

Inferring trophic variation for Antarctic krill (*Euphausia superba*) in the Antarctic Peninsula from the austral fall to early winter using stable isotope analysis

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Abstract

The Antarctic krill (*Euphausia superba*) is a key species in the Southern Ocean ecosystem and an important link in the food web of the Antarctic ecosystem. The trophic information for this species during the transition from the austral fall to the winter is important to understand its poorly known overwintering mechanisms. However, the few studies on the topic differ in their results, in terms of both spatial and temporal variables. We investigated the size dependence and monthly and regional variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of adult krill in the Antarctic Peninsula, in the austral fall (April to May) and the early winter (June). We aimed to examine the trophic variations of krill occurred during this period, and the relationship between krill and their feeding environment in the Antarctic marine ecosystem. The following results were obtained: (1) no significant relationship was observed between size and the $\delta^{13}\text{C}$ value of krill, but the $\delta^{15}\text{N}$ value of krill presented a remarkable association with size; (2) the $\delta^{13}\text{C}$ values of krill increased during the austral fall, but no remarkable variation existed at the onset of winter, and the $\delta^{15}\text{N}$ values were not significant different during this period; (3) mean $\delta^{15}\text{N}$ values of krill differed significantly between the Bransfield Strait and the South Shetland Islands. Our data imply that adult krill present size-, season-, and region-dependent trophic variation during the transition from austral fall to early winter in the Antarctic Peninsula.

Key words: *Euphausia superba*, stable isotope, trophic variation, Antarctic Peninsula, feeding habit

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1 Introduction

Antarctic krill (*Euphausia superba* Dana, 1850; hereafter, krill) is the most important link in the Antarctic food web, and is considered a key species of Antarctic ecosystem (Everson, 2000) because of its high biomass and importance as a prey for penguins, flying birds, marine mammals, fishes, and benthic invertebrates (Atkinson et al., 2009). It is important to understand the trophic condition of krill in hotspots such as the South Shetland Islands and the Antarctic Peninsula (Kokubun et al., 2015), given the significant warming in the region (Atkinson et al., 2004; Trivelpiece et al., 2011), coupled with increasing krill-fishing operations (Nicol and Foster, 2016).

Considering the important role of krill in the Southern Ocean food web, its feeding habits, particularly the diet of krill in the austral summer, have been widely studied (Barkley, 1940; Kils, 1983; Hopkins, 1985; Croxall et al., 1999; Schmidt and Atkinson, 2006). More recently, biomarker analyses have been introduced to complement the conventional dietary analysis and to understand the diet and trophic levels of animals, and stable isotope

analysis is one of the promising approaches that has emerged as a valuable tool for examining trophic relationships (e.g., Michener and Schell, 1994). Stable nitrogen isotope ($\delta^{15}\text{N}$) values indicate the trophic position of a consumer (Vander Zanden and Rasmussen, 2001), whereas stable carbon isotope ($\delta^{13}\text{C}$) values can be used as a proxy for the source of primary production, as well as the inshore and benthic versus offshore and pelagic feeding preferences of a consumer (Hobson and Welch, 1992; France, 1995). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis has developed into a major approach for determining the source of food in pelagic/benthic systems and the trophic structure of marine organisms in marine food webs (Wada et al., 1987). Food source (Frazer, 1996; Schmidt et al., 2006), ontogenetic niche expansion (Polito et al., 2013), and trophic relationships of krill (Schmidt et al., 2003; Corbisier et al., 2004; Stowasser et al., 2012; Kokubun et al., 2015) have been examined in different regions of the Southern Ocean using stable isotope analysis. The extant studies indicate spatial-temporal and ontogenetic differences in the food source and the trophic relationships of krill. However, the trophic status of krill

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during the austral late fall to early winter has received little attention and the trophic variation of krill during the onset of austral winter is very important to understand the overwintering mechanism of this species. Therefore, the objectives of the present study were: (1) to understand the trophic status of krill in the Antarctic Peninsula, and (2) examine the monthly (seasonal) differences (if any) in the food sources of krill, particularly during the austral late fall to early winter. The results would be important in developing a comprehensive understanding of the relationship between krill and their feeding environment in the Antarctic marine ecosystem, particularly during the transition from austral fall to early winter, when krill prepare for the long-term overwintering period.

