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Feeding strategies of *Euphausia superba* in the eastern South Shetland Islands in austral summer

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Abstract

Euphausia superba is a key species in the Southern Ocean that serves as a link between primary production and higher trophic levels. To investigate the feeding strategies of *E. superba* from the eastern South Shetland Islands, fatty acid biomarkers, stable isotope signatures, and an incubation experiment were conducted. The results of the incubation experiment proved that adult *E. superba* mainly fed on 2–20 μm particles, demonstrating the importance of nanoplankton in their diet. Moreover, significant positive relationships between δ^{15}N and body size demonstrated that size-related dietary shifts were present in *E. superba*. Evidence from principal component analysis and the C16:1ω7/C18:4ω3 ratio showed that juveniles preferentially fed on dinoflagellates and adults were more likely to feed on diatoms. Fatty acid profiles in adult *E. superba* roughly mirrored the different trophic conditions and feeding strategies between stations. Adult *E. superba* at Stas D2-07, D5-07, DA-01 and DA-02 exhibited elevated levels of C16:1ω7, C18:4ω3, C18:1ω9 and C18:1ω9/C18:1ω7, indicating higher levels of feeding on both phytoplankton and higher trophic diets. In contrast, adult *E. superba* at Stas D1-03 and D1-04 were characterized by high levels of polyunsaturated fatty acids/saturated fatty acids ratios and low levels of C16:1ω7, C18:1ω7, C18:4ω3, C18:1ω9 and total fatty acids. We inferred that adult krill at Stas D1-03 and D1-04 still suffered from difficult dietary conditions after overwintering. The different dietary conditions between stations suggest a highly plastic feeding strategy of *E. superba* in the eastern South Shetland Islands.

Key words: *Euphausia superba*, South Shetland Islands, fatty acids, stable isotopes

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1 Introduction

Euphausia superba is widely distributed in the Southern Ocean around the Antarctic continent and sub-Antarctic islands, with a biomass of up to hundreds of millions of tons (Falk-Petersen et al., 2000; Nicol et al., 2000). As the key species in the Southern Ocean ecosystem, *E. superba* directly links primary production with secondary consumers such as fish, birds and marine mammals (Smetacek and Nicol, 2005; Yoshida et al., 2011). Therefore, studies on the trophodynamics of *E. superba* are important for our understanding of the food web structure of the Southern Ocean ecosystem.

Due to various hydrographic conditions and the seasonality of food availability, krill from different regions exhibit distinct feeding strategies (Schmidt and Atkinson, 2016; Schmidt et al., 2014). For example, krill from South Georgia mainly feed on diatoms, but the proportions of flagellates increase in the Scotia Sea, Bransfield Strait and Lazarev Sea, especially during summer and autumn (Schmidt and Atkinson, 2016). Comparison between South Georgia and the Lazarev Sea suggests that in productive shelf areas, postlarval krill are likely to supplement their diet with seabed material, whereas in the deep ice-covered ocean, they feed more carnivorously on copepods and protozoans (Schmidt

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and Atkinson, 2016; Schmidt et al., 2014). In addition, ontogenetic differences are reflected in the feeding activities and diets of juvenile and adult krill (Schmidt and Atkinson, 2016). Due to higher metabolic rates and lower lipid stores, juveniles have higher feeding activities and are more closely associated with ice algae during winter (Quetin et al., 1994; Schmidt and Atkinson, 2016). Compared to younger individuals, adult krill explore a wider dietary niche and have increased capacity to capture larger motile prey, such as copepods (Polito et al., 2013; Schmidt et al., 2014). Because of their comparatively larger lipid stores, adult krill can also survive for long periods of food scarcity in winter (Schmidt et al., 2014; Töbe et al., 2010).

Early studies on thoracic leg morphology classified *E. superba* as a filter feeder (Hamner, 1988). However, gut content analysis and incubation experiments have demonstrated that in addition to phytoplankton, euphausiids also consume protozoans, copepods and detritus (Atkinson et al., 2002; Meyer et al., 2009; Polito et al., 2013), yet these traditional methods only provide a limited view of the dietary composition of *E. superba*. Recently, a variety of laboratory and field studies assessing profiles of fatty acids and stable isotopes, which are highly variable between ontogenetic stages, seasons, and regions, have effectively provided information on the feeding activities of *E. superba* over long time scales (Hagen et al., 2007; Ko et al., 2016; Meyer et al., 2009; Polito et al., 2013). In most cases, studies on the diet of krill have employed a single method, with very few studies applying multiple approaches (El-Sabaawi et al., 2009).

In previous work, we studied the influence of hydrographic factors on the population structure of *E. superba* in the eastern South Shetland Islands in austral summer (Zhang et al., 2016). Based on the results, in the present study, we investigated the dietary conditions of *E. superba* using a combined approach of fatty acid biomarker and stable isotope assessment and an incubation experiment. We aimed to explore the feeding habits and strategies of *E. superba* in the eastern South Shetland Islands.

2 Materials and methods

2.1 *Study area and environmental conditions*

This survey was carried out in February 2014 during the 30th Chinese National Antarctic Research Expedition (CHINARE). The study area is located in the eastern South Shetland Islands of the Antarctic Peninsula (Fig. 1). Stations DA-01 and DA-02 are in the Scotia Ridge, which is influenced by the Antarctic Circumpolar Current (ACC), the Antarctic Slope Front (ASF) and Weddell Sea waters. Station D2-07 is located in the ASF and Sta. D5-07 at the southern edge of the Weddell-Scotia Confluence (WSF). Stations D1-03 and D1-04 are strongly influenced by the ACC (Flexas et al., 2015; Hewitt et al., 2004; Heywood et al., 2004; Thompson et al., 2009). Seawater temperature and salinity were recorded using a Sea-Bird 911 plus CTD onboard the R/V *Xuelong*. Water samples for chlorophyll *a* (Chl *a*) measurements were collected from 0, 25, 50, 75, 100, 150 and 200 m layers using 20 L Niskin bottles. For each Chl *a* sample, 500 mL of seawater was filtered through a 25 mm diameter Whatman GF/F glass fiber filter (pore size 0.70 μm) and immediately stored at –20°C. Chl *a* was extracted with 90% aqueous acetone for 24 h at 4°C, and concentrations were determined fluorometrically using a Turner Designs Fluorometer 7200.

