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Ontogenetic diet shift in Antarctic krill (*Euphausia superba*) in the Prydz Bay: a stable isotope analysis

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Abstract

As one of the most common and dominant species in the Southern Ocean, Antarctic krill (*Euphausia superba*) play a significant role in food web structure and the process of energy flow. The diet of Antarctic krill in the Prydz Bay during austral summer of 2012/2013 was investigated and the ontogenetic shift in krill diet was evaluated using the stable isotope method. The nitrogen stable isotope values (δ^{15}N) of adults ((2.78±0.58)‰) were much higher than those of juveniles ((1.69±0.70)‰), whereas the carbon stable isotope values (δ^{13}C) of adults (–(28.26±1.08)‰) were slightly lower than those of juveniles (–(27.48±1.35)‰). Particulate organic matter (POM) from 0, 25, and 50 m depth combined (0/25/50 m) represented phytoplankton food items. The results showed that phytoplankton food items in surface water and mesozooplankton were two essential food items for Antarctic krill in the Prydz Bay during summer. POM (0/25/50 m) contributes 56%–69% and 26%–34% to the diet of juvenile and adult krill, respectively, whereas mesozooplankton composes 13%–34% and 58%–71% of the diet of juvenile and adult krill, respectively. Thus, an ontogenetic diet shift from POM (0/25/50 m), which consists mainly of phytoplankton, to a higher trophic level diet containing mesozooplankton, was detected. The capacity for adults to consume more zooplankton food items may minimize their food competition with juveniles, which rely mostly on phytoplankton food items. This suggests "diet shift with ontogeny" which may somehow help krill keep their dietary energy budget balanced and well adapted to the Antarctic marine ecosystem as a dominant species.

Key words: Antarctic krill, Prydz Bay, diet shift, stable isotope, IsoSource

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1 Introduction

Antarctic krill (*Euphausia superba*) are widely distributed in the Southern Ocean and are an important component of the Antarctic ecosystem, as they serve as a link between primary producers and secondary consumers (Everson, 2000). Krill commonly are thought to graze primarily on phytoplankton, but they actually consume considerable amounts of heterotrophic prey (mostly zooplankton) as well (Schmidt et al., 2003). Krill have been successful at acclimating to the seasonal cycles of food availability and habitat in the Southern Ocean. In spring and summer when phytoplankton is growing rapidly, krill mainly feed on phytoplankton as the main food source (Quetin and Ross, 1991). In autumn and winter when food is in short supply, krill (and especially larval krill) likely depend on sea ice for both food and habitat (Daly, 1990). Different developmental stages also may have different food preferences and survival strategies, as larvae and juveniles need more energy to survive winter to develop into adults (Nicol, 2006). The diet composition and diversity of feeding strategies of Antarctic krill likely interact with the energy and material flow of the Antarctic ecosystem. Thus, it is necessary to clarify the feeding strategy of Antarctic krill and how the grazing impact differs among stages in the seasonally ice-dominated Antarctic habitat.

Many traditional methods have been applied to investigate krill feeding activities and diet compositions. Stomach and gut content analyses provide a snap shot of what a specimen actually ingested at a given time. Using these methods, Maciejewska (1993) reported that diatoms and flagellates were major food items and that the size of ingested food particles increased with increasing size of animals. Feeding experiments can provide information about food selectivity. Price et al. (1988) showed that krill can feed very efficiently on zooplankton prey and have high-

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er clearance rates of phytoplankton than previously believed. These approaches are useful, but they also have disadvantages. For example, stomach and gut content analyses provide information about food recently ingested in the field, but they do not provide long-term dietary information (Båmstedt et al., 2000). In addition, the role of zooplankton in the diet may be underestimated because very small amounts of chitinous material reach the stomach and they are difficult to identify (Ponomareva, 1954). As for incubation experiments, it is not easy to simulate the natural environment, and zooplankton might behave unnaturally under artificial conditions, and bottle effects are unavoidable (Boyd et al., 1984). Finally, these approaches are mostly qualitative rather than quantitative.

The stable isotope method has been broadly applied to quantitatively describe diet and to determine trophic positions (Neill and Cornwell, 1992). As a biomarker, stable isotopes provide data about assimilated food that is integrated over a long period of time, thus serving as a method complementary to gut content analysis. The carbon isotope signature is relatively conservative across trophic levels, increasing by ~0.5‰–1‰ per trophic level, and is therefore indicative of dietary sources. Conversely, the nitrogen isotope signature increases by 3‰–4‰ per trophic level and is thus more indicative of trophic level (Post, 2002). Researchers have already used stable isotope analysis to study the diet of Antarctic krill in the Antarctic ecosystem. Their results indicated a pelagic and mainly herbivorous diet for *E. superba* in April in the Lazarev Sea, whereas ice and copepods seemed not to be important (Schmidt et al., 2003). Analysis of carbon and nitrogen isotope signature also provided evidence for an ontogenetic niche expansion of Antarctic krill in the South Shetland Islands, as adults had higher and more variable δ^{15}N values compared to those of juveniles (Polito et al., 2013).

The Prydz Bay is the third largest marine area extending into the Antarctic landmass, ranking behind the Weddell Sea and the Ross Sea (Pu and Dong, 2003). Three zooplankton communities were identified along the continental shelf edge of the Prydz Bay: the neritic community, the offshore oceanic community, and the krill-dominated community along the shelf slope (Hosie and Cochran, 1994). This community distribution pattern is strongly correlated with temperature, chlorophyll *a* (Chl *a*) concentration, and sea ice extent and distribution. As important residents in the Antarctic Ocean, Antarctic krill exhibited a patchy distribution and overall low abundance in the Prydz Bay (Hosie et al., 1988). Seasonal variability in the extent of sea ice affects the growth conditions and food availability of Antarctic krill. In austral winter, sea ice covers nearly the entire bay and provides ice biota as a food source for krill. In spring, sea ice retreats and water column phytoplankton blooms supply food for krill and other zooplankton (Atkinson et al., 2004). The success of krill recruitment depends on many factors, including growth conditions, food availability, and environmental conditions, especially the extent of sea ice in the previous winter. However, details of krill diet are still unclear, for example, the main diet of krill in the Prydz Bay during summer and whether there are differences in diet preference between juvenile and adult krill.

IsoSource is a linear mixing model applied to quantitatively determine the feasible contributions of multiple food sources based on isotopic values (Phillips and Gregg, 2003; Phillips et al., 2005). As a well-tested model, IsoSource has been applied in numerous dietary analyses as part of ecological studies (Benstead et al., 2006; Norkko et al., 2007; Hellmann et al., 2013). In the East Sea (Sea of Japan), this model revealed a trend towards increasing detritivory with ontogeny in *Euphausia pacifica* (Park et al., 2011). A disadvantage of this model is that it does not provide detailed dietary information, but instead yields information about higher level trophic groups (phytoplankton, zooplankton, detritus etc.) (Ogle et al., 2014). Nevertheless, we used this linear mixing model to provide a general understanding of the krill diet in the Prydz Bay.

