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Trophodynamics of euphausiids in the Amundsen Sea during the austral summer by fatty acid and stable isotopic signatures

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ABSTRACT

The Amundsen Sea is characterized by a continental shelf, long-term sea ice, and many coastal polynyas with high biological productivity. *Euphausia superba* and *Euphausia crystallorophias*, which are dominant Antarctic krill, are major prey for most predators, such as fishes, birds, and marine mammals. An understanding of the feeding ecology of krill may provide the information for the structure and function of the Amundsen Sea ecosystem. Thus, we applied two biochemical approaches (fatty acids and stable isotopes) to determine the trophodynamics of adult krill in the Amundsen Sea. There were no significant differences in lipid contents between the two species, but the dominant storage lipids were different. Triacylglycerol (TAG) was dominant in *E. superba*, but wax esters (WE) were dominant in *E. crystallorophias* due to their different living strategies. Furthermore, the lipid content of *E. crystallorophias* displayed a spatial variation, being highest on the glacial edge. It was difficult to understand the feeding strategy and food source using only the fatty acid compositions of krill and in situ particulate organic matter. However, we found that specific FA ratios (18:1ω9/18:1ω7 and PUFA/SFA) and the nitrogen isotope ratio ($\delta^{15}N$) provide more insight into the feeding ecology of krill, such as feeding strategy and trophic position. These ratios suggest that *E. crystallorophias* consistently showed a higher degree of carnivorous feeding than *E. superba* in the Amundsen Sea during the austral summer. In conclusion, adult *E. superba* might more directly obtain their energy from in situ primary producers in the open sea, but, in the Amundsen Sea Polynya, adult *E. crystallorophias* seems to obtain their energy mainly through the microbial loop (microzooplankton). If so, *E. crystallolophias* would be a key player not only to transfer the energy from microbes to higher trophic levels but also to control the carbon and nitrogen cycle in the Amundsen Sea Polynya.

1. Introduction

Antarctic krill are abundant and widespread zooplankton and micronekton (sometimes adult krill called as micronekton due to their size) in the Southern Ocean. They transfer energy from low to high trophic levels as a major consumer of primary producers and are a major prey for fishes, birds, and marine mammals in Antarctic pelagic ecosystems (El-Sayed, 1985; Sakshaug, 1997). In the Southern Ocean, *Euphausia superba* and *Euphausia crystallorophias* are the predominant and common krill species with a biomass of hundreds of millions of tons. *E. superba* is known to have a wide distribution around the Antarctic continent and Southern Ocean (Falk-Petersen et al., 2000), whereas *E. crystallorophias* (called ice krill) is the most common euphausiid in high latitude Antarctic neritic waters (John, 1936). Although most *Euphausia* spp. are known to be omnivores, their food abundance and composition are spatially and temporally variable, particularly in the polar region. Therefore, they can effectively switch their feeding strategy from omnivore to carnivore or herbivore depending on the available food (Schnack, 1985; Price et al., 1988; Hopkins et al., 1993). Furthermore, they take advantage of other metabolic and morphological strategies (i.e., storing lipids, lowering their metabolism, and shrinking their body size) to overcome the extreme conditions (low food availability) during winter (Ikeda and Dixon, 1982; Quetin et al., 1994; Torres et al., 1994; Hagen et al., 1996; Falk-Petersen et al., 2000; Ju and Harvey, 2004). Willis (2014) revealed that population of krill (*E. superba*) can be controlled by various predators, such as whales, seals, and penguins. As mentioned above, many studies of Antarctic krill,

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especially *E. superba* have been conducted to better understand the structure and function of polar ecosystems.

Antarctica, especially the Amundsen Sea, is characterized by a narrow or lacking continental shelf, a large amount of sea ice that has persisted for a long-time, and a number of coastal polynyas located near to large ice shelves (Arrigo and van Dijken, 2003). Fragoso and Smith (2012) confirmed that highly productive and nutrient-enriched polynyas, and continental shelves are the optimal regions for phytoplankton blooms within coastal polynyas during spring and summer. In Antarctica, the continental shelf has high biological productivity (Smith and Nelson, 1985; Arrigo et al., 1998), and the polynyas provide critical habitats for organisms of multiple trophic levels, such as microzooplankton, copepods, krill, and mammals (Hosie and Cochran, 1994; Gill and Thiele, 1997; Li et al., 2001). Among them, the dominant krill can obtain energy from low trophic levels or particulate organic matter (POM) in the Amundsen Sea Polynya. This energy is then supplied to other polar ecosystems (the regions with relatively low productivity; non-polynya areas and the Ross Sea Polynya) (Yager et al., 2012). Despite the key function of krill in the Amundsen Sea, our understanding of the Antarctic krill's role in the Amundsen Sea ecosystem is still lacking due to the accessibility and harsh weather conditions.