2.2 *Sample collection*

Particulate organic matter (POM) samples for stable isotopic analysis were collected from 0–200 m at Stas D1-03 and DA-02. Water samples from the 0, 25, 50, 75, 100, 150 and 200 m layers were mixed and successively filtered through 200, 70 and 20 μm sieves and precombusted Whatman GF/F glass fiber filters (47 mm diameter, 0.70 μm pore size). POM samples from each size category (except 0.70 μm) were flushed from the sieves and filtered onto precombusted Whatman GF/F glass fiber filters and then stored at –80°C until analysis.

Zooplankton samples were collected using a Norpac net (330 μm mesh size, 0.5 m^2 mouth size), which was towed vertically from a depth of 200 m to the surface layer at an average speed of 1 m/s. Samples in the cod-end were preserved in 5% formalin seawater solution. *Euphausia superba* specimens were identified and counted in the laboratory using a Nikon SMZ 745 stereo microscope. The population structures of *E. superba* around the South Shetland Islands have been reported (Zhang et al., 2016).

For fatty acid and isotopic analyses, additional vertical hauls were conducted using a Norpac net at six stations, as marked by the open circles in Fig. 1. Samples in the cod-end were diluted into a 20 L bucket filled with *in situ* seawater. Specimens of *E. superba* were picked out and cultured in filtered seawater (filtered by 0.45 μm acetate fiber filters) for 2 h to evacuate the gut contents. Total length (TL) was measured from the front of the eyes to the tip of the telson. Krill ≤35 mm TL were considered juven-

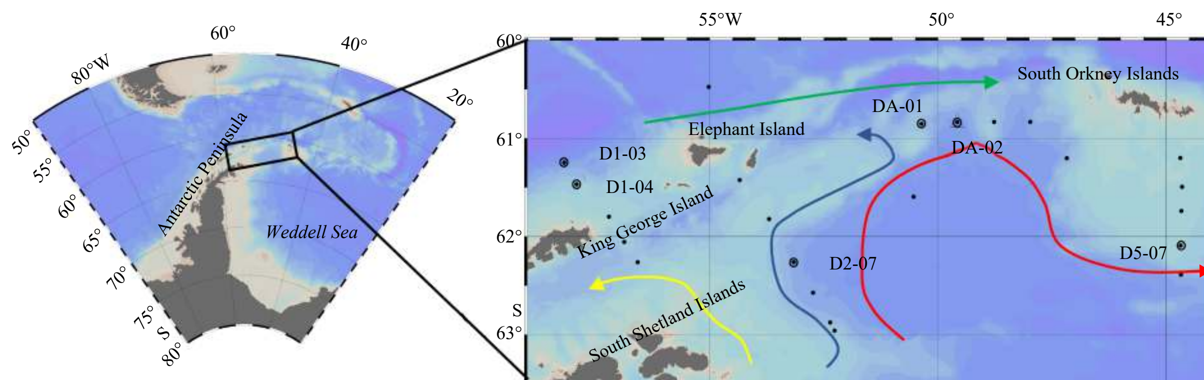

Fig. 1. Map of the sampling stations in the eastern South Shetland Islands. Dots represents Norpac net stations, open circles *E. superba* collected for fatty acid and isotopic analysis, open triangle *E. superba* incubation experiment, green line the Southern Boundary of the Antarctic Circumpolar Current (SBACC), yellow line the Antarctic Coastal Current (ACC), blue line the Antarctic Slope Front (ASF), and red line the Weddell Front (WF) (Flexas et al., 2015; Hewitt et al., 2004; Heywood et al., 2004; Thompson et al., 2009).

iles (including larvae); krill >35 mm TL were deemed adults (Miller and Trivelpiece, 2007; Polito et al., 2013). The specimens were then rinsed with filtered seawater and stored at –80°C until transported to the laboratory for further analysis.

2.3 *Feeding experiment*

The feeding experiment of *E. superba* was conducted onboard the R/V *Xuelong* on February 12, 2014, at Sta. DA-02. For the experiment, actively swimming and healthy adult *E. superba* (average TL (39.27±0.94) mm) were picked out using a spoon and placed in a 4 L bucket filled with 0°C (the *in situ* sampling temperature) seawater. Seawater for the incubation was collected from the Chl *a* maximum layer (approximately 25 m) using 20 L Niskin bottles and filtered through 200 μm mesh before use. For gross Chl *a* concentrations (initial), 500 mL of seawater was filtered through 25 mm diameter Whatman GF/F glass fiber filters (pore size 0.70 μm). For size-fractionated (>20, 2–20 and 0.70–2 μm) Chl *a* concentrations (initial), duplicate 500 mL seawater samples were successively filtered through nylon mesh nets (47 mm diameter, 20 μm pore size), acetate fiber filters (47 mm diameter, 2 μm pore size) and Whatman GF/F glass fiber filters (25 mm diameter, pore size 0.70 μm). Three *E. superba* specimens were added to a 1 L Nalgene polycarbonate bottle filled with well-mixed seawater (treatment). Three replicates and three controls with no animals added were incubated in a dark incubator at (0±0.5)°C for 24 h. The bottles were gently inverted every 6 h during the incubation to suspend the phytoplankton. After a 24 h incubation, duplicate samples of 450 mL seawater from each bottle were filtered for gross and size-fractionated Chl *a* concentrations. All Chl *a* samples were immediately stored at –20°C. Chl *a* concentrations were measured fluorometrically as described above. The remaining seawater in each bottle (including the initial, control and treatment) was preserved in 5% buffered formalin seawater solution to determine the cell/particle size spectrum. No krill were found dead at the end of the experiment. In the laboratory, the size spectrum of food particles was analyzed using a Coulter Counter (BECKMAN Multisizer™ 3) with a 100 μm aperture.