To evaluate the diet of *E. superba* and its dietary shift with ontogeny in the Prydz Bay in austral summer of 2012/2013, we first measured the δ^{13}C and δ^{15}N values of *E. superba* juveniles and adults and those of potential food items. We subsequently quantified the feasible contributions of potential food items for juveniles and adults, and assessed the ontogenetic dietary shift in krill using a mixing model.

2 Materials and methods

2.1 *Study site and environmental conditions*

The main survey was conducted in the Prydz Bay area in the whole February of 2013 as part of the 29th Chinese National Antarctic Research Expedition cruise except sea ice samples were collected on December 2 to 4 of 2012 when the ice was dense (Fig. 1). During the main survey period, the floating ice was mostly thawed from the north to 69°S according to our visual observation. Temperature and salinity were measured using a CTD on board. Water samples for Chl *a* concentration analysis were collected with 10-L Niskin bottles from 0, 50, and 100 m depths. For each Chl *a* sample, 500 mL of seawater were filtered onto a Whatman GF/F (glass fiber) filter (0.70-μm pore size) and immediately stored at –20°C for no more than a month. Chl *a* was extracted using 90% acetone for 24 h at 4°C and the fluorescence of Chl *a* then was measured with a Turner Designs 10AU fluorometer.

2.2 *Sample collection and preparation*

Three types of nets were used to collect zooplankton samples, and all the trawls were carried out when we arrived at each station (Fig. 1). A Norpac net (0.5-m^2 opening, 330-μm mesh size) was towed vertically from 200 m to the surface. The volume of water filtered by the Norpac net was obtained by multiplying the net open area and trawl depth (which was 200 m), resulting in approximately 100 m^3. A Hydro-Bios multinet (0.5-m^2 opening, 200-μm mesh size) composed of five stratified nets was towed vertically at 11 stations using the 3 000-m winch. At deep stations where the sea bottom depth was greater than 1 500 m (P6-03, P5-01, P5-03, P4-01, P3-01, and P3-06), the multinet was dropped to 1 500 m to obtain samples of five water layers (0–100, 100–200, 200–500, 500–1 000, and 1 000–1 500 m). The sea bottom depth was 1 000–1 500 m at Sta. P4-05, so the nets were dropped to 1 000 m and the five water layers sampled were 0–100, 100–200, 200–500, 500–800, and 800–1 000 m. At neritic stations where the sea bottom depth was no more than 500 m (P6-09, P5-09, P5-12, and PA-01), the five stratified water layers sampled were 0–50, 50–100, 100–200, 200–300, and 300–the approximate bottom depth (350, 480, 500 and 450 m, respectively). The volume of water filtered by the multinet was obtained by multiplying the net open area and the depth of each corresponding water stratum. A single Isaac-Kidd Midwater Trawl net (2-m^2 opening, 6-mm mesh size) was towed obliquely at a speed of 1.5–2 m/s to collect Antarctic krill within water layers shallower than 50 m. The zooplankton samples were preserved in 5% buffered formalin seawater solution and later identified and counted using a dissecting microscopescope (Nikon SMZ 745T) in the laboratory. Antarctic krill samples were picked from several stations for stable

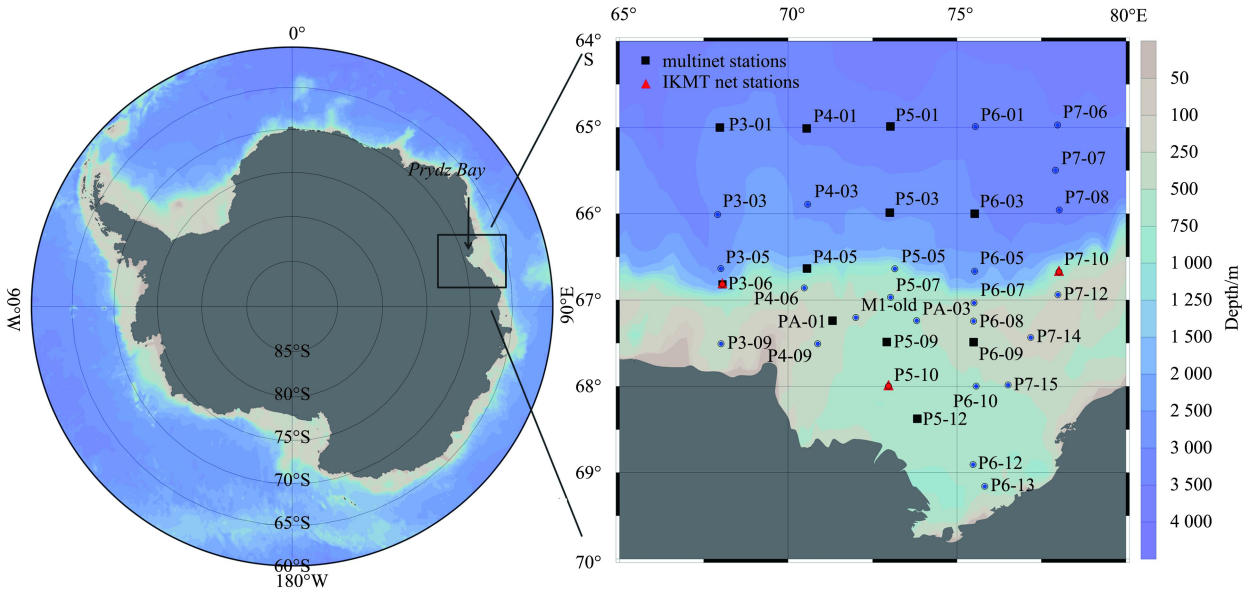

Fig. 1. Study site and sampling stations during the Prydz Bay during December 2012–February 2013. Stations sampled using the Multinet and Isaac-Kidd Midwater Trawl net are marked as squares and triangles, respectively.

isotope analysis. They were washed of debris and kept alive in 0.70-μm filtered seawater for a few hours to allow clearance of gut contents. They then were frozen individually at –80°C before further treatment.

Particulate organic matter (POM), mesozooplankton, and ice biota are considered to be prey of krill. POM samples for isotope analysis were collected with Niskin bottles from five water layers (0, 25, 50, 100, and 200 m) at most stations, and they were filtered through precombusted (450°C for 4 h) GF/F filters (0.70-μm pore size) after screening through a 200-μm sieve to exclude large prey items. To evaluate the POM composition, one liter water samples were collected with Niskin bottles from five of seven water layers (0, 25, 50, 100, 200, 500, 1 000, and 2 000 m) depending on the depth of a given station (e.g., for a 250-m deep station, samples were collected at 0, 25, 50, 100, and 200 m; for a 1 500-m deep station, samples were collected at 0, 100, 200, 500, and 1 000 m). These water samples were preserved in Lugol's solution and stored cool and in darkness. Later the species in water samples were identified and counted under a Zeiss microscope in the laboratory. The mesozooplankton sample was collected from the 0–100 m water layer using the multinet at Sta. P5-03. We towed twice at this station. The second sample was filtered through a precombusted GF/F filter for isotope analysis. Samples of a mixture of snow and one-year sea ice (hereafter named ice biota) were collected near the Zhongshan Station (69°22′24″S, 76°22′40″E) on December 2 to 4 of 2012. The ice biota samples were melted and filtered on GF/F filters. All krill diet samples for stable isotope analysis were frozen at –80°C before further treatment.