To understand the feeding ecology of zooplankton in marine ecosystems, various approaches, each with its own strengths and drawbacks, have been used. Among the traditional methods, stomach content analysis under the microscope provides a direct snap shot of the recently consumed food items. While this indicates the diet over short periods (hours to a day), it cannot represent the long-term feeding history due to the different digestion rates for different types of diets (soft vs. hard). Feeding experiments can determine the feeding rate and food selectivity, but are conducted under artificial conditions over short periods ranging from a few hours to a day. The feeding ecology of *Euphausia pacifica* has been investigated through a stomach content analysis (Kakagawa et al., 2001) and in situ feeding experiments (Du and Peterson, 2014) in the Pacific Ocean. To compensate for the biases of traditional approaches, fatty acid (FA) analysis has been used (Cripps et al., 1999; Hagen et al., 2001; Ju and Harvey, 2004). Because specific FAs can be synthesized only by primary producers (i.e., phytoplankton), these are used to determine the diet. Additionally, the ratios of some grouped FAs (polyunsaturated FA/saturated FA: PUFA/SFA) or individual FAs (18:1ω9/18:1ω7) have been used to interpret the feeding strategy of krill (Atkinson et al., 2002; Meyer et al., 2002). Zooplankton feeding on metazoans and protists is known to have relatively high concentrations of 18:1ω9, while 18:1ω7 is indicative of feeding on phytoplankton by zooplankton (Falk-Petersen et al., 2000). Therefore, the ratio of 18:1ω9/18:1ω7 has been used to indicate the relative degree of carnivory–omnivory–herbivory of zooplankton (Dalsgaard et al., 2003). However, the lipid may sometimes be transformed during the metabolic process (i.e. elongation, desaturation: Kattner and Hagen, 1998; Falk-Petersen et al., 2000), making interpretation of the specific origin difficult. The food source and trophic relationship in the food web can be explained through the use of stable carbon ($\delta^{13}C$) and nitrogen isotope ($\delta^{15}N$) ratios because the $\delta^{13}C$ of the primary producer is essentially conservative through the trophic level but $\delta^{15}N$ steadily increase at higher trophic levels in a food web, on account of the preferential incorporation of heavy isotopes and the excretion of light isotopes in organisms (DeNiro and Epstein, 1981; Michener and Kaufman, 2007; Caut et al., 2009). During the austral winter, the stable isotope ratios were analyzed for *E. superba* and in potential food sources (i.e., POM) to understand their weeks–months feeding source (Frazer, 1996; Frazer et al., 1997). The ratios were spatially and temporally variable throughout the Antarctic Peninsula because they change with the environment, and therefore do not always indicate a specific diet. These biochemical approaches, such as FA and stable isotope analysis, can indicate the dietary history over both the short- (weeks) and long-term (months). Recently, multiple approaches have been applied to understand the prey–predator relationship in the food web of marine ecosystems, because they can provide complementary information than the use of a single method. Atkinson et al. (2002) used multiple approaches (i.e., stomach content analysis, feeding experiments, and FA analysis) for the feeding and energy budgets of *E. superba* at the onset of winter in the Antarctic Ocean. It was also established that protozoans are a significant food source for *E. superba* from a combination of stomach content analysis, FAs, and stable isotopes (Schmidt et al., 2006). With exception of these two studies, the rest of the studies on the diet of *Euphausia* spp. have used a single method, with very few studies applying multiple approaches in different marine ecosystems (El-Sabaawi et al., 2009).

Therefore, we applied two complementary approaches (i.e., FA and stable isotopes) to determine the food source of *E. superba* and *E. crystallorophias*, and its role in energy transfer from lower to higher trophic levels in the Amundsen Sea ecosystem during austral summer (January 2011).

2. Materials and methods

2.1. Study area, sampling, and preparation

The Amundsen Sea is located in the West Antarctica between the Bellingshausen Sea and Ross Sea. The sea is characterized with a continental shelf, sea ice, and a number of coastal polynyas (Arrigo and van Dijken, 2003).

Antarctic krill (*E. superba* and *E. crystallorophias*) were collected at selected stations (open sea, continental shelf, polynya, and glacial edge) using a bongo net (mesh size: 333 and 505 μm). The sampling depth was selected by acoustic transects from the open sea to the glacial edge of the Amundsen Sea during January 2011, onboard the IBRV *Araon* (Fig. 1). The surface water was collected using a Rosette sampler in three regions (i.e., open sea, continental shelf, and polynya), and then POM, which was considered to be a potential food sources (i.e., phytoplankton) was sampled by filtering the surface water onto pre-combusted (450 °C) 47 mm GF/F filters under a gentle vacuum. All samples were stored at −80 °C prior to biochemical analysis. Before the analysis, the adults of *E. superba* and *E. crystallorophias* were sorted out based on their morphological differences (i.e., the shape of the rostrum and eye) (Baker et al., 1990), and then their size (total length) and wet weight were measured. Mean total lengths of krill used for biochemical analysis were 46.2 ± 8.1 mm for *E. superba* and 32.4 ± 2.6 mm for *E. crystallorophias* corresponding for the adult phase (Ikeda, 1985; Brinton and Townsend, 1991). Further details (i.e., location, depth, and environmental conditions) regarding the sampling stations were provided in Table 1.