2.4 *Fatty acid methyl ester preparation and analysis*

In the laboratory, krill were weighed (wet weight: WW) before thawing, and fractions of muscle samples for fatty acid and stable isotope analyses were dissected from the abdomen. Muscle samples were lyophilized at –45°C for 48 h and then measured for dry weight (DW).

A fraction of the muscle samples was separated for extraction and analysis of fatty acids. Total lipids were extracted following the procedures of Folch et al. (1957) and Parrish (1999). Briefly, samples were placed in DCM:MeOH (dichloromethane:methanol) at a proportion of 2:1 (V/V) with 0.01% BHT (butylhydroxytoluene) as an antioxidant and C19:0 fatty acid methyl ester (FAME) as an internal standard. The organic extracts were combined after three extractions and then evaporated under high-purity nitrogen. For gas chromatographic analysis, total lipids were transesterified in methanol containing 3% concentrated sulfuric acid at 80°C for 4 h (Hagen et al., 2001; Kattner and Fricke, 1986). FAMEs were recovered from the mixture using hexane. Analysis of fatty acids was carried out using an Agilent 7890A Gas Chromatography instrument equipped with a DB-FFAP capillary column (30 m length, 0.25 mm inner diameter and 0.25 μm film thickness). The temperature programming was as follows: 150°C for 1 min and hold at 220°C for 33 min after heating at 3°C/min. The temperatures of the injector and the detector were maintained at 220°C and 280°C, respectively.

2.5 *Isotopic analysis*

Freeze-dried samples for isotopic analysis were ground in an agate mortar (Schmidt et al., 2004). Carbon and nitrogen stable isotope ratios were analyzed using an Isotope Ratio Mass Spectrometer (DELTA V Advantage) combined with an elemental analyzer (Flash EA1112 HT). Lipids were not removed from the samples prior to stable isotope analysis (Schukat et al., 2014). All isotope abundances are expressed in δ notation according to the following equation:

$$\delta X = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 10^3, \quad (1)$$

where X is ^{13}C or ^{15}N and R is the corresponding ^{13}C:^{12}C or ^{15}N:^{14}N. PeeDee Belemnite carbonate and atmospheric nitrogen were used as the standards for carbon and nitrogen, respectively. Measurement precision was approximately 0.1‰ for δ^{13}C and 0.2‰ for δ^{15}N.

2.6 *Data analysis*

Fatty acids were quantitatively evaluated according to the internal standard C19:0 FAME. Principal component analysis (PCA) was conducted using Canoco 5 software (Ter Braak and Šmilauer, 2012) to discriminate differences in the fatty acid compositions of *E. superba* between stations. Percentage data were arcsine transformed before PCA. Because arcsine transformation strongly increases the relative influences of rare components, we removed fatty acids with values less than 1%. Statistical comparisons of fatty acid markers between stations were performed using nonparametric Kruskal–Wallis one-way ANOVA because the sample size was too small to apply parametric statistical tests. Pearson correlation analysis was carried out between stable isotopes and selected fatty acid ratios. Kruskal–Wallis one-way ANOVA and Pearson correlation analysis were conducted using IBM SPSS Statistics 22. The significance levels for the tests were set at $p<0.05$ or $p<0.01$.

3 Results

3.1 *Environmental conditions*

The vertical profiles of temperature, salinity and Chl *a* (from 200 m depth to the surface) at the sampling stations are shown in Fig. 2. The average temperatures (Fig. 2a) were relatively high at Stas D1-03 and D1-04 and then gradually decreased toward the east, ranging from –0.87°C to 0.78°C. Vertically, the six stations showed similar trends, with temperatures decreasing with depth and reaching the lowest values at approximately 70–200 m; temperatures then increased markedly with depth. At deeper stations, such as D1-03, DA-01, DA-02 and D2-07, the temperature decreased slowly below the permanent thermocline. Similarly, salinity increased from the surface to the bottom of the water column at the six stations, with the lowest salinity occurring at Sta. D5-07.

Average concentrations of Chl *a* (Fig. 2c) were comparatively higher at Stas D1-04 and DA-01 (0.388 and 0.589 mg/m^3, respectively), with the minimum value observed at Sta. DA-02 (0.136 mg/m^3). Both Stas D1-04 and DA-01 showed maximum Chl *a* values at the surface that decreased gradually with depth. At Sta. D1-03, the maximum Chl *a* value was found at 75 m.

3.2 *Feeding experiment*

The average diameter and gross volume of food particles in the feeding experiment are presented in Table 1. The initial dia-

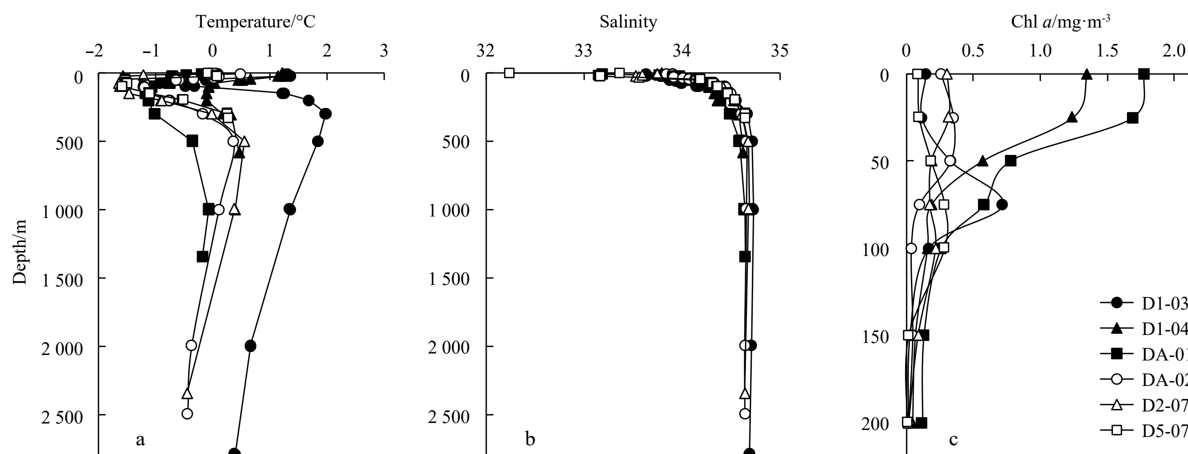

Fig. 2. Vertical distributions of temperature (a), salinity (b) and Chl *a* concentrations (c) at sampling stations in the eastern South Shetland Islands.