In this study, Antarctic krill⩽35 mm total length were considered to be juveniles (including larvae), and Antarctic krill>35 mm total length were considered to be adults (Polito et al., 2013). The dry weight of each krill individual was measured, but length data were not collected. Thus, we used regression relationship between body mass (dry weight mg) and total length (mm) to estimate length (Atkinson et al., 2002):

$$\log_{10} W_{\mathrm{d}} = 3.25 - \log_{10} L_{\mathrm{t}} - 3.18 \left(n = 31 \text{ krill},\ R^2 = 0.978\right), \quad (1)$$

where W_{d} is dry weight (mg) and L_{t} is total length (mm). In this study, we considered the dry weight (when L_{t}=35 mm) as the index to differentiate juvenile and adult krill.

Stable isotope samples were freeze dried in a vacuum for 48 h. Inorganic carbonates were not removed from all samples because the effect of pre-analysis acid treatment on both δ^{13}C and δ^{15}N is unclear (Brodie et al., 2011). Each of the krill samples and the mesozooplankton sample were ground to a fine powder with a pestle and agate mortar for 1–3 replicates. Carbon and nitrogen stable isotope ratios of krill and their potential diet samples were then measured using an elemental analyzer (Flash EA 1112HT, Thermo Fisher Scientific, Inc., San Diego, CA, USA) coupled with an isotope-ratio mass spectrometer (Finnigan Delta V Advantage, Thermo Fisher Scientific, Inc.). Isotope abundances are expressed in delta (δ) notation as

$$\delta X = \left[\left(R_{\mathrm{sample}}/R_{\mathrm{standard}}\right) - 1\right] \times 10^3, \quad (2)$$

where X is ^{13}C or ^{15}N and R is ^{13}C/^{12}C or ^{15}N/^{14}N. Pee Dee Belemnite was used as the standard for carbon and atmospheric N_2 (air) was used as the standard for nitrogen. An internal standard (glycine) was run for every 12 samples. Measurement precision was 0.1‰ and 0.2‰ for δ^{13}C and δ^{15}N values, respectively.

In this study, lipid was not extracted from all the samples, and the δ^{13}C values given in the text are uncorrected, original data if not annotated. However, lipid synthesis is known to discriminate against ^{13}C (Deniro and Epstein, 1977), and lipids are lighter in δ^{13}C relative to protein by approximately 6‰ (McConnaughey and McRoy, 1979; Alexander et al., 1996). In contrast, δ^{15}N values are not affected (Rau et al., 1991b). The lipid content of a sample can be predicted accurately from its C/N ratio (McConnaughey and McRoy, 1979; Lesage et al., 2001). Therefore, "lipid normalized" δ^{13}C values were calculated from δ^{13}C values and C/N ratios using the equations in McConnaughey and McRoy (1979) when the C/N ratios were high (C/N ratio greater than 4 in this study).

The trophic levels (TLs) of juvenile and adult Antarctic krill relative to primary consumers were calculated using the following formula:

$$TL_{\mathrm{consumer}} = \left[\left(\delta^{15}\mathrm{N}_{\mathrm{consumer}} - \delta^{15}\mathrm{N}_{\mathrm{primary\ consumer}}\right)/3.4\right] + 2, \quad (3)$$

where $\delta^{15}N_{primary\ consumer}$ is the $\delta^{15}N$ reference baseline value of the primary consumer at TL 2 (Vander Zanden and Rasmussen, 1999). We chose a dominant herbivorous species, *Salpa thompsoni*, as the primary consumer for calculating the trophic position of Antarctic krill following Cherel et al. (2008). *S. thompsoni* was collected by Norpac net. The average $\delta^{15}N$ fractionation value per TL increment was assumed to be 3.4 (Minagawa and Wada, 1984).

2.3 *Data analysis*

We used the stable isotope mixing model IsoSource to investigate the contributions of multiple food sources to the diet of Antarctic krill (Phillips and Gregg, 2003). The model iteratively calculates all possible combinations of source proportions and selects only those that match the target mixture within the variability allowed by the tolerance setting (0.1‰ with an increment of 1%). Both original and lipid-corrected $\delta^{13}C$ data were used in the model, and both outputs were considered and illustrated. Ocean Data View 4 was used to plot stations, environmental factors (temperature, salinity, and Chl *a* concentrations), and the horizontal distribution of Antarctic krill in the study area. One-way analysis of variance (ANOVA) was conducted to assess isotopic differences of POM in the 0, 25, and 50 m layers. Linear regression analysis was applied to clarify the relationship between krill body mass and isotope values using SPSS 17.0 software.

3 Results

3.1 *Environmental conditions*

The sea ice had retreated at all stations during our sampling time period. The sea surface temperatures (SSTs) ranged from –1.36°C to 0.74°C, and they were higher in the oceanic region than in the neritic region (Fig. 2a). The coldest surface waters (–1.36°C) occurred to the east of Prydz Bay around the Cape Darnley (P3-09). The salinities of surface water ranged from 32.83 to 34.10 (Fig. 2b). Chl *a* concentrations ranged from 0.01 μg/L to 0.97 μg/L in the surface waters. The maximum values were 0.97 μg/L at P6-12 and 0.73 μg/L at P7-12 (Fig. 2c), and these results