2 Materials and methods

2.1 Survey area and sampling

Krill samples were collected randomly by Chinese scientific observers aboard a large-scale trawler, *Kaili* (total of length, 120.7 m; gross registration tonnage, 7 847 t; main engine 5 296 kW; codend mesh size 20 mm), from May 26 to June 7, 2012, and April 9 to May 28, 2015. The sampling areas were located off the South Shetland Islands (between Snow Island and Rugged Island, SSI) and in the Bransfield Strait (BS) (Fig. 1).

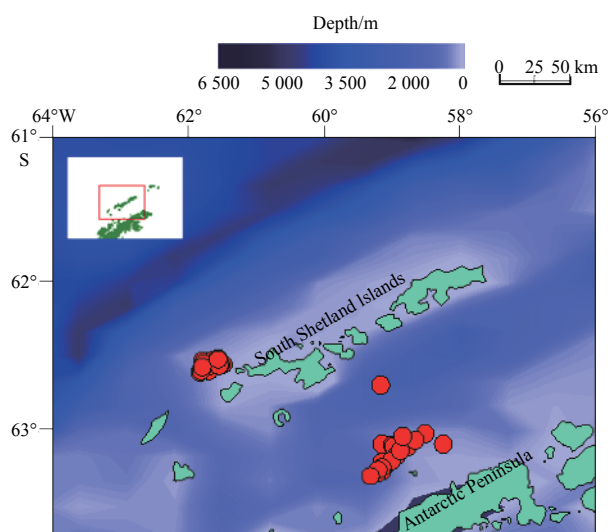


Fig. 1. The study area with sampling locations (solid circles).

2.2 Sample preparation and stable isotopic analyses

In the laboratory at the Shanghai Ocean University (SHOU), individual krill were homogenized and freeze-dried for 48 h in an oven at -60°C , after measuring their total length (from the tip of the rostrum to the tip of the uropod, TL , mm) and wet weight (WW , g), examining the sex, and removing the head/shell. Sex and the maturity stage were identified following Makarov and Denys (1981). The samples were analyzed using a system that coupled an elemental analyzer (Elementar Vario Cube CN series) with a continuous-flow isotope ratio mass spectrometer (CF-IRMS; Isoprime, GV Instruments, U.K.). All isotope analyses were carried out at the Laboratory of Stable Isotope Analysis, SHOU. Stable isotope abundance was expressed in delta (δ) notation, as the magnitude of deviation from the conventional standard Pee Dee Belemnite (PDB) for carbon and air N_2 for nitrogen, in parts per thousand (‰), according to the equation: $\delta X = ([R_{\text{sample}}/$

$R_{\text{standard}}] - 1) \times 10^3$, where X is ^{13}C or ^{15}N , and R is the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratio, respectively (Fry and Sherr, 1989). Sucrose (ANU $\text{C}_{12}\text{H}_{22}\text{O}_{11}$; NIST, Gaithersburg, MD) and ammonium sulfate ($[(\text{NH}_4)_2\text{SO}_4]$; NIST) were used for the internal ^{13}C and ^{15}N calibration, respectively. Sample precision was 0.1‰ and 0.2‰ for the ^{13}C and ^{15}N values, respectively.

2.3 Statistical analysis

Analysis of variance (ANOVA) was performed to determine the monthly difference in size distribution. Analysis of covariance (ANCOVA) was used to determine the effect of sex on weight-length relationship of krill. To investigate the relationships of size with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of krill, linear regressions analyses were conducted. Size-, monthly- and regional-differences in ^{13}C or ^{15}N values of krill were examined using Student's t -test for two groups or ANOVA for three or more groups. All the tests were two-tailed with a significance level of $p < 0.05$. Data are presented as mean \pm SD, unless stated otherwise. Statistical analyses were carried out using SPSS version 17.0 (SPSS Inc., Chicago, IL, USA).