Table 1. Particle sizes in the *E. superba* feeding experiment

	Average diameter/μm	Gross volume/10^6 μm³·mL⁻¹
Initial (n=3)	21.63±13.54	1.08
Control (n=3)	38.03±15.95	2.28
Treatment (n=3)	35.47±15.43	2.46

meter and gross volume of particles were (21.63±13.54) μm and 1.08×10^6 μm³/mL, respectively. After a 24 h incubation, the particle diameter increased to (38.03±15.95) μm in the control and (35.47±15.43) μm in the treatment, with gross volumes of particles increasing to 2.28×10^6 and 2.46×10^6 μm³/mL, respectively.

As shown in Fig. 3, the averaged gross Chl *a* concentrations in the initial, control and treatment groups were 0.063, 0.093 and 0.097 mg/m³, respectively. Chl *a* concentrations in the 2–20 μm size category were relatively higher in the control than in the treatment group (p>0.05). Chl *a* was not detected in the <2 μm and >20 μm size classes in the control.

3.3 *Fatty acid profiles in E. superba*

Euphausiids used for biochemical analysis were highly variable in size, weight and fatty acid concentration (Table 2). TL (26–55 mm) and WW (0.12–1.20 g) were lg-transformed, and a positive linear relationship was distinguished based on all specimens from the six stations, suggesting a trend toward longer krill also being heavier. The corresponding regression equation was as follows:

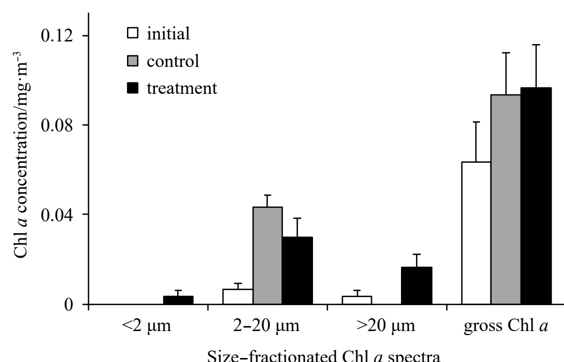

Fig. 3. Chlorophyll *a* concentrations in the *E. superba* feeding experiment.

$$\lg WW = 3.079\ \lg TL - 5.303$$
$$(n = 26, R = 0.962, F = 608.765, p < 0.001)\,.$$

However, accumulation of fatty acids appeared to have no relationship with either krill size (26 to 55 mm) or WW (0.12 to 1.20 g) (p>0.05), with the total fatty acids (TFA) content varying from 23.34 to 145.11 mg/g. Krill from Sta. D1-04 were evidently smaller in size ((31.75±7.04) mm) and lighter in weight ((0.23±0.14) g), as three of the four individuals were juvenile (TL⩽35 mm). However, the minimum TFA value did not occur at Sta. D1-04 ((52.5±15.22) mg/g) but at Sta. D1-03 ((28.24±6.92) mg/g).

The major fatty acids in *E. superba* were as follows: saturated C14:0 and C16:0; monounsaturated C16:1ω7, C18:1ω7 and C18:1ω9; and polyunsaturated C18:3ω3, C18:4ω3, C20:5ω3 and C22:6ω3 (Table 2). Among them, C20:5ω3, C16:0 and C22:6ω3 were present in the highest proportions, ranging from 22.5% to 38.9%, 17.0% to 23.5% and 5.1% to 21.1%, respectively. Krill from the six stations differed clearly in fatty acid composition. Briefly, krill from Sta. D1-03 exhibited significantly higher levels of C20:5ω3 and C22:6ω3 (p<0.05) than did krill from Stas DA-01 and D2-07. In addition, values of C18:3ω3 were significantly higher at Sta. D1-04 than at the other stations (p<0.05). Although the maximum values of C18:4ω3 were found at Sta. D1-04, a significant difference was detected only between D1-03 and D1-04 (p<0.05).

PCA was carried out to distinguish differences in fatty acid compositions based on all krill samples from the six stations (Fig. 4). Together, the first two principal components (PCs) explained 83.33% of the total variance, with PCs 1 and 2 accounting for 66.03% and 17.30%, respectively. We discriminated all krill samples into four categories according to the PCA. Adult krill from D1-03 and D1-04 were distinguished from the other samples by the first principal component. The fatty acids that contributed most to PC 1 were C18:2ω6, C20:5ω3 and C22:6ω3 in the positive direction and C14:0, C16:1ω7 and C18:1ω9 in the negative direction. On the positive axis of PC 2, individuals from Sta. D1-04 with TLs⩽35 mm showed a discrete distribution away from the other samples. These juveniles were characterized by high contents of C18:4ω3, C18:3ω3 and C18:2ω6. Individuals from Stas D5-07 and D2-07 were situated mainly in the negative direction of PC 2, with C16:1ω7, C18:1ω7 and C18:1ω9 as the featured fatty acids.