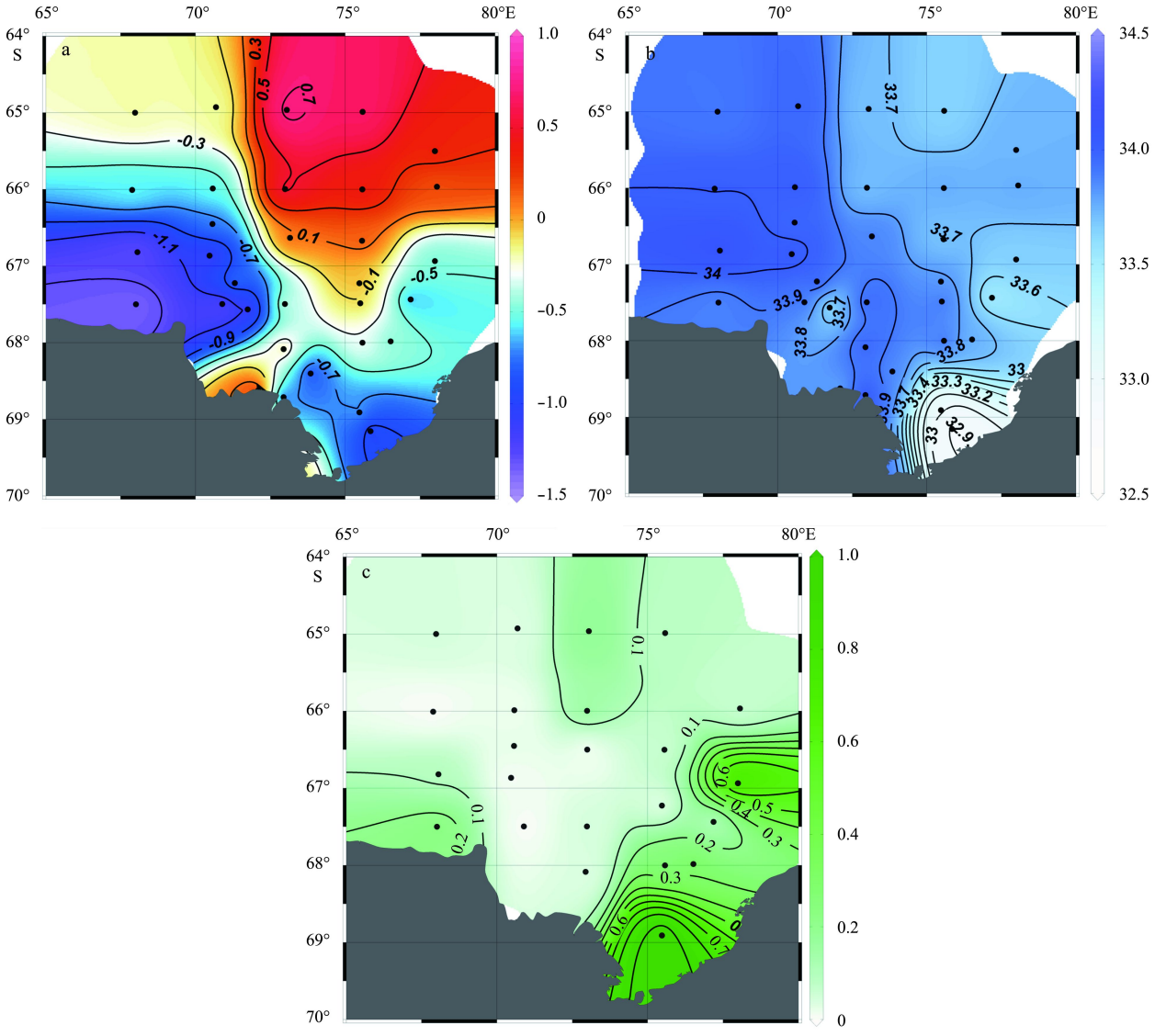

Fig. 2. Surface hydrological conditions in the Prydz Bay: a. surface water temperatures (SSTs) ranged from –1.36°C to 0.74°C, b. salinities of surface water ranged from 32.83 to 34.10, and c. Chl *a* concentrations of surface water ranged from 0.01 μg/L to 0.97 μg/L. The marked dots indicate the stations at which the data were collected.

were supported by remote sensing data (Yin et al., 2014). Based on the fluorescence values, the maximum Chl *a* concentrations generally occurred in water layers between 40 m and 70 m. Generally, our results are in agreement with reported hydrographic conditions of the Prydz Bay in previous studies (Smith et al., 1984; Hosie and Cochran, 1994).

3.2 *Distribution and abundance of juvenile and adult krill*

Figure 3 shows the horizontal distribution and abundance of Antarctic krill based on the Norpac net samples, expressed as individuals (ind.) per 1 000 m^3 based on the Norpac net samples. The abundance of juvenile krill was 10–880 ind. per 1 000 m^3 and that of adult krill was 10–100 ind. per 1 000 m^3. Adult krill were found at only three stations: 100 ind. per 1 000 m^3 at P5-09, 20 ind. per 1 000 m^3 at P5-05, and 10 ind. per 1 000 m^3 at P4-03. Generally, Antarctic krill were more abundant at the neritic stations south of 68°S than at the shelf slope. The relationship between the horizontal abundance of Antarctic krill (ind. per 1 000 m^3) and Chl *a* concentrations of the surface water (μg/L) was significant (r^2= 0.691, p<0.001).

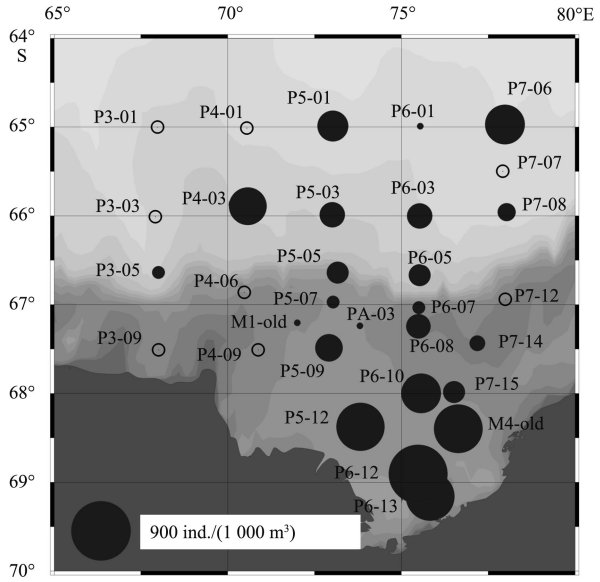

Fig. 3. Horizonal distribution and abundance of Antarctic krill in the Prydz Bay are expressed as individuals per 1 000 m^3. The sized dots are proportional to total abundance. Stations at which no Antarctic krill were collected by Norpac net are marked as open circles.

Vertical distribution and abundance of Antarctic krill were determined based on the multinet samples. Antarctic krill were collected at six of the 11 stations (Fig. 4). At the deep stations (P3-06, P5-03, and P4-05), adult krill were found in deeper water (P5-03, P4-05), whereas juveniles were found in upper water (P5-03). At neritic stations (P6-09, P5-09, and PA-01) with depths less than 500 m, both adults and juveniles were found (PA-01, P5-09).

3.3 *Compositions of potential diets: POM and mesozooplankton*

We calculated the mean abundance of food groups in every water layer based on POM compositions (Table 1). Diatoms constituted the major group: two pennate diatoms, *Nitzschia* spp. and *Fragilariopsis* spp., were the two most abundant species, followed by three centric diatoms, *Corethron* sp., *Chaetoceros* spp., and *Eucampia* sp. Most species were concentrated in the upper 200 m.

The mesozooplankton sample contained mainly heterotroph-

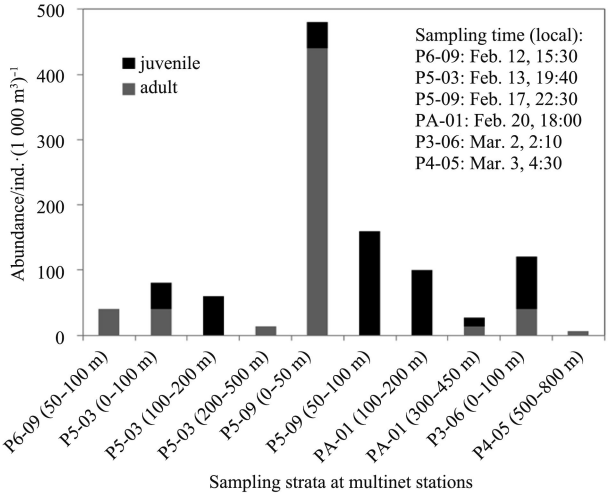

Fig. 4. Vertical distribution and abundance of Antarctic krill (juvenile and adult) in water strata in our study area expressed as individuals per 1 000 m^3.

