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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