2.2. Lipid content and class composition analysis

After weighing the freeze-dried individuals, the lipids were extracted three times in a mixture of CH_2CL_2:MeOH (dichloromethane:methanol = 1:1) by gun sonication using the modified Bligh and Dyer extraction method (Berndmeyer et al., 2014). The organic solvents in the lipid extracts were dried under a gentle stream of nitrogen gas, and then the extracted lipids were redissolved in a mixture of CH_2CL_2:MeOH (dichloromethane: methanol = 2:1) to analyze the lipid content and class composition. Aliquots (0.5–1.0 μl) of the redissolved lipid extracts were spotted onto silica chromarods (Mitsubishi Kagaku Iatron, Tokyo, Japan), focused with a mixture of CH_2CL_2:MeOH (dichloromethane: methanol = 1:1), and then developed in a mixture of hexane: diethyl ether:formic acid (85:15:0.2) for separation of the major lipid classes. Lipid classes were separated on the rod and quantified by thin-layer chromatography coupled with a flame ionization

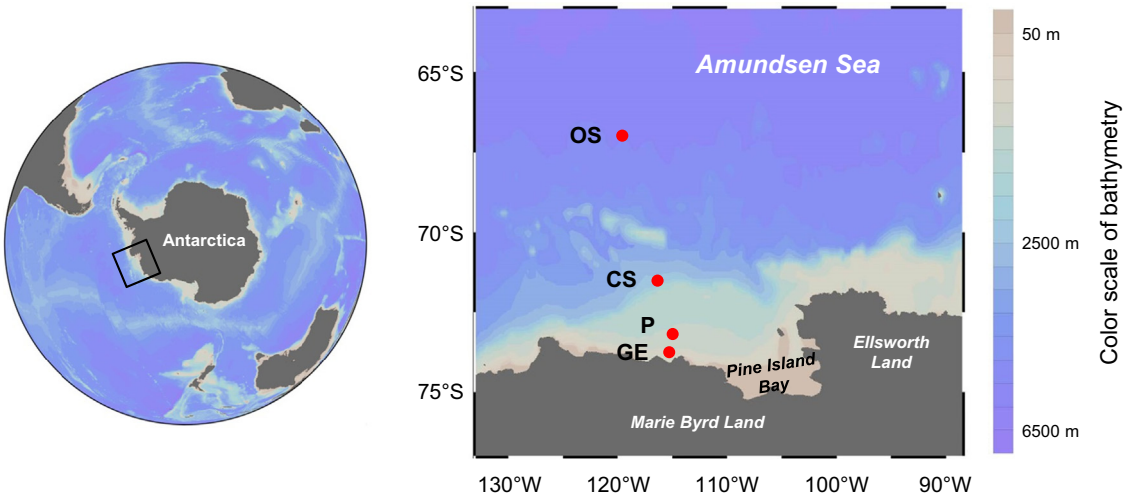

Fig. 1. Map of the study area with sampling stations (indicated as red circles) for Antarctic krill *Euphausia superba* (OS) and *Euphausia crystallorophias* (CS, P, and GE) in the austral summer of 2011 in the Amundsen Sea with bathymetry. OS: open sea; CS: continental shelf; P: middle of polynya; GE: polynya near glacial edge.

Table 1
General information of the sampling stations with basic environmental data in the Amundsen Sea in January 2011.

Station	Latitude (°S)	Longitude (°W)	Date (UTC) (mm/dd/yy)	Water depth (m)	Temperature (°C)	Salinity (psu)	Chl-a (μg/L)	Sea ice concentration (%)
GE (polynya near glacial edge)	74.08	115.72	01/02/2011	1076	−0.62	33.93	3.83	0
P (middle of polynya)	73.25	115.00	01/01/2011	830	−0.79	33.74	11.60	0
CS (continental shelf)	71.56	117.08	01/08/2011	1364	−1.57	33.58	0.23	60–80
OS (open sea)	67.00	120.00	01/12/2011	4520	−0.93	33.01	0.64	0

detector (TLC–FID), using a Mark-V Iatroscan (Iatron Laboratories, Tokyo, Japan) (Ko et al., 2011). Each lipid class was identified and calibrated by a comparison with commercially available standards: 1,2-dipalmitoyl-rac-glycero-3-phosphocholine hydrate for phospholipids (PL), cholesterol for cholesterol (CS), n-nonadecanoic acid for free fatty acids (FFA), glyceryl trioleate for triacylglycerol (TAG), and palmitoleic acid stearyl ester for wax esters (WE) (Sigma-Aldrich Co., St Louis, MO, USA). The peak areas of each lipid class were integrated using the ChemStation software 2001–2007 (Agilent Technologies, Santa Clara, CA, USA) to determine the quantity of each class. Total lipid content was obtained through the summation of all lipid classes determined by TLC–FID.