Table 1. Mean abundance (ind./L) of food groups in water samples from different depths

Food group	Depth of water samples/m							
	0 (n=20)	25 (n=12)	50 (n=19)	100 (n=20)	200 (n=20)	500 (n=13)	1 000 (n=6)	2 000 (n=3)
Diatoms								
Centric diatoms								
Corethron sp.	147.0	165.0	556.3	57.5	10.5	5.4	3.3	6.7
Chaetoceros spp.	114.5	138.3	114.7	113.0	23.5	0.8	3.3	0.0
Eucampia sp.	52.5	22.5	29.5	12.5	18.5	0.0	5.0	0.0
Others	53.0	110.8	48.9	45.5	18.0	13.1	5.0	3.3
Pennate diatoms								
Nitzschia spp.	1 102.0	1 205.8	369.5	570.5	120.0	23.1	3.3	10.0
Fragilariopsis spp.	730.5	1 231.7	606.3	858.5	538.0	60.8	13.3	3.3
Others	12.0	7.5	10.0	21.5	21.5	11.5	1.7	13.3
Dinoflagellates	21.5	48.3	15.3	11.5	9.1	4.6	3.3	23.3
Chrysophytes	28.0	19.2	24.2	14.5	1.0	0.0	0.0	0.0
Ciliates	38.0	42.5	34.7	22.0	7.5	2.3	1.7	0.0

Note: n is number of stations.

ic zooplankton such as copepods. *Oithona similis* was the most abundant species (163 ind./m^3), followed by *Ctenocalanus citer* (15.5 ind./m^3), *Metridia gerlachei* (14.1 ind./m^3), *Calanoides acutus* (2.9 ind./m^3), and *Calanus propinquus* (2.2 ind./m^3). Other species were less abundant.

3.4 *δ^{13}C and δ^{15}N values of Antarctic krill and their food sources*

Table 2 shows the δ^{13}C and δ^{15}N values of Antarctic krill and their potential food sources. Both original and lipid-corrected δ^{13}C values are listed. The mean δ^{13}C of adult krill (–28.26‰) was lower than that of juveniles (–27.48‰), whereas the mean δ^{15}N of adults (2.78‰) was higher than that of juveniles (1.69‰). The C/N ratios of krill were 3.44–5.74, meaning that the different lipid content explains a difference of ⩽1.4‰ of their original δ^{13}C values. For juvenile krill, the lipid-corrected δ^{13}C values were slightly higher than those original ones. This can be attributed partly to their low lipid contents indicated by their low C/N ratios (3.44–4.29). Three sources of POM (0 m), POM (25 m), and POM (50 m) were combined to represent the shallow water POM (0/25/50 m) because no significant differences were observed among them for δ^{13}C (Kruskal-Wallis test: df=39, p=0.246) or δ^{15}N (ANOVA: df=39, p=0.184). POM in the shallow layers usually had lower δ^{13}C and δ^{15}N values than POM in the deeper layers. Mesozooplankton had a much lower δ^{13}C value (–28.86‰) than ice biota (–23.65‰), but their δ^{15}N values were similar. The primary consumer, *S. thompsoni*, had a relatively low δ^{15}N value (1.88‰).

Table 2. δ^{13}C and δ^{15}N values (mean±SD) of krill and their food sources in the Prydz Bay during December 2012–March 2013

	n	δ^{13}C/‰	δ^{15}N/‰	lipid-corrected δ^{13}C/‰	C/N ratios	*TL*
POM (0/25/50 m)	42	–27.45±1.28	0.13±1.16	–26.64±1.49	4.94±1.23	
POM (100 m)	14	–26.30±1.18	4.64±0.92	–25.62±1.25	4.75±1.01	
POM (200 m)	3	–26.02±1.44	5.84±0.94	–25.71±1.73	3.69±1.88	
Mesozooplankton	1	–28.86	3.83	–28.75	4.10	
Ice biota	15	–23.65±2.09	3.87±1.12	–23.32±2.09	4.31	
Euphausia superba (juvenile)	9	–27.48±1.35	1.69±0.70	–27.45±1.31	3.74±0.25	1.95±0.21
Euphausia superba (adult)	10	–28.26±1.08	2.78±0.58	–27.46±1.15	4.92±0.52	2.27±0.17
Salpa thompsoni	16	–28.76±2.02	1.88±1.76	–27.71±1.73	5.34±0.81	2.00±0.52

Note: *n* is numbers of sample analyzed and *TL* trophic level.

To better understand the changes of δ^{13}C and δ^{15}N values with developmental stage, we tested the relationship between krill body mass and δ^{13}C and δ^{15}N values (Fig. 5). Krill δ^{13}C values were lower in heavier krill, but the correlation was weak (R^2=0.092, p=0.207), which indicates that to a small extent larger krill may have lower δ^{13}C values. δ^{15}N values for krill were positively correlated with body weight (R^2=0.438, p=0.002), meaning that larger krill usually had higher δ^{15}N values. Based on mean values, the δ^{15}N value of adult krill was 1.09‰ higher than that of juvenile krill (Table 2), which suggests that diet of krill changes with its size.

3.5 *Stable isotope multiple-source mixing model results*

The IsoSource model was used to estimate the feasible contribution of different food sources to the diet of Antarctic krill (Fig. 6). Lipid-corrected δ^{13}C values are also marked in this figure. Both the original and lipid-corrected δ^{13}C values were used in the IsoSource model, and the calculated results are listed in Table 3. The mixing polygon was broad, with the mixtures falling near one end in both figures. For *E. superba* juveniles, POM (0/25/50 m) appeared to constitute the majority of the diet (56%–69%), with mesozooplankton as an important secondary food source (13%–34%); POM (100 m), POM (200 m), and ice biota at 0%–24%, 0%–19%, and 0%–13%, respectively, apparently contributed less to the diet, and these values had lower precision (Fig. 6a). Because the lipid-corrected δ^{13}C values of juveniles (–27.45±1.31) were close to original values (–27.48±1.35) as a result of low C/N ratios, the two outputs were similar. For *E. superba* adults, mesozooplankton was the major food source (58%–71%), followed by POM (0/25/50 m) (26%–34%); other potential food sources made

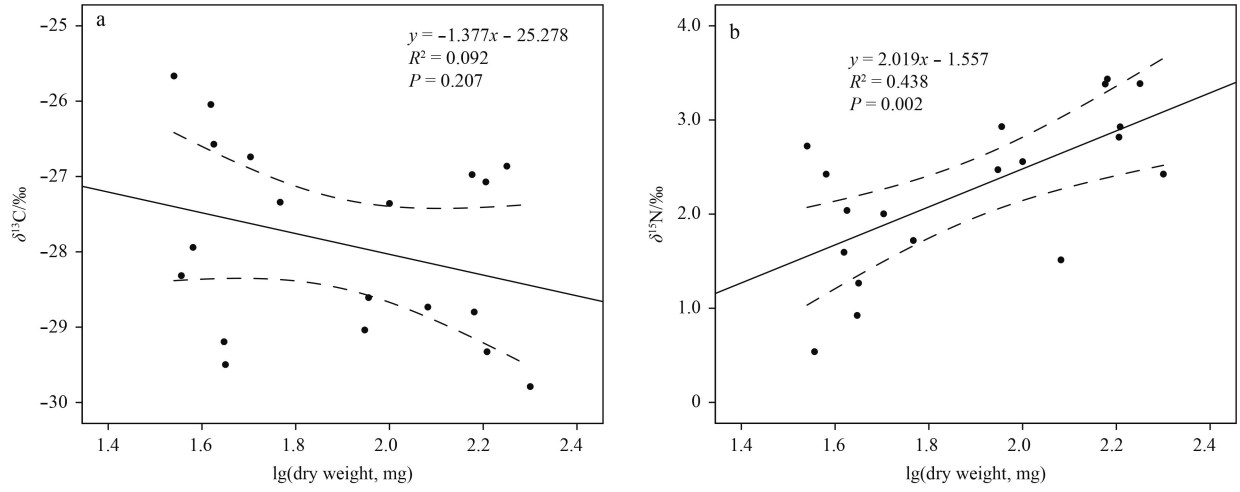

Fig. 5. Relationship between body mass and stable isotope values (δ^{13}C and δ^{15}N) in Antarctic krill. Linear regression lines, 95% confidence intervals, and test statistics are provided.