3 Results

3.1 The relationship between weight and length

The TL ranged from 35.10 mm to 58.93 mm (48.19 ± 9.06 mm) and the wet weight ranged from 0.180 2 g to 1.438 3 g ($0.774 7 \pm 0.365 8$ g). The length distribution showed no monthly difference (ANOVA; $F=2.64$, $p=0.08$, $n=52$). Sex differences could not be found for the weight-length relationship within the samples (Fig. 2) (ANCOVA; $F=3.909$, $p>0.05$), which can be expressed as $W=6.753 4 \times 10^{-7} TL^{3.565 4}$ ($R^2=0.972 1$, $p<0.01$, $n=52$) for the combined samples.

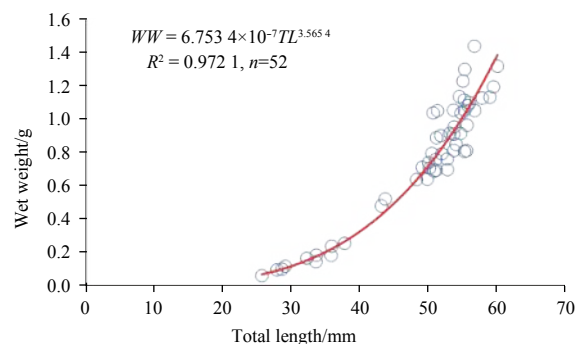


Fig. 2. The relationship between total length (TL) and wet weight (WW) of Antarctic krill (*Euphausia superba*).

3.2 The relationship of size with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of krill

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of krill ranged from -30.0‰ to -22.3‰ ($-26.3\text{‰} \pm 1.65\text{‰}$) and 3.0‰ to 5.6‰ ($4.6\text{‰} \pm 0.62\text{‰}$). The differences between females and males were not detected for $\delta^{13}\text{C}$ (Student's t -test; $t=0.471 5$, $p=0.639 6$) and $\delta^{15}\text{N}$ (Student's t -test; $t=0.494 7$, $p=0.623 3$) values of krill, so the samples were combined. There was no significant relationship between size and the $\delta^{13}\text{C}$ value ($R^2=0.000 7$, $p=0.856 8$, $n=52$) of krill (Fig. 3). However, the $\delta^{15}\text{N}$ value of krill demonstrated a significant positive correlation with size ($R^2=0.172 4$, $p=0.002 2$, $n=52$) (Fig. 4).

3.3 The monthly variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of krill

The mean $\delta^{13}\text{C}$ values of krill were $-27.2(\pm 1.06)\text{‰}$, $-25.9(\pm 1.54)\text{‰}$, and $-26.3(\pm 2.21)\text{‰}$ in April, May and June, respectively. A weak monthly difference was found for the mean

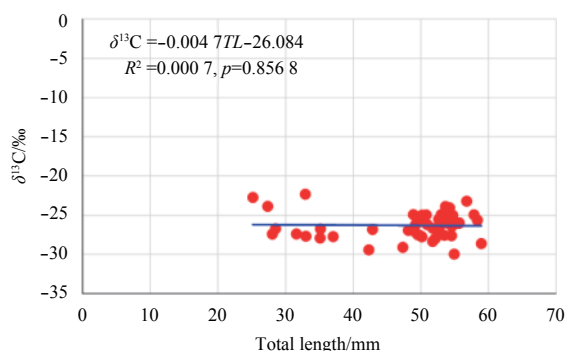


Fig. 3. The $\delta^{13}\text{C}$ (‰) value in relations to size (total length, TL , mm) of krill (*Euphausia superba*).

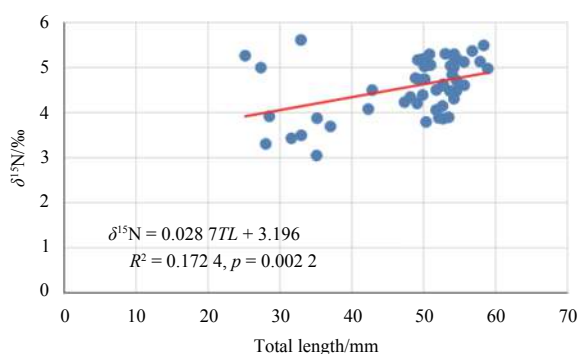


Fig. 4. The $\delta^{15}\text{N}$ (‰) value in relations to size (total length, TL , mm) of krill (*Euphausia superba*).