2.3. Fatty acid analysis

Aliquots (ca. 70–200 μl) of the lipid extracts from *Euphausia* spp. and POM were used for the FA analysis. An internal standard (n-nonadecanoic acid; Sigma-Aldrich Co.) was added to each aliquot, and then the remaining organic solvents were dried under nitrogen gas. The samples were subjected to alkaline hydrolysis using 0.5 N methanolic KOH, with gentle heating at 70 °C for 30 min. After cooling at room temperature, the lipid fraction containing the FAs was separated following acidification to pH 2, dried under nitrogen gas, and then converted to the FA methyl ester (FAME) using boron trifluoride methanol (BF_3-MeOH), with heating at 70 °C for 30 min. FAMEs were isolated by partitioning into hexane: diethyl ether (9:1). A subsample of FAMEs was treated with dimethyl disulfide (DMDS) to determine the position of double bonds in unsaturated FAs (Nichols et al., 1986; Destaillats and Angers, 2002). FAMEs were quantified by gas chromatography and flame ionization detector (GC–FID; model 7890A, Agilent Technologies) with a ZB-5 ms coated 5% phenyl-arylene and 95% dimethylpolysiloxane column (60-m length, 0.32-mm internal diameter, 0.25-μm film thickness; Phenomenex) using helium as the carrier gas. The samples were injected in splitless mode at an initial oven temperature of 50 °C, an injector temperature of 250 °C, and a detector temperature of 320 °C. Then, the oven temperature was ramped at 10 °C/min to 120 °C and 4 °C/min to a final temperature of 300 °C, and maintained at 300 °C for 5 min. The total duration of the analysis for a sample was 57 min. Individual FA compounds were structurally identified by gas chromatography–mass spectrometry (GC–MS; Agilent 7890A GC, with Agilent 5975 C MS) operating at 70 eV, with a mass acquisition range of 50–700 amu. The setting and column for the GC–MS were the same as those used for GC–FID.

2.4. Stable isotope analysis

Bulk stable isotope ratios were analyzed from freeze-dried and powdered individuals. Considering the depletion of ^{13}C and the inflation of the $\delta^{13}C$ value by carbonates in biota samples, the lipids from the samples for the $\delta^{13}C$ analysis were removed as explained above (see Berndmeyer et al. (2014)), and then the lipid-free samples were washed with hydrochloric acid. The samples for the $\delta^{15}N$ analysis were not washed with hydrochloric acid, and the lipids were not removed because these processes may influence $\delta^{15}N$ values (Bunn et al., 1995). All samples were dried for 24 h and placed in tin capsules, and the $\delta^{13}C$ and $\delta^{15}N$ ratios were obtained using an elemental analyzer (EA 3000-D, Eurovector, Milan, Italy) coupled with an isotope ratio mass spectrometer (IsoPrime; GV instruments, Cheadle Hume, UK).

$\delta^{13}C$ and $\delta^{15}N$ ratios were expressed as

$$\delta^{13}C \text{ or } \delta^{15}N\ (‰) = \left[\left(R_{sample}/R_{standard}\right)-1\right] \times 10^3$$

where R_{sample} and $R_{standard}$ are the ratios of $^{13}C/^{12}C$ (for $\delta^{13}C$) or $^{15}N/^{14}N$ (for $\delta^{15}N$) in the sample and standard, respectively. The standards used for carbon and nitrogen were Vienna Peedee

Belemnite (VPDB) and atmospheric nitrogen, respectively. The reference materials were IAEA-CH6 (mean ± SD, $\delta^{13}C = -10.45 \pm 0.04‰$) and IAEA-N1 ($\delta^{15}N = 0.4 \pm 0.2‰$). The analytical precision was within 0.2‰ and 0.5‰ for carbon and nitrogen, respectively.

2.5. Statistical analysis

Statistical comparisons of lipid contents and stable isotope signatures between species and among stations for euphausiids were carried out using the non-parametric Mann–Whitney test and Kruskal–Wallis test because the number of samples was not enough to satisfy the normality and homogeneity of variances for applying parametric statistic tests.

3. Results

3.1. Lipid content and class composition

The mean total lipid contents of adult *E. superba* and *E. crystallorophias* in January 2011 were 9.1 ± 2.2% and 8.5 ± 3.9% of dry mass (DM), respectively (Fig. 2). The lipid contents of the two species were not significantly different (Mann–Whitney $U = 27.000$, $p > 0.05$). For *E. crystallorophias*, the spatial variability of the lipid contents was significant (Kruskal–Wallis = 7.500, $p < 0.05$). Individuals from the glacial edge (13.0 ± 3.4% of DM, $n = 6$) contained a significantly higher lipid content than those from the continental shelf (6.4 ± 1.3% of DM, $n = 8$) and polynya (6.3 ± 2.1% of DM, $n = 12$). While the lipid reserves of *E. superba* were mainly composed of the PL (24–31% of total lipids) and TAG (57–64% of total lipids), for *E. crystallorophias*, the PL (42–66% of total lipids) and WE (23–45% of total lipids) were the dominant lipid classes. There were also spatial variations in the relative abundance of each lipid class in *E. crystallorophias*.

3.2. Fatty acid composition

Euphausia spp. contained 22 different FAs, ranging from C_{14} to C_{24} (see Table 2). Although the dominant FAs were 16:0, 18:1ω9, 18:1ω7, 20:5ω3, and 22:6ω3 for both species, the relative abundances of these FAs varied between species and among sampling stations. *E. superba* contained an abundance of SFAs containing 16:0, whereas the relative abundance of 18:1ω9 was lower than in *E. crystallorophias*. For *E. crystallorophias*, the relative abundance of monounsaturated FAs (MUFAs), mainly 18:1ω9 and 18:1ω7, was higher at the glacial edge than at the continental shelf and polynya. However, the abundance of PUFAs (mainly the algal origin fatty acids: 20:5ω3 and 22:6ω3) was highest at the polynya and lowest at the glacial edge. Although there were relatively small changes compared with the other FAs, the highest abundance of the branched FAs (BrFAs), known as bacterial origin FAs, were found in the open sea for *E. superba*.