Dietary fatty acids (mg/g) and fatty acid ratios are presented in Fig. 5. Compared to adults at Sta. D1-03, adults at Stas DA-01

Table 2. Mean values of individual fatty acids (%), krill size (mm), wet weight (g), and total fatty acids (mg/g) in *E. superba*

	D1-03 (*n*=3)	D1-04 (*n*=4)	D2-07 (*n*=6)	DA-01 (*n*=3)	DA-02 (*n*=6)	D5-07 (*n*=4)
C14:0	2.85±2.52	5.13±1.82	8.28±2.74	9.17±1.52	7.03±2.33	9.40±0.70
C15:0	0.32±0.27	0.37±0.07	0.44±0.08	0.41±0.04	0.36±0.08	0.56±0.13
C16:0	17.78±1.12	20.80±0.91	21.68±0.90	22.26±1.51	21.70±1.40	21.18±1.19
C16:1ω7	2.24±1.23	2.48±0.56	5.93±1.93	4.72±1.80	4.19±1.46	5.87±0.25
C17:0	0.29±0.09	1.01±0.42	1.06±0.18	0.87±0.08	1.00±0.36	0.98±0.25
C18:0	0.89±0.08	0.98±0.33	1.04±0.06	0.98±0.31	1.28±0.24	0.90±0.23
C18:1ω7	6.51±0.61	6.88±1.62	10.84±0.38	10.94±1.50	10.76±1.25	10.13±0.63
C18:1ω9	6.07±1.03	5.70±0.90	8.19±1.00	7.73±0.76	7.29±0.88	7.01±0.54
C18:2ω6	3.28±0.17	2.07±0.24	0.08±0.02	1.63±0.01	1.68±0.30	0.10±0.02
C18:3ω6	n.d.	n.d.	0.26±0.03	0.18±0.07	0.12±0.10	0.30±0.05
C18:3ω3	1.42±0.42	3.52±0.79	1.25±0.26	1.53±0.30	1.10±0.15	1.11±0.10
C18:4ω3	1.19±1.11	5.79±2.21	3.09±1.09	4.01±1.11	3.66±0.68	2.76±0.89
C20:0	n.d.	n.d.	0.04±0.02	0.02±0.01	0.06±0.08	0.04±0.04
C20:1ω9	0.10±0.17	0.41±0.16	0.80±0.19	0.9±0.15	0.74±0.30	0.46±0.11
C20:2ω6	0.34±0.07	0.19±0.03	0.15±0.02	0.18±0.05	0.17±0.03	0.33±0.04
C20:3ω6	0.23±0.05	0.05±0.04	0.09±0.01	0.05±0.02	0.07±0.04	0.14±0.02
C20:3ω3	1.66±0.38	0.58±0.23	0.65±0.12	0.43±0.06	0.67±0.25	0.83±0.21
C20:4ω6	0.34±0.12	0.51±0.08	0.22±0.09	0.21±0.02	0.14±0.06	0.21±0.03
C20:5ω3	35.79±4.38	30.79±3.54	26.95±2.01	24.49±2.91	27.53±3.10	27.80±1.79
C22:1ω9	0.16±0.05	0.31±0.14	0.60±0.18	0.81±0.32	0.57±0.34	0.44±0.10
C22:2ω6	0.08±0.07	0.08±0.05	0.12±0.01	0.14±0.02	0.15±0.02	0.14±0.01
C22:6ω3	18.48±3.23	12.36±3.54	8.23±1.77	8.33±1.20	9.74±2.99	9.34±1.15
TFA/mg·g^{-1}	28.24±6.92	52.5±15.22	79.54±34.01	85.73±14.38	69.82±32.93	62.14±19.07
TL/mm	47.33±7.51	31.75±7.04	42.50±6.32	45.67±5.51	48.67±3.08	38.00±2.55
WW/g	0.80±0.40	0.23±0.14	0.53±0.21	0.64±0.21	0.83±0.29	0.37±0.14

Note: n.d. means not detected, TFA total fatty acids, TL total length, and WW wet weight.

Fig. 4. Biplot of stations and fatty acid profiles of *E. superba* based on PCA. Bacteria: C15:0+17:0; and copepod: C20:1+22:1.

and D2-07 showed significantly higher levels of C16:1ω7, C18:1ω7 and C18:1ω9 ($p<0.05$). Adults at Sta. D1-03 showed the minimum value of C18:4ω3, which was significantly lower than those at Stas D1-04 and DA-01 ($p<0.05$). Due to higher levels of C18:4ω3, juveniles at Sta. D1-04 showed the lowest level of C16:1ω7/C18:4ω3 compared to adults at other stations ($p<0.05$). Polyunsaturated fatty acids/saturated fatty acids ratios (PUFA/SFA), which were negatively correlated with C18:1ω9/C18:1ω7 ($p<0.05$), exhibited significantly higher levels at Sta. D1-03 than at Stas DA-01, DA-02, D2-07 and D5-07 ($p<0.05$).

3.4 *$\delta^{13}C$ and $\delta^{15}N$ values in particulate organic matter (POM) and E. superba*

For POM, $\delta^{13}C$ values at both Stas D1-03 and DA-02 were higher in the 20–70 μm size class and lower in the 70–200 μm and >200 μm size classes. However, $\delta^{15}N$ values in POM exhibited distinct patterns between the two stations. For example, $\delta^{15}N$ values at Sta. D1-03 were notably higher in the 20–70 μm and 70–200 μm size classes than in the other classes. At Sta. DA-02, higher levels of $\delta^{15}N$ were detected in the 20–70 μm and >200 μm size classes (Table 3).