$\delta^{13}\text{C}$ values across the three months (ANOVA; $F=3.19$, $p=0.05$) (Fig. 5). A significant increase in the $\delta^{13}\text{C}$ values was observed from April to May (Student's t -test; $t=2.02$, $p=0.007$), but no significant variation existed from May to June (Student's t -test; $t=2.03$, $p=0.58$).

The mean $\delta^{15}\text{N}$ values of krill were $4.2(\pm 0.56)\text{‰}$, $4.6(\pm 0.66)\text{‰}$, and $4.8(\pm 0.51)\text{‰}$ in April, May, and June, respectively. The $\delta^{15}\text{N}$ values showed a slight increase from April to June (Fig. 5), although there were not statistically significant (ANOVA; $F=1.97$, $p=0.15$). They were not significantly different from April to May either (Student's t -test; $t=2.02$, $p=0.15$) or from May to June (Student's t -test; $t=2.03$, $p=0.43$).

3.4 The regional variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of krill

The mean $\delta^{13}\text{C}$ values of krill were $-26.6(\pm 1.59)\text{‰}$ and $-25.8(\pm 1.66)\text{‰}$ in the BS and off the SSI, respectively (Fig. 6). The mean $\delta^{15}\text{N}$ values of krill were $4.40(\pm 0.67)\text{‰}$ and $4.84(\pm 0.45)\text{‰}$ in the BS and off the SSI, respectively. The mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values increased from the BS towards the SSI; however, there was no significant difference in the mean $\delta^{13}\text{C}$ values between the BS and the SSI (Student's t -test; $t=2.01$, $p=0.06$), but mean $\delta^{15}\text{N}$ values of krill presented a significant difference between the BS and the SSI (Student's t -test; $t=2.01$, $p=0.01$).

4 Discussion

4.1 The relationship of trophic position with krill size

The present study indicated that the $\delta^{13}\text{C}$ value of krill had no relationship with size, but a significant relationship was inferred between the $\delta^{15}\text{N}$ value and size. Similar results were obtained by Frazer (1996), who observed no statistical relationship between

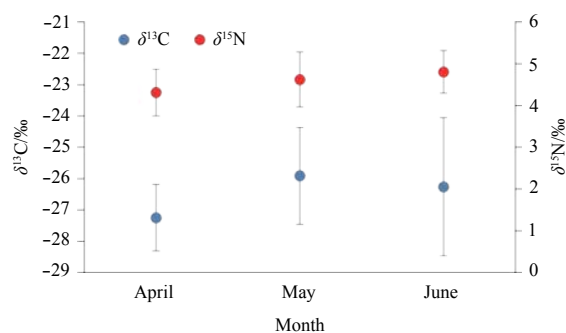


Fig. 5. The monthly variation on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of krill (*Euphausia superba*). The vertical bar signifies ± 1 standard deviation.

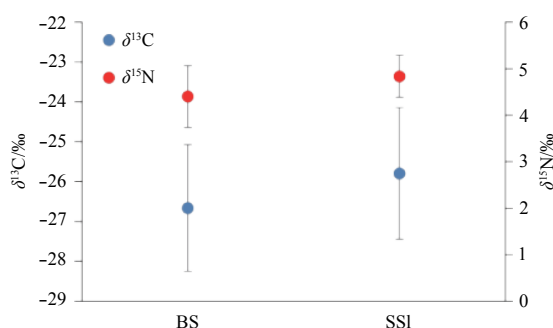


Fig. 6. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of krill (*Euphausia superba*) in the Bransfield Strait (BS) and off the South Shetland Islands (SSI). The vertical bar signifies ± 1 standard deviation.