We considered the ratios of specific FAs (PUFA/SFA and 18:1ω9/18:1ω7) to understand the relative degree of carnivorous feeding in krill (i.e., a higher ratio indicates more carnivorous feeding). Based on these ratios, the degree of carnivorous feeding was different between species (Table 2). *E. crystallorophias* displayed relatively higher ratios than *E. superba*. However, *E. cyrstallorophias* displayed an almost identical ratio at all sampling stations.

The FA composition of POM was given in Table 3. In the open sea, it was dominated by SFA (42.1% of total FAs), mainly 14:0, whereas POM from the continental shelf was composed mainly of SFA (33.4% of total FAs) and PUFA (35.9% of total FAs). POM from the polynya contained an abundance of SFAs (44.7% of total FAs) and MUFAs (36.5% of total FAs). Although the amount of BrFA present was minor, its relative abundance exhibited spatial variation, with high levels in the open sea (5.2% of total FAs) but low levels in the glacial edge (< 0.1% of total FAs).

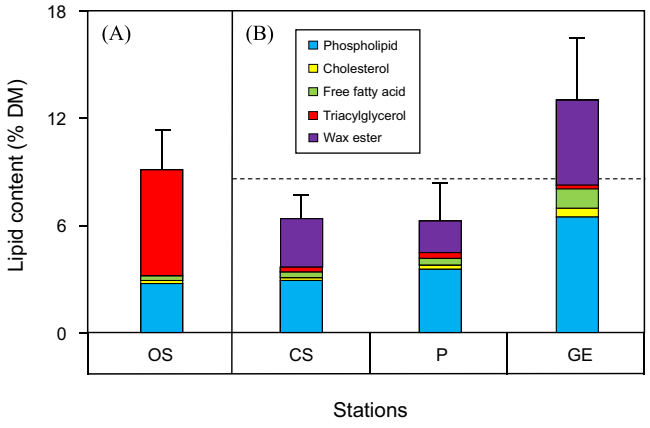

Fig. 2. Lipid content (% DM; means and standard deviations) and class composition of (A) *Euphausia superba* and (B) *Euphausia crystallorophias* in January 2011 in the Amundsen Sea. The dotted line indicates the mean lipid content of *E. crystallorophias* at all stations. OS: open sea; CS: continental shelf; P: middle of polynya; GE: polynya near glacial edge.

Table 2
Relative abundances of individual fatty acids (FAs) as a percentage of total FAs (means and standard deviations) in *Euphausia superba* and *Euphausia crystallorophias*. OS: open sea; CS: continental shelf; P: middle of polynya; GE: polynya near gracial edge; SFA: saturated FA; MUFA: monounsaturated FA; PUFA: polyunsaturated FA; BrFA: branched FA.

Fatty acids	*Euphausia superba*	*Euphausia crystallorophias*		
	OS ($n=13$)	CS ($n=8$)	P ($n=12$)	GE ($n=6$)
n-saturates				
14:0	6.3 ± 2.9	2.2 ± 0.4	2.9 ± 0.2	1.1 ± 0.5
16:0	25.9 ± 5.0	13.9 ± 3.0	14.0 ± 2.2	14.8 ± 1.6
18:0	3.2 ± 0.8	3.3 ± 0.9	6.9 ± 4.1	1.8 ± 0.6
20:0	0.2 ± 0.1	0.1 ± 0.1	Tr	Tr
Monounsaturates				
16:1ω9	0.3 ± 0.1	2.5 ± 1.9	0.2 ± 0.0	0.1 ± 0.0
16:1ω7	6.6 ± 2.6	3.3 ± 2.7	3.0 ± 1.3	2.5 ± 0.7
16:1ω5	0.9 ± 0.4	0.7 ± 1.0	0.3 ± 0.0	0.1 ± 0.0
16:1ω3	0.4 ± 0.3	0.3 ± 0.3	0.2 ± 0.1	0.1 ± 0.1
18:1ω9[a]	13.0 ± 2.5	29.6 ± 1.3	28.4 ± 1.5	43.5 ± 5.2
18:1ω7	12.7 ± 2.9	14.9 ± 6.9	10.4 ± 4.1	13.6 ± 1.5
18:1ω5	0.7 ± 0.4	0.6 ± 0.6	0.2 ± 0.2	0.3 ± 0.0
20:1ω11	0.3 ± 0.2	0.2 ± 0.0	0.2 ± 0.0	0.2 ± 0.0
20:1ω9	0.5 ± 0.2	0.3 ± 0.2	0.2 ± 0.1	0.2 ± 0.0
22:1+24:1[b]	1.4 ± 1.0	0.6 ± 0.3	0.4 ± 0.3	Tr
Polyunsaturates				
16:3[c]	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.1 ± 0.1
18:2ω6+18:4ω3	3.5 ± 1.3	3.0 ± 0.5	2.7 ± 0.3	2.3 ± 0.2
20:4[c]	1.5 ± 0.5	1.2 ± 0.2	1.4 ± 0.2	0.9 ± 0.3
20:5ω3	13.9 ± 5.1	14.0 ± 7.2	14.6 ± 0.1	9.3 ± 4.0
20:2[c]	0.7 ± 0.4	0.7 ± 0.3	0.5 ± 0.1	0.8 ± 0.1
22:5[c]	0.6 ± 0.2	0.4 ± 0.2	0.6 ± 0.1	Tr
22:6ω3	6.0 ± 2.9	7.7 ± 3.8	12.5 ± 3.1	8.2 ± 4.1
ΣSFA	35.6 ± 5.2	19.6 ± 1.7	23.8 ± 1.7	17.7 ± 2.2
ΣMUFA	36.9 ± 4.8	52.8 ± 8.5	43.6 ± 4.5	60.6 ± 6.6
ΣPUFA	26.4 ± 7.5	27.2 ± 10.2	32.3 ± 2.7	21.7 ± 8.3
ΣBrFA	1.2 ± 0.7	0.4 ± 0.1	0.3 ± 0.0	Tr
18:1ω9/18:1ω7	1.1 ± 0.3	2.2 ± 0.9	3.0 ± 1.3	3.2 ± 0.3
PUFA/SFA	0.8 ± 0.3	1.4 ± 0.6	1.4 ± 0.0	1.3 ± 0.7