Table 3. Mean proportions and the 1–99th percentile ranges of the percentage frequency distributions of five food sources in Antarctic krill diet using IsoSource

Preys of Antarctic krill	Juvenile krill with original δ^{13}C		Juvenile krill with lipid-corrected δ^{13}C		Adult krill with original δ^{13}C		Adult krill with lipid-corrected δ^{13}C	
	Mean/%	Range/%	Mean/%	Range/%	Mean/%	Range/%	Mean/%	Range/%
POM (0/25/50 m)	62.1	56–69	62.5	56–71	29.9	26–34	35.3	26–46
POM (100 m)	6.9	0–24	6.7	0–23	2.9	0–11	9.9	0–32
POM (200 m)	5.4	0–19	6.2	0–21	2.2	0–9	9.1	0–30
Mesozooplankton	22.1	13–34	20.5	9–33	63.7	58–71	39.8	26–57
Ice biota	3.6	0–13	4	0–14	1.4	0–6	5.9	0–20

up the remainder of the diet (Fig. 6b): POM (100 m) (0%–11%), POM (200 m) (0%–9%), and ice biota (0%–6%). It should be noted that the lipid-corrected δ^{13}C values of adults (–27.46±1.15) were about 0.80‰ higher than those of original δ^{13}C values (–28.26±1.08), so the two outputs differed in their distribution of contributions of food sources, especially for mesozooplankton. Because each of the feasible source combinations is constrained to sum to 100%, there are tradeoffs among these food sources within their feasible ranges. This means that if one source was at its maximum feasible contribution, some of other sources must contribute amounts closer to the lower end of their range (Phillips and Gregg, 2003). Based on original data, the mean values indicate that as *E. superba* matured, the contribution of POM (0/25/50 m) to the diet decreased from an average of 62.1% to 29.9% while that of mesozooplankton increased from an average of 22.1% to 63.7%; this represents an ontogenetic diet shift from POM (0/25/50 m) to mesozooplankton.

4 Discussion

In this study, POM, mesozooplankton, and ice biota were considered to be potential food items for krill based on results of previous studies (Atkinson and Snÿder, 1997; Hansson and Tranvik, 2003). The δ^{15}N values of krill and their diet increased in the following order: POM (0/25/50 m) (0.13‰) < *E. superba*, juvenile (1.69‰) < *S. thompsoni* (1.88‰) < *E. superba*, adult (2.78‰) < mesozooplankton (3.83‰) < ice biota (3.87‰) < POM (100 m) (4.64‰) < POM (200 m) (5.84‰). These values are generally consistent with results from East Antarctica: POM (0.5‰) < *E. superba*, juvenile (1.0‰) < *S. thompsoni* (1.8‰) < *E. superba*, adult (3.1‰) < other zooplankton (Wada et al., 1987). POM sampled from the Weddell Sea varied widely from –5.4‰ to 41.3‰ in δ^{15}N values, with a significant trend towards higher values with increasing depth. This may due to the selective loss of ^{14}N during POM diagenesis and respiration in aphotic waters (Wada et al., 1987; Rau et al., 1991b). The original δ^{13}C values in this study increased in the following order: mesozooplankton (–28.86‰) < *S. thompsoni* (–28.76‰) < *E. superba*, adult (–28.26‰) < *E. superba*, juvenile (–27.48‰) < POM (0/25/50 m) (–27.45‰) < POM (100 m) (–26.30‰) < POM (200 m) (–26.02‰) < ice biota (23.65‰). The δ^{13}C values (–29.60‰ to –24.35‰) of POM were generally consistent with the δ^{13}C values (–29.68‰ to –26.30‰) of POM reported for the Weddell Sea (Wada et al., 1987). The POM δ^{13}C values also showed a trend towards higher values with increasing depth as a result of the selective loss of ^{12}C during metabolism and degradation of POM once it is removed from the euphotic zone (Wada et al., 1987; Rau et al., 1991b). The isotope values for POM are influenced in part by oceanographic conditions, such as nutrients and CO_2 concentrations in the water, and are unlikely to be the same as pure phytoplankton due to the other potential materials such as bacteria, detritus, and heterotrophs (Rau et al., 1991c; Stowasser et al., 2012). However, POM originates from phytoplankton, and the latter may be represented by samples of POM from open water (Pelagic-POM), especially compared with POM originating from ice algae (Wada et al., 1987; Søreide et al., 2006). Therefore, we consider it reasonable to regard POM as a phytoplankton food source for krill, as POM consists mostly of phytoplankton (Maciejewska, 1993; Gurney et al., 2001; Meyer et al., 2002).

The δ^{15}N values of Antarctic krill in this study (1.69‰ for juveniles and 2.78‰ for adults (Table 2)), were similar to values from a previous study (1.0‰ for juveniles and 3.1‰ for adults) conducted in East Antarctica (Wada et al., 1987). Several previous studies indicated that Antarctic krill in the Prydz Bay had a relatively low δ^{15}N value (0.4‰ to 3.2‰) and high δ^{13}C value (–29.8‰ to –26.5‰) compared to krill from other Antarctic areas (Rau et al., 1991a; Schmidt et al., 2003; Stowasser et al., 2012), although other studies reported high δ^{15}N values (3.0‰–4.0‰) of krill from the Prydz Bay (Hodum and Hobson, 2000; Tierney et al., 2008). The δ^{15}N value of a consumer is affected by its food sources and the isotopic fractionation that occurs during the feeding process. Isotopic fractionation of nitrogen seems to be constant regardless of habitat (Cabana and Rasmussen, 1996). Thus, the different δ^{15}N values of krill from different areas of the Southern Ocean likely are due to the different primary food items they consume, both directly and indirectly.