$\delta^{13}\text{C}$ value and size, but a weak positive correlation between $\delta^{15}\text{N}$ value and size of larval krill in the austral winter, and Polito et al. (2013), who reported that, with ontogenetic niche expansion, adult krill have higher and more variable $\delta^{15}\text{N}$ values but consistent $\delta^{13}\text{C}$ values than juveniles do during the austral summer around the SSI. This indicated that both adults and juveniles were feeding on phytoplankton, but the adults also fed on prey from higher trophic levels (Polito et al., 2013). Stowasser et al. (2012) also reported a positive and significant correlation between $\delta^{15}\text{N}$ values and body mass of krill. This was also supported by Agersted et al. (2014), who found that the largest species, *Meganyctiphanes norvegica*, had the highest trophic position in the Arctic Ocean. The swimming capability of krill at different stages can partly explain the ontogenetic differences in size and food requirements. Larger krill, with their stronger swimming capabilities (Huntley and Zhou, 2004), can explore a wider range of habitats, which increases the ability to encounter motile prey (Schmidt and Atkinson, 2016).

4.2 The monthly (seasonal) trophic variation of krill

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of krill did not show a monthly variation in the present study, suggesting that the diet had no significant effect during the transition from austral fall to early winter; however, larger individuals had higher $\delta^{15}\text{N}$ values. A possible explanation is that phytoplankton likely remained an important food resource from austral summer to early winter, but food items became more scarce and krill resorted to more opportunistic or carnivorous feeding after the end of phytoplankton blooms during the austral early winter, and larger individuals had a strong capacity to find food sources and feed on prey at

higher trophic positions (Schmidt and Atkinson, 2016). A significant increase in the $\delta^{13}\text{C}$ values was observed from April to May, but no remarkable variation existed from May to June, when the effect of monthly length can be neglected, suggesting that primary production increased in the austral fall, but remained stable during the transition to early winter. Meyer et al. (2010) also indicated that, compared with the austral winter, the carbon content of krill was higher in the austral fall; however, the nitrogen content was relatively stable from the austral fall to winter. A plausible explanation is that, in the transition period before the onset of austral winter, krill was still physiologically active but feeding was slow due to a winter close down (Atkinson et al., 2002). From Fig. 7, it can be seen that the trophic position of krill varied regionally, if the effect of the sampling process is not considered. For the SSI, the trophic variation of adult krill in the austral late fall to early winter was significant than that in the austral summer (Fig. 7 and Table 1), implying that the food sources of krill were similar in the summer; however, krill would feed on food items with wider trophic positions in the austral fall. Furthermore, the samples in the present study were collected during

two years; although a sampling month overlapped (May), the potential effect of inter-annual differences on seasonal variation needs to be considered.

4.3 The regional trophic variation of krill

No significant difference was observed on mean $\delta^{13}\text{C}$ values between the BS and the SSI, but krill in the SSI presented significantly higher $\delta^{15}\text{N}$ values than krill in the BS during the austral fall to early winter, indicating that the food sources of krill were not different, but food items with higher trophic positions were available in the SSI. From Fig. 1, it can be seen that the krill sampled in the SSI were closer to the shore than those in the BS. Given the similar foraging habitats between the two regions, krill closer to the shore consumed food sources at higher trophic positions during the austral fall to early winter (Nishino and Kawamura, 1996). Based on the stomach content analysis of krill-feeding penguins, Kokubun et al. (2015) indicated that $\delta^{13}\text{C}$ values of krill did not differ between on-shelf and off-shelf trips, but krill from off-shelf trips had higher $\delta^{15}\text{N}$ values than those from on-shelf trips during the austral summer (December to January). Although Kok-

Table 1. The $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ values of krill in the different regions of the Southern Ocean