Tr, trace amount (< 0.1% of total concentration).
[a] 18:3ω3 might be co-eluted.
[b] Sum of minor amounts of fatty acids (includes 22:1 and 24:1).
[c] Double bond position unidentified.

Table 3
Relative abundances of individual fatty acids (FAs) as a percentage of all FAs in particulate organic matter (POM). OS: open sea; CS: continental shelf; P: middle of polynya; SFA: saturated FA; MUFA: monounsaturated FA; PUFA: polyunsaturated FA; BrFA: branched FA.

Fatty acids	Particulate organic matter (POM)		
	OS	CS	P
n-saturates			
14:0	26.8	6.5	14.5
16:0	5.3	19.7	19.7
18:0	9.0	6.8	10.0
20:0	1.1	0.3	0.5
Monounsaturates			
16:1ω9	1.8	0.9	3.3
16:1ω7	0.6	8.8	7.9
16:1ω5	0.0	Tr	0.8
16:1ω3	0.4	0.6	0.5
18:1ω9[a]	5.1	12.9	17.5
18:1ω7	2.0	2.8	3.4
18:1ω5	0.5	0.4	0.3
20:1ω11	0.7	0.3	1.5
20:1ω9	0.4	0.4	0.7
22:1+24:1[b]	2.8	1.1	0.6
Polyunsaturates			
16:3[c]	1.3	0.5	0.3
18:2+18:4[c]	4.1	10.1	6.3
20:4[c]	3.9	1.4	0.6
20:2[c]	0.8	1.3	1.5
20:5ω3	11.5	12.5	3.3
22:5[c]	2.4	1.2	0.3
22:6ω3	14.2	9.0	3.1
Σ SFA	42.1	33.4	44.7
Σ MUFA	14.4	28.3	36.5
Σ PUFA	38.3	35.9	15.3
Σ BrFA	5.2	2.4	3.5

Tr, trace amount (< 0.1% of total concentration).
[a] 8:3ω3 might be co-eluted.
[b] Sum of minor amounts of fatty acids (includes 22:1 and 24:1).
[c] Double bond position unidentified.

Table 4
Carbon and nitrogen isotope ratios of *Euphausia superba* and *Euphausia crystallorophias* at the OS (open sea), CS (continental shelf), P (middle of polynya), and GE (polynya near gracial edge) stations.

	E. superba	*E. crystallorophias*		
	OS (n=5)	CS (*n*=3)	P (*n*=2)	GE (*n*=6)
$\delta^{13}C$	−25.7 ± 0.5	−23.2 ± 0.5	−23.9 ± 0.8	−25.0 ± 0.4
$\delta^{15}N$	5.1 ± 0.3	8.4 ± 0.6	8.9 ± 0.5	8.2 ± 0.4

3.3. Stable carbon and nitrogen isotope ratios

The $\delta^{13}C$ and $\delta^{15}N$ values of *Euphausia* spp. were presented in Table 4. Overall, *E. superba* (−25.7 ± 0.5‰ and 5.1 ± 0.3‰) had lower $\delta^{13}C$ and $\delta^{15}N$ values than *E. crystallorophias* (−24.1 ± 0.9‰ and 8.5 ± 0.4‰) ($\delta^{13}C$: Mann–Whitney=3.500, $p < 0.05$; $\delta^{15}N$: Mann–Whitney=0.000, $p < 0.05$). The $\delta^{13}C$ of *E. crystallorophia* differed significantly among stations. Krill from the continental shelf and polynya were more enriched with ^{13}C than those from the glacial edge (Kruskal–Wallis=7.741, $p < 0.05$), whereas no significant enrichment was detected for ^{15}N throughout the sampling stations (Kruskal–Wallis=7.500, $p > 0.05$). However, the trophic position of *E. crystallorophias* could be one level higher than that of *E. superba*, based on trophic enrichment (3.3 ± 0.26‰) of $\delta^{15}N$.

