanism for the observed seasonal differences in krill spatial distributions, and modeling suggests active directed movements by krill significantly enhance their growth and reproductive sucess (Siegel 1988, 2005, Lawson et al. 2004, Richerson et al. 2015). These earlier studies suggesting such an active inshore migration did not sample the very near shore region studied here, and thus found lower overall abundances in winter as compared to other seasons (Marr 1962, Siegel 1988, 2005, Lawson et al. 2004). This new data showing very high densities and abundances of krill within the coastal fjords supports the concept of an active seasonal on-off shore migration, and helps to account for the previously missing krill in winter. Krill are sometimes classified as 'micronekton' rather than plankton because of their swimming abilities. On small spatial scales, krill swimming is important in maintaining desired loca-

tions, likely associated with opportunities for feeding, reproduction or reduced predation risk (Mackas et al. 1997, Tarling et al. 1998, Zhou et al. 2005). Krill have also been observed to use their swimming abilities in large-scale movements. Krill have been observed swimming against a current and swarms use this ability to maintain positions even in the main flow of the Antarctic Circumpolar Current (Marr 1962, Tarling & Thorpe 2014). In East Antarctica krill swarm movements have been tracked over multiple weeks, covering distances up to 185 km (Kanda et al. 1982). These aggregations migrated at speeds of 0.11 to 0.13 m s^{-1}, at which speeds krill could move from the shelf edge to the inner area of a coastal fjord in 2 to 3 wk.

Minimizing advective losses

An active migration such as we hypothesize for krill in the WAP would require energy expenditure by the krill, and thus for such a strategy to have developed and become widespread in the population it must offer significant benefits to krill survival or reproduction. One potential benefit to krill of spending the winter within fjords is the minimization of advective losses from the favorable WAP region or minimization of energetic expenditures from counter-current swimming to maintain position. The WAP is a highly productive area, with high primary productivity fed by nutrient enrichment from circumpolar deep water (Ducklow et al. 2007). It would thus be beneficial for krill to stay within the WAP region. It remains unclear to what extent this is the case, with indications that krill within the WAP region are a self-sustaining population (Quetin & Ross 2003), and models suggest that krill may complete their full life cycle there (Hofmann & Husrevoglu 2003), but also that krill populations within the WAP area may be maintained by both local recruitment and advective input of larvae from other regions (Piñones et al. 2013).

The WAP area is a highly advective environment, with the Antarctic Circumpolar Current carrying water, and potentially krill, to the northeast and out of the area, while the coastal current could advect individuals away to the southwest (Nicol 2006). Entering bays, in which current flows are much lower than in the Bransfield Strait and broader shelf region, would prevent krill from being advected out of the area, or allow krill to reduce energy expenditures on swimming to maintain position. Reduced advection out of the WAP area, or energy savings from reduced maintenance swimming, may be particularly beneficial during the winter season with low food resources. In Marguerite Bay, in fall and winter, krill are most abundant where currents and current sheer are lowest (Lawson et al. 2008), which might suggest krill selecting retentive environments as habitat. In addition to the broadscale current flows, katabatic winds blowing down the glaciers and over the fjords may move surface waters offshore. Krill within fjords were observed not to be present within these surface layers of cold fresh water, while in the more offshore areas without such strong stratification and katabatic winds, they were present in even the shallowest layers. This is consistent with a strategy of minimizing advective losses.

Differences between individuals in swimming ability may also play a role in the different benefits of such minimization of advection to each krill. Krill swimming ability is a function of length with maximal sustained speeds around 8 body lengths s^{-1}(Kils 1981). As a result krill will segregate by size while migrating. Within fjords, krill length distributions showed a single peak, with slight indications of a higher secondary peak in Andvord Bay. This peak length corresponds to krill of age 1+, that is those hatched around January 2012. Smaller YOY krill were observed in the further off-shore samples, and larger krill corresponding to age 3 and greater were very rare in our sampling. It is possible that the smallest and youngest individuals are not able to make a seasonal migration all the way into the fjords (although other possibilities are discussed below). Larger krill may find maintaining position against a current to be less of a metabolic burden than age 1+ krill, and may choose to stay in an area with fewer predators than the coastal fjords. The observed abundance of age 1+ krill could also be related to multiyear patterns in krill recruitment, as 2013 was a particularly high recruitment year for krill in the WAP region (Steinberg et al. 2015), although the lack of a strong age 2+ year class within the fjords suggests recruitment variability is not the full explanation for the observed length distributions as 2012 was also a strong krill recruitment year (Steinberg et al. 2015).