Euphausia superba $\delta^{13}C$ and $\delta^{15}N$ values ranged from –28.44‰ to –24.43‰ and 1.06‰ to 4.47‰, respectively. Although adult krill at Sta. D1-03 exhibited surprisingly lower levels of TFA than did the specimens from other stations, they did not show significant differences in $\delta^{13}C$ and $\delta^{15}N$ levels. Values of both $\delta^{13}C$ and $\delta^{15}N$ were highest at Sta. DA-02, with minimum values occurring at Stas DA-01 and D1-04, respectively (Table 4). Pearson correlation analysis was carried out between $\delta^{13}C$ and $\delta^{15}N$ and selected fatty acid ratios (Table 5). $\delta^{15}N$ was positively correlated with $\delta^{13}C$ ($p<0.05$), WW ($p<0.01$) and krill size ($p<0.01$). C18:1ω9/C18:1ω7 was positively correlated with both $\delta^{13}C$ and $\delta^{15}N$, whereas PUFA/SFA was negatively correlated with $\delta^{15}N$.

4 Discussion

4.1 *Food size of adult krill*

Euphausia superba feeding involves the integrated action of thoracopods, mouthparts and mandibles, and the special mechanical characteristics of the feeding apparatus help *E. superba* set upper and lower size limits for particles that can be consumed (Schmidt and Atkinson, 2016). Morphological studies on the

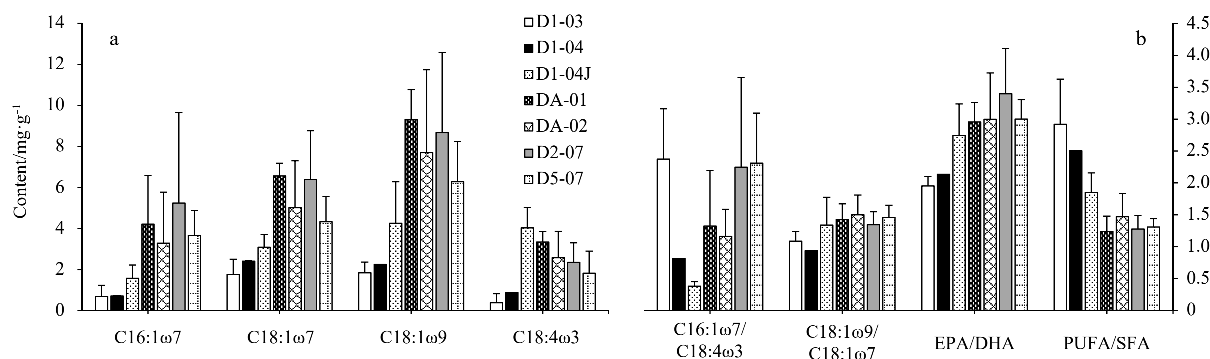

Fig. 5. Concentrations of major fatty acids (a) and fatty acid ratios (b) in *E. superba*. J represents juveniles, EPA C20:5ω3, DHA C22:6ω3, SFA saturated fatty acids, and PUFA polyunsaturated fatty acids.

Table 3. $\delta^{13}C$ and $\delta^{15}N$ values in POM from Stas D1-03 and DA-02

Station	Size/μm	$\delta^{13}C$/‰	$\delta^{15}N$/‰
D1-03	>200	–30.91	3.15
D1-03	70–200	–30.35	4.93
D1-03	20–70	–27.92	5.31
D1-03	0.7–20	–29.82	3.16
DA-02	>200	–28.09	4.67
DA-02	70–200	–28.14	2.07
DA-02	20–70	–26.52	4.66
DA-02	0.7–20	–27.32	n.d.

Note: n. d. means not detected.

feeding apparatus have found that the filtering area of the feeding basket increases from ~70 mm² in juveniles to ~277 mm² in adults but that the minimum mesh size remains within a fine range of 2–3 μm (Suh and Nemoto, 1987), indicating that even adult *E. superba* can ingest particles as small as 2–3 μm. This condition helps *E. superba* feed efficiently on nano- and microplankton and reach substantial growth rates even when food concentrations are extremely low (Schmidt and Atkinson, 2016; Zhu, 1993). Previous research based on a diet composition analysis of 340 *E. superba* individuals from the South Shetland Islands found that the gut contents mainly comprised diatoms (60%) and protozoa (15.5%), with approximately 85% of the food particles being smaller than 20 μm (Zhu, 1993). Similar results were found in our incubation experiment, in which Chl *a* concentrations in the 2–20 μm size category were higher in the control than in the treatment group, verifying that adult *E. superba* mainly feed on particles 2–20 μm in size. However, the feeding activity of *E. superba* is far more complicated than merely filter-feeding of small phytoplankton particles and also includes raptorial capture of zooplankton, handling of giant diatoms, and grasping of ice algae in different habitats and food environments (Schmidt and Atkinson, 2016).

4.2 *Phytoplankton feeding preferences of E. superba*

Most of the primary production in the Southern Ocean is dominated by diatoms, with dinoflagellates and other species abundant only during bloom conditions (Dalsgaard et al., 2003). Results for typical microalgal markers C16:1ω7 and C18:4ω3 in *E. superba* indicate that this krill species primarily feeds on diatoms and dinoflagellates (Hagen et al., 2001; Schmidt et al., 2014; Stübing and Hagen, 2003). In addition, C18:1ω7, which is derived from chain elongation of the diatom marker C16:1ω7, is also an indicator of dietary uptake of either diatoms or bacteria (Dalsgaard et al., 2003; Falk-Petersen et al., 1999).