The IsoSource output indicated that phytoplankton food items in surface water represented by POM (0/25/50 m) were a substantial food source for krill, as POM (0/25/50 m) constituted a high proportion of the diet, especially for juvenile krill (56%–69%) (Fig. 6a). In summer in the Prydz Bay, a positive relationship exists between krill distribution and Chl *a* concentration in surface water. At this time of year, freshly collected krill have a dark green hepatopancreas, which illustrates that krill rely on phytoplankton as their main food (although the Chl *a* concentrations were not high during the study period). Other studies also indicated that krill feed mainly on phytoplankton in epipelagic waters (Haberman et al., 2003a, b; Schmidt et al., 2006). Stomach content analysis revealed that juveniles preferred larger particle sizes (about 30–40 μm) than adults (about 10–30 μm), that stomachs of juveniles contained larger amounts of ingested food particles than adults, and that adults had more diversified food compositions (Maciejewska, 1993). The different feeding patterns indicate that juvenile krill may meet their energy needs by eating a large proportion of phytoplankton particles of a similar size, whereas adults are relatively independent of the size and type of phytoplankton. These findings confirm the greater importance of phytoplankton food source for juvenile krill compared to adult krill and that phytoplankton in surface water contributes quantitatively more to the diet of juveniles than to that of adults. In the Prydz Bay, species assemblages were distinguished by their respective narrow ranges of δ^{13}C values: Pennate diatoms, such as *Nitzschia curta* and *Nitzschia subcurvata*, appeared

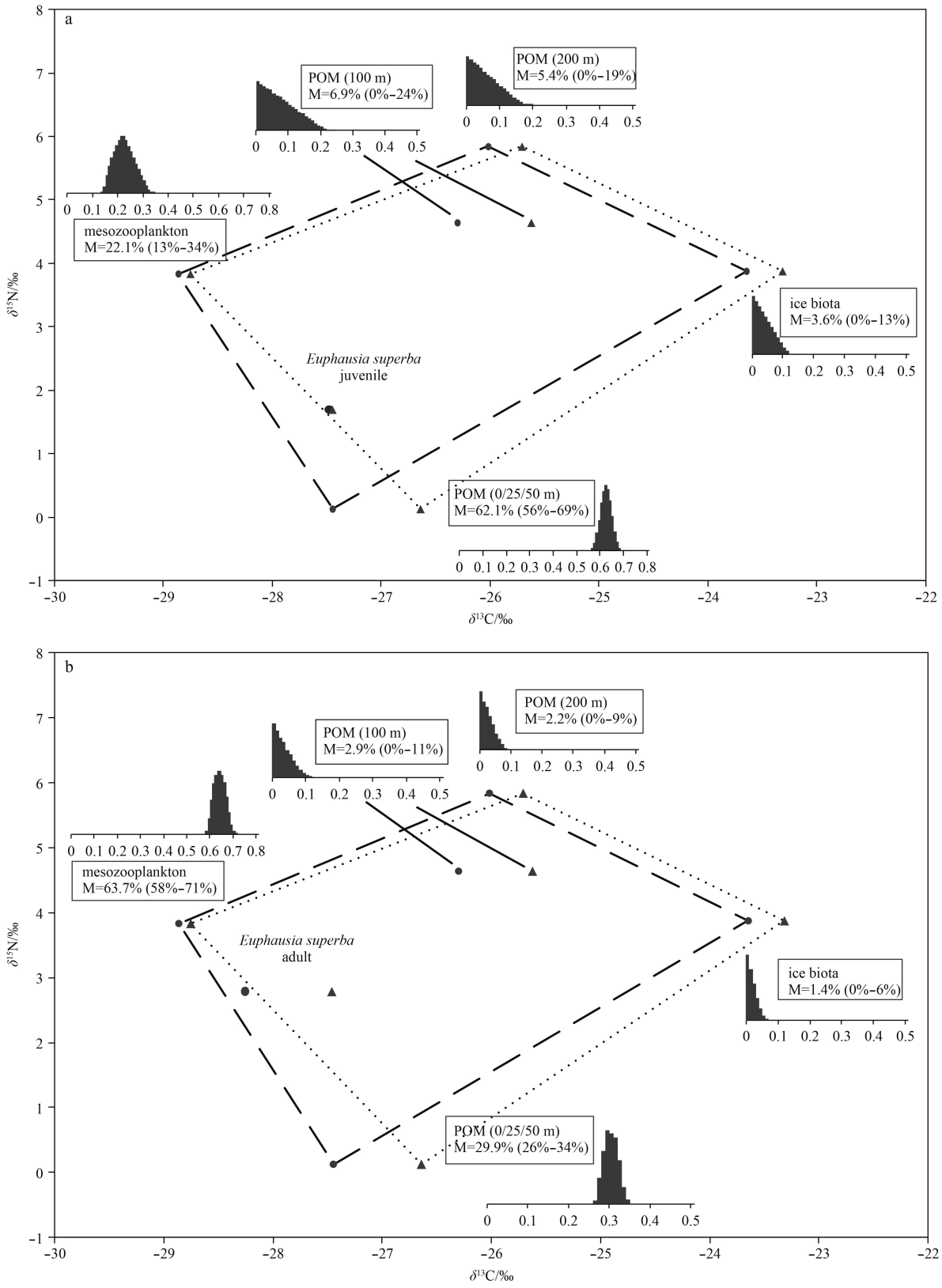

Fig. 6. Mixing polygon for δ^{13}C and δ^{15}N values of five food sources for *E. superba* juveniles (a) and adults (b). Histograms show the distribution of feasible contributions from each possible source to the krill diet; M equals mean value (1–99 percentile ranges) for these distributions. Lipid-corrected δ^{13}C values are also marked as triangles in this figure.

to have made the greatest imprint on the highest δ^{13}C values (–20.12‰ to –22.37‰), whereas Phaeocystis, naked flagellates, autotrophic dinoflagellates, and centric diatoms likely caused the lower values (–24.50‰ to –26.65‰; –29.73‰ to –31.85‰) (Kopczyńska et al., 1995).

The model output showed that mesozooplankton was also an

important food source for Antarctic krill, especially for adults, as it accounted for 58%–71% of the diet of adults (Fig. 6b). Mesozooplankton was the only food source that had a δ^{13}C value lower than those of juveniles and adults on the basis of isotopic balance in the mixing model, which suggests that it is an indispensable dietary component in addition to phytoplankton in surface layers. This result is consistent with the mainstream view that krill are omnivorous feeders, especially in summer (Hopkins and Torres, 1989; Atkinson et al., 1999). During austral summer, phytoplankton concentrations in the water column vary widely over space and time, and Chl *a* concentrations generally range between 0.1 and 13 μg/L, with most reported values being less than 1.0 μg/L (Perissinotto et al., 2000; Atkinson et al., 2004). When phytoplankton concentrations are low, all stages of krill tend to feed omnivorously (Daly, 1990; Daly and Macaulay, 1991). Our mesozooplankton sample contained zooplankton that consisted mostly of small and large copepods. These heterotrophic food items constitute a considerable proportion of the diet of krill (Perissinotto et al., 2000), and fatty acid trophic markers indicate that they are consistently part of diet (Schmidt et al., 2014).