Region	Sampling date	Total length/mm (mean±SD)	Sex/life stage	$\delta^{13}\text{C}/\text{‰}$ (mean±SD)	$\delta^{15}\text{N}/\text{‰}$ (mean±SD)	Source	Code
South Shetland Islands	Mar. 2000	unknown	larvae	-25.1±0.9	4.2±0.4	Schmidt et al. (2004)	1
South Shetland Islands	Jan. 2007	28.9±3.4	larvae	-26.8±0.7	2.7±0.2	Polito et al. (2013)	2
South Shetland Islands	Jan. 2009	33.1±2.1	larvae	-27.0±0.7	2.4±0.3	Polito et al. (2013)	3
South Shetland Islands	Mar. 2000	unknown	adult female	-28.3±0.7	2.9±0.4	Schmidt et al. (2004)	4
South Shetland Islands	Jan. 2007	47.8±4.5	adult female	-26.2±1.0	3.6±0.7	Polito et al. (2013)	5
South Shetland Islands	Jan. 2009	47.2±5.5	adult female	-26.6±1.0	3.3±0.6	Polito et al. (2013)	6
South Shetland Islands	Jan. 2007	45.2±5.1	adult male	-26.4±1.0	3.5±0.6	Polito et al. (2013)	7
South Shetland Islands	Jan. 2009	44.6±5.1	adult male	-26.8±1.0	3.1±0.6	Polito et al. (2013)	8
South Shetland Islands	Jan. 2008	unknown	adult	-26.5±0.4	3.2±0.4	Polito and Goebel (2010)	9
South Shetland Islands	Dec. 2009/Jan. 2010	45.67±1.56	adult	-26.83±0.89	4.03±0.24	Kokubun et al. (2015)	10
South Shetland Islands	Dec. 2009/Jan. 2010	46.66±0.61	adult	-27.19±0.75	4.05±0.43	Kokubun et al. (2015)	11
South Shetland Islands	Dec. 2009/Jan. 2010	46.58±0.69	adult	-27.37±0.53	3.78±0.29	Kokubun et al. (2015)	12
South Shetland Islands	Dec. 2009/Jan. 2010	45.87±1.45	adult	-26.8±0.9	4.22±0.28	Kokubun et al. (2015)	13
South Shetland Islands	Apr. 2015	49.23±5.95	adult	-27.2±1.1	4.31±0.6	present study	14
South Shetland Islands	May 2012/May 2015	46.01±10.67	adult	-25.9±1.5	4.62±0.7	present study	15
South Shetland Islands	Jun. 2012	53.20±3.77	adult	-26.2±2.2	4.8±0.5	present study	16
Antarctic Peninsula	Mar. 1989	unknown	adult	-29.8±0.6	3.6±0.2	Dunton (2001)	17
Marguerite Bay	Mar. 2000	unknown	adult	-28.2	4.9	Schmidt et al. (2003)	18
Marguerite Bay	Feb. 2000	unknown	CIII	-26.1	5.7	Schmidt et al. (2003)	19
Marguerite Bay	Feb. 2000	unknown	FI-III	-24.7	6.1	Schmidt et al. (2003)	20
Lazarev Sea	Apr. 1999	unknown	juvenile	-31.2	2.1	Schmidt et al. (2003)	21
Lazarev Sea	Apr. 1999	unknown	FIII	-27.5	2.1	Schmidt et al. (2003)	22
Lazarev Sea	Apr. 1999	unknown	adult	-31.3	3.6	Schmidt et al. (2003)	23
Scotia Sea	Jan.-Feb. 2008	unknown	unknown	-22.3±3.1	4.3±1.0	Stowasser et al. (2012)	24
South Georgia Island	summer 2012	unknown	unknown	-18.3±0.6	6.2±0.3	Anderson et al. (2009)	25
Lazarev Sea	Apr. 1999	unknown	larvae	-31.1±0.7	2.1±0.9	Schmidt et al. (2004)	26
East Antarctic	Jan. 1984	unknown	larvae	-28.1	1	Wada et al. (1987)	27
Lazarev Sea	Apr. 1999	unknown	adult	-31.3±0.7	3.6±0.4	Schmidt et al. (2004)	28
East Antarctic	Jan. 1984	unknown	adult	-29.3	2.7	Wada et al. (1987)	29
Amundsen Sea	Jan. 2011	46.2±8.10	adult	-25.70±0.5 to -23.2±0.5	5.1±0.3 to 8.9±0.5	Ko et al. (2015)	30
East Antarctic	Sep. to Oct. 2007/ Sep. to Nov. 2012	unknown	furcilia	-25.85±0.38	5.65±0.56	Jia et al. (2015)	31
East Antarctic	Sep. to Oct. 2007/ Sep. to Nov. 2012	unknown	juvenile	-25.66±0.23	3.14±0.23	Jia et al. (2015)	32
East Antarctic	Sep. to Oct. 2007/ Sep. to Nov. 2012	unknown	adult	-26.39±0.66	2.84±0.33	Jia et al. (2015)	33