In PCA, juvenile *E. superba* at Sta. D1-04 were separated from other specimens by the dinoflagellate markers C18:4ω3 and C18:3ω3, indicating a dinoflagellate-featured diet in juveniles. Moreover, the content of C18:4ω3 was significantly higher than that of the diatom marker C16:1ω7 in juveniles at Sta. D1-04 (p=0.05), with an average C16:1ω7/C18:4ω3 ratio of only 0.38 (Fig. 5). The ratio of C16:1ω7/C18:4ω3, which is independent of total lipid levels, has proven to be an appropriate index for a diatom- vs. a dinoflagellate-biased diet in krill (Stübing and Hagen, 2003). Furthermore, the extremely low level of C16:1ω7/C18:4ω3

Table 4. $\delta^{13}C$ and $\delta^{15}N$ values in *E. superba*

	D1-03 (n=3)	D1-04 (n=4)	DA-01 (n=6)	DA-02 (n=3)	D2-07 (n=6)	D5-07 (n=4)
$\delta^{13}C$/‰	–27.18±1.09	–27.06±0.84	–27.31±0.94	–25.60±0.82	–26.42±1.82	–26.22±0.72
$\delta^{15}N$/‰	3.21±0.32	2.61±1.07	3.73±0.33	3.79±0.39	3.70±0.50	3.17±0.17

Table 5. Pearson correlation analysis between $\delta^{13}C$ and $\delta^{15}N$ and selected fatty acid ratios

	C16:1ω7/ C18:4ω3	C18:1ω9/ C18:1ω7	PUFA/SFA	WW	TL	$\delta^{13}C$	$\delta^{15}N$
C16:1ω7/C18:4ω3	1						
C18:1ω9/C18:1ω7	–0.002	1					
PUFA/SFA	–0.044	–0.553**	1				
WW	0.232	0.006	0.217	1			
TL	0.279	–0.028	0.110	0.927**	1		
$\delta^{13}C$	–0.260	0.162	–0.025	0.330	0.367	1	
$\delta^{15}N$	0.087	0.238	–0.221	0.535**	0.692**	0.427*	1

Note: * Correlation is significant at the 0.05 level (2-tailed); ** correlation is significant at the 0.01 level (2-tailed). SFA represents saturated fatty acids, PUFA polyunsaturated fatty acids, WW wet weight, and TL total length.

allows for the conclusion that D1-04 juveniles feed preferentially on dinoflagellates, as opposed to diatoms. Similar results have also been published by Hagen et al. (2001) and Ju and Harvey (2004), who reported clearly higher levels of C18:4ω3 in furcilia than in adults. According to C16:1ω7/C18:4ω3 results, adult *E. superba* were more likely than juveniles to feed on diatoms, with the ratio exceeding 1 in almost all specimens (Fig. 5b).

4.3 *Validity of carnivorous and omnivorous indicators*

Previous gut content analyses have revealed that *E. superba* switches to more omnivorous and carnivorous feeding during nonbloom periods and utilizes food items such as protozoans, copepods, and invertebrate eggs (Atkinson et al., 2002; Cripps et al., 1999; Schmidt et al., 2006). Although these food items are much more nutritious than phytoplankton, their contributions to the diet of krill are not as large as we presumed (Stübing et al., 2003).

It is broadly accepted that herbivorous copepods can biosynthesize the monounsaturated fatty acids C20:1 and C22:1 from C18:1 and C20:1 via chain elongation. Hence, the marker C20:1+22:1 can be used as an indicator of feeding on herbivorous copepods by carnivorous predators (Dalsgaard et al., 2003). In our study, C20:1+22:1 was nearly absent in *E. superba*. Low proportions of C20:1+22:1 in krill and high levels in fecal pellets have demonstrated the poor assimilation and rapid catabolism of this marker in *E. superba* (Stübing et al., 2003), and this indicator is therefore controversial. Accordingly, despite possible ingest of copepods, the marker C20:1+22:1 is of limited use as an indicator for *E. superba*.

C18:1ω9, C18:1ω9/C18:1ω7 and PUFA/SFA have been employed to evaluate carnivorous-omnivorous feeding in *E. superba* (Cripps and Atkinson, 2000; Dalsgaard et al., 2003; Ko et al., 2016; Schmidt et al., 2006). However, adult krill from Stas D1-03 and D1-04, which were less carnivorous and omnivorous according to C18:1ω9 and C18:1ω9/C18:1ω7 results, exhibited far higher levels of PUFA/SFA (Fig. 5b). Cripps and Atkinson (2000) reported an increase in PUFA/SFA in *E. superba* after the addition of copepods as a diet. In the field, krill can become carnivorous and feed on PUFA-rich copepods when phytoplankton abundance is low, which might also lead to an increase in PUFA/SFA (Cripps et al., 1999). Nevertheless, an increase in PUFA/SFA can also occur after a period of starvation, in which SFA-rich storage lipids are preferentially metabolized (a detailed discussion is presented in the next section) (Cripps et al., 1999; Dalsgaard et al., 2003). Another contradiction appeared when we applied correlation analysis between δ^{15}N and the two carnivorous markers PUFA/SFA and C18:1ω9/C18:1ω7 (Table 5). The negative correlation between δ^{15}N and PUFA/SFA appeared to demonstrate the invalidity of PUFA/SFA as a carnivorous indicator in our study. In our opinion, the application of PUFA/SFA as a carnivorous marker should be carried out with caution.

4.4 *Differences in feeding patterns of adult E. superba between stations*

In the present study, krill exhibited obvious station-based differences in fatty acid profiles. In PCA, the diatom markers C16:1ω7 and C18:1ω7 and carnivorous marker C18:1ω9 discriminated adult krill at Stas D2-07 and D5-07, indicating comparatively high levels of feeding on diatoms and animal diets such as copepods and protozoans at these stations (Dalsgaard et al., 2003). Compared to adults from Stas D1-03 and D1-04, individuals from Stas DA-01 and DA-02 also showed relatively higher levels of feeding on diatoms and animal diets (Fig. 5).

In general, these four stations are closely related to the Weddell Sea waters. D5-07 is situated at the southern edge of the WSC, and DA-01 and DA-02 are located on the Scotia Ridge, where the SBACC merges with the ASF and the Weddell Sea waters (Thompson et al., 2009). Due to the transport and mixture of different water masses, the WSC is one of the most biologically rich areas of the Southern Ocean (Hofmann et al., 1998). The highest abundance of *E. superba* in our study occurred in areas around the South Orkney Islands, with the population dominated by calyptopis I (Zhang et al., 2016). Interestingly, this area coincides with extremely low levels of Chl *a*, indicating a top-down control by the krill population (Zhang et al., 2016). Compared to Stas DA-01, DA-02 and D5-07, which are in the range of the WSC, Sta. D2-07 is mainly influenced by the ASF. However, no significant differences in fatty acid indicators were detected between the four stations, indicating that the diet condition at Sta. D2-07 was similar to that at the other stations.