The ice biota δ^{13}C values in this study ranged from –27.91‰ to –19.41‰ and agree with the ice core values of –26‰ to –18‰ in the southeastern Weddell Sea (Fischer, 1991). Rau et al. (1991b) reported that ice biota throughout the Southern Ocean had a wide range of δ^{13}C (–26‰ to –18‰) and δ^{15}N (2‰ to >10‰) values, and Søreide et al. (2006) found that Ice-POM was generally more enriched in ^{13}C than Pelagic-POM. The ice biota are considered to be an available food source, especially in austral winter (Legendre et al., 1992; Ross et al., 2004; Quetin and Ross, 2009). However, in our study, ice biota only constituted 0%–10% and 0%–4% of the diet of juveniles and adults, respectively, suggesting that ice biota contribute little to the diet of krill at this time (Fig. 6, Table 3). In spring, phytoplankton production increases explosively, as the melting sea ice along the Amery Ice Shelf releases algae mixtures into the water and creates vertical exchanges in the water column (Quetin and Ross, 1991; Yin et al., 2014). By summer, the sea ice has mostly melted, and both phytoplankton and zooplankton are in the water column and provide food for higher consumers. At this time, krill may not need to exploit ice biota anymore, or the algae and other food materials in the sea ice have been released into waters already. This premise is in agreement with laboratory incubation results suggesting that in the Lazarev Sea in autumn *E. superba* larvae mainly feed herbivorously rather than feed within the ice biota (Schmidt et al., 2003).

The IsoSource output indicated that krill in different developmental stages had different foraging strategies. POM (0/25/50 m) and mesozooplankton were the two major dietary components for Antarctic krill. For juveniles, POM (0/25/50 m) constituted most (56%–69%) to the diet, followed by mesozooplankton (13%–34%). For adults, the contribution of mesozooplankton (58%–71%) to the diet was much greater than that of POM (0/25/50 m) (26%–34%). However, because of the impact of lipid content in adult krill, the output changed a little when lipid-corrected δ^{13}C values were used. For example, mesozooplankton contributed 26%–57% of the adult krill diet when lipid-corrected data were used, whereas the range was 58%–71% using original δ^{13}C data. Thus, we might have overestimated the diet proportion of mesozooplankton. However, it is essential to be aware that the mixing model output is highly sensitive to whether or not carbon isotope ratios of predators and/or prey have been corrected for lipid content (Kiljunen et al., 2006), and output must be interpreted with causion. Another problem we should pay attention to is that we only have one mesozooplankton sample. We used the POM isotope value distribution data to estimate the spatial distribution of mesozoopalntkon isotope values using a constant trohic enrichment of ($\delta^{15}N_{zooplankton}$–$\delta^{15}N_{POM}$ at P5-03) in order to improve the "sample size". The output indicated that the proportions of contribution to main juvenile krill diet are: 66.1% POM (0/25/50 m) (61%–72%), and 18% mesozooplankton (11%–28%). The other three minor sources POM (100 m), POM (200 m), and ice biota contribute exactly the same proportions as results calculated from the original data. For adult krill, the proportion of diet contributions is: 41.4% POM (0/25/50 m) (38%–45%), 51.8% mesozooplankton (47%–58%), 3% POM (100 m) (0%–12%), 2.3% POM (200 m) (0%–9%), and 1.4% ice biota (0%–6%). Compared to the results from original data, mesozooplankton contributed more and POM (0/25/50 m) contributed less to the adult diet after mesozooplankton isotope value was lipid-corrected. Although the specific distributions of diet contributions are different among these outputs, the main conclusion does not change. We could still infer that in austral summer in the Prydz Bay, an ontogenetic diet shift occurs in krill, with a change from phytoplanktonic to mesozooplanktonic food sources. In fact, Antarctic krill can ingest a wide size range of food particles (2–3 μm to nearly 1 000 μm) due to their efficient filter feeding basket (Suh and Nemoto, 1987; Maciejewska, 1993). The filter mesh size of krill is consistent throughout ontogeny (McClatchie and Boyd, 1983); however, the feeding filter area in *E. superba* tends to increase with increasing body length. This suggests that larger krill would capture more food particles per unit time when filtering in the same way (Suh and Choi, 1998). A large filter area would increase the successful capture of zooplankton, which are more capable of moving than phytoplankton. Moreover, gut content analysis also showed that larvae contained high but variable proportions of diatom markers, whereas in postlarvae the role of copepods increased with krill body length (Schmidt et al., 2014). This dietary pattern is consistent with growing evidence suggesting that krill adults consume a relatively greater proportion of heterotrophic prey than juveniles during austral summer (Atkinson et al., 2002).

In our study, the δ^{15}N values of krill were positively related to body mass (Fig. 5), meaning that larger krill usually had higher δ^{15}N values. The broad range of δ^{15}N values observed in this study (0.45‰–3.45‰) also suggests that krill in the Prydz Bay area are omnivorous feeders, and the mean *TL* of adults is 0.32 level higher than that of juveniles. This increase in TL with ontogeny, which was confirmed by stomach content analysis (Schmidt et al., 2014), means that large and mature krill would be in higher trophic positions and consume more heterotrophic prey compared to juveniles. In fact, copepod ingestion of krill was reported to increase with krill body length (Polito et al., 2013; Schmidt et al., 2014). The ability for adults to consume more zooplanktonic food items may minimize food competition with juveniles, which rely mostly on phytoplankton food items (Polito et al., 2013).

The distribution of krill may be indicative of their food sources, as it identifies where they eat. The environmental conditions especially Chl *a* may have an impact on the krill distribution. Based on Norpac samples, Antarctic krill were mostly distributed with the surface phytoplantkon. It is known that another Antarctic resident, *Euphausia crystallorophias*, was found to be mainly on the continental shelf (Thomas and Green, 1988; Hosie, 1991). While in our survey, *E. crystallorophias* were found only at two stations (P5-12 and P6-09), thus it was not dominant in the

Prydz Bay during this summer. Based on multinet samples, juvenile krill were found in the top 200 m, whereas adult krill were distributed from the sea surface down to deep water (500–800 m at P4-05). Previous research in the Prydz Bay area indicated that juveniles were always found in waters close to the surface and that female adults were mostly found in the deeper hauls (Miquel, 1991). Studies in other regions of the Southern Ocean reported similar vertical diatributions (Siegel et al., 1990; Quetin and Ross, 1991; Nordhausen, 1994; Taki et al., 2008). It is reasonable to assume that Antarctic krill prey in the upper ocean, where fresh phytoplankton is their main food source. However, other foraging patterns may exist. For example, epibenthic sampling and the examination of stomach contents suggested that Antarctic krill may migrate to deep waters and forage on the seabed for detritus and copepods (Schmidt et al., 2011). This foraging pattern could affect krill δ^{15}N values. It is possible that adult krill has higher δ^{15}N values because they migrated to the seabed to forage for zooplanktonic food or detritus.

In conclusion, our one season results show that Antarctic krill mainly consume phytoplankton food items in surface water (POM (0/25/50 m)) and mesozooplankton in the Prydz Bay during austral summer of 2012/2013. Ice biota contributes little to diet of krill. Our data indicate that Antarctic krill are opportunistic consumers, as they exploit different food sources when available (Daly, 2004). The large proportion of POM (0/25/50 m) in the diet of juveniles and mesozooplankton in the diet of adults illustrates that a conversion, or ontogenetic diet shift, from phytoplanktonic to zooplanktonic occurs. In this case, adult krill are likely to be more flexible and independent in food selectivity, whereas juveniles may rely predominately on phytoplankton food items. This “diet shift with ontogeny” may help Antarctic krill maintain a dietary balance, avoid competition among stages, and acclimate to the Antarctic marine ecosystem as a dominant species.

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