4. Discussion

The lipid contents of *Euphausia* spp. from the Amundsen Sea during the austral summer were slightly lower than those from the Weddell Sea and Ross Sea (Hagen et al., 1996; Kattner and Hagen, 1998). On average, the phytoplankton bloom in the Amundsen Sea Polynya (January) occurs later than in the Ross Sea Polynya (December) (Smith et al., 2006). Therefore, it could be inferred that the krill in the Amundsen Sea Polynya start to accumulate lipids from their food supply after the onset of the phytoplankton bloom, which is about 1 month later than for krill in the Ross Sea Polynya. There was a spatial variability in the lipid contents of adult *E. crystallorophias*, which decreased from the near-shore to continental shelf. *E. crystallorophias,* as the dominant krill species in the Amundsen Sea Polynya, had the highest lipid content in the glacial edge of the Getz Ice Shelf (Fig. 2). This spatial pattern of lipid levels in krill resulted from the enhanced primary and secondary production in the polynya near the ice-shelf (Yager et al., 1995; Arrigo and van Dijken, 2003; La et al., 2015). Generally, large amounts of Fe and nutrients from freshwater and melting ice-shelves are supplied to the polynya (Yager et al., 2012), which enhances primary production. This leads to a high Chl-a concentration, with the dominance of *Phaeocystis antarctica* (Lee et al., 2012) in the Amundsen Sea Polynya as shown in Table 1. However, lipid levels in *E. crystallorophia* did not correspond exactly to the Chl-a concentration within the two polynya stations. We speculate that lipid accumulation in krill occurs a few days to weeks later than the timing of the algal bloom (Falk-Petersen et al., 2000). It has been reported that the algal bloom in the Amundsen Sea Polynya develops from the near ice-shelves to the continental shelf (Yager et al., 2012). The combination of the spatial time lag of the algal bloom and lipid metabolism might be caused by the different level of lipid accumulation in *E. crystallorophias* within the polynya, which may be also reflected into the accumulation of storage lipids, particularly two fold increments of WE at the glacial edge.

The lipid class composition of adult krill displayed interspecies differences. TAG was the dominant storage lipid in *E. superba*, while WE were dominant in *E. crystallorophias*. This difference in composition is well known and stems from the different living strategies (particularly overwintering and timing of spawning) of krill species to survive under the extreme conditions (i.e., cold temperature, limited food, and dark). For *E. crystallorophias*, which lives in the neritic regions (colder than the open sea) and with an early timing of reproduction before the spring bloom, it is more efficient to store WE as energy reserves because the WE have lower melting points and higher energy costs per weight than TAGs (Kattner and Hagen, 1998; Falk-Petersen et al., 2000; Ju and Harvey, 2004; Ju et al., 2009).

The FA profile has been used to understand the feeding ecology and energy sources of krill from the Arctic and Antarctic Oceans (Virtue et al., 1996; Cripps et al., 1999; Hagen et al., 2001). A comparison of the FA composition between krill and natural prey assemblages (i.e., POM) suggested that the feeding strategy (carnivore/omnivore/herbivore) of *E. superba* varied spatially and seasonally in the Antarctic (Cripps et al., 1999). In this study, the FA composition of POM, as potential prey, was compared with those of adult *E. superba* and *E. crystallorophias* in the Amundsen Sea (Tables 2 and 3). In the continental shelf and polynya, adult *E. crystallorophias* had a similar pattern of FA composition to POM, which was characterized by the dominance of 16:0 and 18:1ω9. There are phytoplankton blooms, which are mainly composed of diatoms in the open sea and prymensiophyte *P. antarctica* in the polynya during the austral summer (Buck and Garrison, 1983; Fryxell and Kendrick, 1988; Davidson and Marchant, 1992; Alderkamp et al., 2012; Lee et al., 2012). Nichols et al. (1991) reported that *Phaeocystis* sp. during the bloom had none or minor