The lowest levels of C16:1ω7, C18:1ω7, C18:4ω3 and C18:1ω9, as well as TFA, occurred in adults at Stas D1-03 and D1-04, demonstrating restricted feeding on both phytoplankton and animal diets in adults from this region. In addition to the low levels of TFA, adults at Stas D1-03 and D1-04 were also characterized by high proportions of C20:3ω3, C20:5ω3 and C22:6ω3, and elevated PUFA/SFA. During austral spring and summer, *E. superba* accumulates the more easily metabolized triacylglycerols as the major lipid stores (Dalsgaard et al., 2003; Ko et al., 2016), and the stored lipids are largely consumed to provide energy during overwintering (Hagen et al., 2001), intensive reproduction (Clarke, 1980; Nicol et al., 1995), or periods of starvation (Cripps et al., 1999; Meyer et al., 2009).

Euphausia superba around the Antarctic Peninsula mainly spawn in January and February (Spiridonov, 1995). At Stas D1-03 and D1-04, the population was mainly composed of late calyptopis and furcilia stages, with the population size remaining small (Zhang et al., 2016). In general, *E. superba* accumulates the maximum amount of lipids in autumn and depletes these stores to a minimum in early spring (Hagen et al., 2001). The sampling in our study was carried out in February, a time when *E. superba* should have fed on phytoplankton blooms for some time and recovered from overwintering. However, it appeared that the depletion of lipids in adult krill from Stas D1-03 and D1-04 was not the result of reproduction or overwintering.

In addition to the temporal and spatial differences in diet availability, fatty acid profiles are also influenced by different assimilation and catabolism rates (Hagen et al., 2001; Meyer et al., 2009; Phleger et al., 2002). Overall, C16:0, C20:5ω3 and C22:6ω3 are incorporated into phospholipids, as opposed to triacylglycerols, in *E. superba*, indicating their important roles in cell membrane construction (Falk-Petersen et al., 2000; Lee et al., 2006). Most structural fatty acids in phospholipids are more stable and independent of dietary changes than fatty acids in stored lipids (Falk-Petersen et al., 2000; Kattner et al., 2007). In a study published by Hagen et al. (2001), SFA in triacylglycerols prevailed over PUFA, especially in the later stages of *E. superba*. In contrast, in phospholipids, PUFA (especially the structural fatty acids C20:5ω3 and C22:6ω3) exceeded 50% in all developmental stages, with the proportion of SFA remaining less than 30%. Under poor food conditions, krill decrease their metabolism and utilize stored lipids (Cripps et al., 1999; Meyer et al., 2009). In summary, the high portions of the structural fatty acids C20:5ω3, C20:3ω3 and C22:6ω3, and the elevated PUFA/SFA in adult krill from Stas D1-03 and D1-04 were likely the result of preferential metabolism of SFA-rich triacylglycerols. In contrast to the other four sta-

tions, Stas D1-03 and D1-04 are mainly influenced by the ACC. Although Chl *a* was elevated at Sta. D1-04, the low levels of fatty acid indicators revealed that adult krill in this region were still suffering from poor dietary conditions after overwintering. The ongoing phytoplankton bloom would be beneficial to their future reproduction and population recruitment.

4.5 *Trophic information from stable isotopes*

Proportions of phytoplankton, heterotrophic organisms and organic detritus influence the stable isotopic signature of POM (Park et al., 2011; Yang et al., 2016), and higher isotopic values in the POM of 20–70 μm size fraction are derived from higher concentrations of heterotrophic organisms such as ciliates (Yang et al., 2016). The different isotopic turnover rates between zooplankton and phytoplankton constituents in POM lead to an inversion of the nitrogen isotope signature (Park et al., 2011), which made it difficult to evaluate the trophic status of *E. superba* in our study.

Size-related dietary shifts are prevalent among many marine fishes and some euphausiids (Graham et al., 2007; Polito et al., 2013). Similar to previous research, δ^{15}N values in our study were positively correlated with body size and WW, verifying that larger *E. superba* individuals ingested more heterotrophic diets such as copepods and protozoans (Polito et al., 2013; Schmidt et al., 2004, 2011; Zhu et al., 2018). The lowest level of δ^{15}N occurred at Sta. D1-04, demonstrating more herbivorous feeding by juveniles. Compared to the results published by Zhu et al. (2018), which was carried out in April, May and June (late autumn and early winter) in the South Shetland Islands, our study showed low levels of δ^{15}N in adult *E. superba*. The reason might be that krill generally feed on phytoplankton during summer, and when phytoplankton becomes scarce in autumn and winter the krill switch to higher trophic food, benthic material or ice algae (Schmidt and Atkinson, 2016; Zhu et al., 2018).

We aimed to obtain a comprehensive understanding of the trophic conditions of *E. superba* by means of a combined incubation experiment with fatty acid biomarker and stable isotope assessment. Considering the potential effect of the small sample size, we attempted to discuss the feeding strategies of *E. superba* more carefully according to previously published studies. Evidence from fatty acid markers indicated that juveniles preferentially fed on dinoflagellates and adults on diatoms. Adult *E. superba* from different stations exhibited distinct features in fatty acid profiles, indicating their different trophic conditions. Under the impacts of nutritious Weddell Sea waters, adult krill at Stas D2-07, D5-07, DA-01 and DA-02 exhibited higher levels of feeding on both phytoplankton and higher trophic diets. In contrast, adult krill at Stas D1-03 and D1-04 appeared to remain in a difficult dietary condition after overwintering. The different dietary conditions between stations and different size groups revealed by our study suggest a highly plastic feeding strategy of *E. superba* in the eastern South Shetland Islands.

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