Near-shore food resources

Fjords may also offer food resources not available to krill remaining further out on the shelf in winter. Algal prey, traditionally considered the most important food item for *E. superba*, are at very low levels in winter throughout the WAP region, due to very low

light levels with both short day lengths (approximately 4 h d⁻¹), and low sun angle. The very low abundance of water column algae can be seen in the very low chlorophyll values observed. Similarly, no ice algae were observed at the time of sampling as sea ice was just forming. However, it is clear from the fecal pellets observed within fjords that krill were feeding at least to some degree in these regions in winter. The importance of winter feeding may also vary as krill mature. *E. superba* accumulates storage lipids in summer and depletes these reserves in winter (Hagen et al. 2001). If larger age 2+ and older krill are able to accumulate more lipids, relative to their metabolic needs, than smaller krill, they may be less reliant on winter near-shore feeding and may choose to remain outside of our sampling region. Such larger krill have often been observed over the shelf region and more off-shore areas not sampled in our cruise, although it is again possible that variations in year-class success are partially responsible for the observed patterns (Siegel 1987, Lascara et al. 1999).

Krill may rely on alternative, non-phytoplankton food sources, such as sediments and associated phytodetritus (Schmidt et al. 2011) or mesozooplankton (Nordhausen et al. 1992, Huntley et al. 1994, Atkinson & Snÿder 1997) in the winter period of scarce phytoplankton. Cross-shelf advective flows, described earlier, may bring mesozooplankton into the fjords, enhancing opportunities for carnivorous feeding by krill. Within fjords, mesozooplankton abundances were roughly an order of magnitude lower than further out on the shelf, suggesting potential top-down effects of krill predation on mesozooplankton within the fjords. However, at the low abundances of mesozooplankton observed, it does not seem likely that this was the main food source sustaining the large krill population and leading to the observed fecal pellets. Similarly, YOY krill were at much lower abundances within fjords than they were off-shore, which may potentially reflect cannibalistic feeding by the larger age 1+ krill which dominated the fjords. Cannibalism was observed in our onboard krill incubations (A. C. Cleary unpubl. data), and has been previously documented for *E. superba* (Ligowski 2000).

The most likely food resource for krill within the fjords is sediments and associated detritus. Krill have been suggested to feed on epibenthic diatoms in some regions (Ligowski 2000), or detritus settling out from the water column and preserved by the cold bottom waters as a kind of 'food bank' (Smith et al. 2006, Schmidt et al. 2011). Krill were observed to spend daylight hours in dense aggregations, with the deepest individuals right on the sediment interface. These observations were consistent between acoustics, underwater videography (NBP1304 cruise report), and near-bottom Niskin sampling of krill (E. G. Durbin unpubl. data). There is growing evidence of the importance of epibenthic habitat for *E. superba*. Dense near-bottom aggregations have been observed with ROVs near the shelf break in the Weddell Sea (Gutt & Siegel 1994), and in the deep waters beyond the shelf break in the WAP region (Clarke & Tyler 2008, Brierley 2008). In total over 14 studies have observed epibenthic *E. superba*, with observations covering much of their distributional range (Schmidt et al. 2011). Sediment food resources have been recognized as potentially seasonally important for *E. superba* in the WAP and other relatively shallow coastal regions (Schmidt et al. 2011).

Krill in our study formed dense aggregations near the seafloor during daylight hours, provided the seafloor was shallower than 300 m. At the bottom of these aggregations krill were within a few meters of the seafloor, and were interacting with the sediment (camera observations; E. G. Durbin et al. unpubl. data). A large number of krill (~160) were collected from one of these observed dense aggregations in Andvord Bay simply by closing a 12 l Niskin bottle near the seafloor while within the aggregation. The guts of these near bottom krill were full of dark material, demonstrating that these krill were actively ingesting sediment. When starved krill individuals were placed in incubations with undisturbed sediment and overlaying waters they immediately swam to the sediment and began stirring up particles and actively filtering the stirred up particles with their thoracic limbs (M. Orchard pers. comm.), again suggesting sediments are a common and potentially important food resource for krill in this region in winter.

The relatively shallow depths of the sampled fjords may explain the value of sediment food resources. The availability of such sediment food resources has also been suggested to explain the more rapid maturation of krill in the WAP, as compared to other regions, such as the Lazarev Sea, where sediment food resources are less available to krill (Schmidt et al. 2014). Krill overwintering strategies are known to vary across their geographic range (Schmidt et al. 2014); for *E. superba* i
n the central WAP region at least, it appears that near-shore benthic feeding may be an important component of the overwintering strategy, and may serve as one of the drivers of seasonal in-shore migration by krill in this region.

CONCLUSIONS

E. superba, particularly age 1+ individuals, were observed in very high densities within 3 coastal fjords along the WAP in winter. These aggregations, in combination with previously reported summer distributions, suggest an active, seasonal on-shore migration. Active migration of krill into fjords in winter may help reduce advective losses from the WAP region, or conserve energy spent maintaining position within the advective shelf region. Fjords may also offer important food resources to krill during this period of very low phytoplankton, particularly in the sediments. High-density krill aggregations at the sediment interface suggest epibenthic feeding may be important for *E. superba* in this region in winter, and potentially one of the drivers of onshore migrations. Improved understanding of the role of fjords and epibenthic areas as habitat for krill helps to refine our understanding of the complex ecology of this keystone species. The role of these previously often under-recognized krill habitats may be important to consider in spatial planning and managing the growing fishery for this species to protect geographically limited but potentially ecologically important krill winter habitat.

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