amounts of PUFAs, especially 20:5ω3 and 22:6ω3, whereas the amounts of 14:0 and 18:1ω9 were increased (Skerratt et al., 1995; Skerratt et al., 1998). In this study, we found that the FA composition of POM from the polynya was similar to that reported for *Phaeocystis* sp., but the FAs of POM from the open sea and continental shelf seem to reflect the FA signature for diatoms and *Phaeocystis* sp. However, it is difficult to determine the major food sources for euphausiids using only the composition of FA composition because POM is composed of diverse particles ranging from algae to microzooplankton (and sometimes small copepods). Some FAs are known to be source-specific, for example 20:5ω3 (EPA: eicosapentaenoic acid) from diatoms (Nichols et al., 1993) and 22:6ω3 (DHA: docosahexaenoid acid) from dinoflagellates (Graeve et al., 1994; Falk-Petersen et al., 2000). Additionally, based on the different ratios of selected FAs (i.e., PUFA/SFA and 18:1ω9/18:1ω7), *E. crystallorophias* could be interpreted to be more carnivorous than *E. superba* (Table 2 and Fig. 3). Two independent biochemical tracers; i.e., the ratio of 18:1ω9/18:1ω7 and PUFA/SFA and the $\delta^{15}N$ value, are plotted in Fig. 3. This plot indicates that the enrichment of ^{15}N agrees well with the increment of carnivorous feeding, interpreted through the FA ratios. Although other studies indicated that the feeding habits of Antarctic krill (inferred through the FA ratios and $\delta^{15}N$ value) were varied regionally and seasonally (Table 5), we could infer that adult *E. crystallorophias* may prefer a carnivorous diet, such as protists, ciliates, or small copepods (i.e., early stages of copepods) in the Amundsen Sea Polynya during the austral summer. Lee et al. (2013) reported that larval *E. crystallorophias* were the major consumer of primary producers among the mesozooplankton in the Amundsen Sea polynyna during the austral summer. It is well known that Antarctic krill can make an ontogenetic diet shift from herbivore to carnivore or omnivore. Therefore, larval krill may preferentially feed on algae (including ice algae) in this study region, but adult krill could be more carnivorous. Although our observation was very limited spatially and seasonally, adult *E. superba* from the open ocean seem less carnivorous than adult *E. crystallorophias* from the polynya. It suggests that adult *E. superba* might be more dependent on in situ primary producers than adult *E. crystallorophias* in this region during the austral summer.

In the Amundsen Sea Polynya, adult *E. crystallorophias* seem to play an important ecological role in linking the microbial loop (microzooplankton) to higher trophic levels during the austral summer. They also might indirectly affect microbial biomass and activity (called 'top–down control') in the Amundsen Sea Polynya, which can affect the cycling of essential elements (i.e., carbon and nitrogen). Therefore, the contribution of microbes in biological production in the Amundsen Sea ecosystem should not be overlooked. To more accurately quantify the contribution of microbes to biological production, we need to measure the grazing rate of krill, its consumption efficiency, and its food selectivity on microzooplankton under winter and summer conditions, which would improve our understanding of the structure and function of the

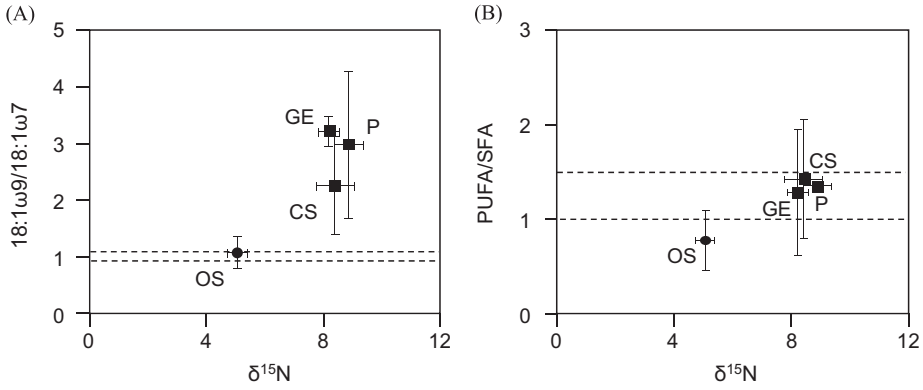

Fig. 3. *Euphausia superba* (•) *and Euphausia crystallorophias* (▪). Interspecies and spatial variation of (A) 18:1ω9/18:1ω7 and (B) PUFA/SFA with $\delta^{15}N$ values. The two dotted lines indicate the standard range (minimum to maximum) of a carnivore (Cripps and Atkinson, 2000; Falk-Petersen et al., 2000; Virtue et al., 2000). OS: open sea; CS: continental shelf; P: middle of polynya; GE: polynya near glacial edge.

Table 5
Comparisons of the specific FA ratios (18:1ω9/18:1ω7 and PUFA/SFA) and $\delta^{15}N$ values of the adult *Euphausia superba* and *Euphausia crystallorophias* from other regions in Antarctica.

	E. superba					*E. crystallorophias*				
	South Georgia & Scotia Sea (summer)[a]	Lazarev Sea (autumn)[b]	Ross Sea (summer)[c]	Marguerite Bay (winter)[d]	Amundsen Sea (summer)[e]	Adelie Land (summer)[f]	Ross Sea (summer)[c]	Marguerite Bay (winter)[d]	Weddell Sea (summer)[g]	Amundsen Sea (summer)[e]
18:1ω9/18:1ω7	1.6 ± 0.3	–	–	1.7 ± 0.1	1.1 ± 0.3	–	–	2.4 ± 0.0	3.1	2.9 ± 0.7
PUFA/SFA	1.9 ± 0.6	–	0.6	0.5	0.8 ± 0.3	–	1.8	0.7	1.3	1.3 ± 0.6
$\delta^{15}N$	4.1 ± 1.1	3.6	–	–	5.1 ± 0.3	6.8 ± 0.7	–	–	–	8.5 ± 0.4

–: no data.

[a] Schmidt et al. (2006).
[b] Schmidt et al. (2003).
[c] Bottino (1974).
[d] Ju and Harvey, (2004).
[e] This study.
[f] Cherel (2008).
[g] Kattner and Hagen (1998).

Amundsen Sea ecosystem and also enable predictions of ecosystem variability under climate change.

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