Note: SD is standardized deviation and code refer to Fig. 7.

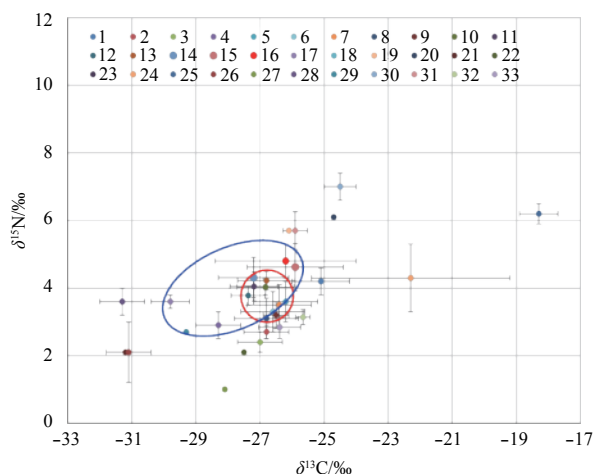


Fig. 7. The $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ values of krill (*Euphausia superba*) in the different regions of the Southern Ocean. The numbers derived from Table 1. Blue (red) circle signify the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of krill (*Euphausia superba*) in the Antarctic Peninsula during the austral summer (fall).

ubun et al. (2015) reported a different result for $\delta^{15}\text{N}$ values, the samples in their study were collected during the austral summer, where the food sources of krill present a seasonal difference (Meyer et al., 2010). Mordy et al. (1995) demonstrated that the microorganism community under the sea ice, which had high $\delta^{15}\text{N}$ values, was very important in the food web during the poor phytoplankton abundance in the austral fall-winter. This provides an explanation for the higher $\delta^{15}\text{N}$ values of krill in the SSI, because sea ice extended gradually to the off-shore region, from the onset of the austral winter, and the microorganisms under the sea ice potentially became the food sources of krill.

The $\delta^{13}\text{C}$ suggested that the marine food sources originated from benthic or pelagic environments (France, 1995), implying that the krill did not have significantly different feeding selectivity for benthic or pelagic food sources between the austral summer and fall to early winter. However, compared with the BS, there were higher (although statistically insignificant) $\delta^{13}\text{C}$ values of krill in the SSI. One possible reason is that the samples in the SSI are spatially closer to the sea bottom and the marginal ice-edge zone, and benthic food sources (e.g., benthic diatoms) have higher $\delta^{13}\text{C}$ values compared to pelagic food sources (e.g., planktonic diatoms) (France, 1995; Kokubun et al., 2015). Another explanation is that krill fed on ice-associated food sources, particularly, ice algae enriched in ^{13}C (Wada et al., 1987; Fischer, 1991).

5 Conclusions

Our study highlights the size- and region-related trophic variation in krill during austral fall to early winter in the Antarctic Peninsula, and provides important data for understanding its overwintering mechanisms, which have been rarely studied. Evidence from the variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of krill due to size, month, and region indicate the important of role of diet. In order to get more detailed insights into the trophic variation of krill, stable isotopic analysis on different tissues, for example, hepatopancreas, carapace, digestive gland, and stomach, would be a crucial and useful approach for understanding the feeding ecology and overwintering of krill. Although stable isotope analysis is a useful method for evaluating the trophic variation of

krill, other methods, such as fatty acid analysis, stomach content analysis, and molecular approach (for example, PCR-DGGE) (Martin et al., 2006), should be also combined to achieve more comprehensive and precise results.

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