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Aspects of krill growth and condition during late winter-early spring off East Antarctica (110–130°E)

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ABSTRACT

Antarctic krill, *Euphausia superba*, is a keystone species in the Southern Ocean. However, information on growth, diet and condition during winter and early spring is limited, hampering our understanding of these fundamental biological parameters at this important period in their lifecycle. Our study assessed diet and condition of larval and postlarval krill collected from open water and below the ice off East Antarctica (110–130°E) in September/October 2007. Condition was assessed using lipid content, growth rates and digestive gland size; feeding history was assessed using fatty acid profiles and stomach content analysis; and a 207-day starvation study investigated the response of krill to long-term food deprivation. Potential food items (*Calanus propinquus* and sea-ice biota) were analysed for lipid and fatty acid composition to compare with krill samples. Krill were found to be in good condition, with mean growth rate of 0.95% per moult for postlarvae and 14.79% for larvae, and mean lipid content of 24.1% for postlarvae and 6.6% for larvae. Fatty acid profiles and stomach content analysis revealed two main feeding strategies - krill below the ice were feeding mostly on sea-ice diatoms, while those in open water were ingesting copepods and detritus. Krill below the ice had larger digestive glands than those in open water. Furciliae fatty acid profiles indicated a diet of heterotrophic flagellates and/or detritus. Postlarval krill survived 207 days of food deprivation by using body protein and lipid reserves for energy. In contrast, krill furciliae were severely depleted after just 5 days of food deprivation, indicating that they must feed continually at this time of year. Krill, copepods and sea-ice biota were all low in polyunsaturated fatty acids, indicating that krill must rely on later spring phytoplankton blooms to obtain these essential nutrients required for reproduction.

1. Introduction

Antarctic krill, *Euphausia superba*, is an important component of the Southern Ocean ecosystem, acting as a major link between primary production and the higher-order predators (Laws, 1985). It is one of the most abundant multicellular species on earth, with an estimated biomass of 500 million tonnes, and is currently the target of the largest fishery in the Southern Ocean (Croxall and Nicol, 2004). Despite the ecological and commercial importance of this species, several aspects of its life history remain poorly understood – one such area is the overwintering biology of krill.

The Southern Ocean is subject to large fluctuations in primary productivity, with major phytoplankton blooms occurring in spring and summer, and very low phytoplankton concentrations in autumn and winter. Southern Ocean organisms thus require special adaptations to enable survival in long periods of low food availability.

Krill have often been observed below the sea ice in winter and early spring, and it has been suggested that they may utilise sea-ice algal communities as an alternative food source at this time of year (Daly, 1990; Flores et al., 2009; Marschall, 1988; Stretch et al., 1988). Detritus and heterotrophic organisms such as copepods may also be utilised as an additional source of energy (Daly and Macaulay, 1991; Huntley et al., 1994; Nishino and Kawamura, 1994; Pakhomov et al., 1997). Non-feeding overwintering strategies may include the use of stored lipid (Hagen et al., 1996; Quetin and Ross, 1991); shrinkage and protein catabolism (Ikeda and Dixon, 1982; Quetin and Ross, 1991); and reduction of metabolic rates (Kawaguchi et al., 1986; Quetin and Ross, 1991; Torres et al., 1994). While krill are known to be capable of using each of these strategies, the relative importance of each in their natural environment is yet to be determined.

Understanding the overwintering of krill is important since it represents a vital stage of the life cycle of this species. A close

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correlation has been observed between winter sea-ice extent and krill recruitment (Kawaguchi and Satake, 1994; Quetin and Ross, 2001; Siegel and Loeb, 1995), suggesting that winter sea ice plays a central role in krill overwintering. This may be as a food source for larvae surviving their first winter (Daly and Macaulay, 1991; Frazer et al., 2002; Hamner et al., 1989), as an important food source for adults prior to the reproductive season (Daly and Macaulay, 1991; Quetin and Ross, 2001), and/or as a physical shelter from predators (Daly and Macaulay, 1991; Frazer et al., 2002; Hamner et al., 1989). The role of sea-ice biota in Antarctic food-webs is poorly understood, but recent studies suggest it may be far more significant than previously thought (van Franeker et al., 1997).

The objectives of this study were: 1) to investigate the availability and nutritional quality of potential food sources for krill within the sea-ice zone in the key transitional period of late winter/early spring; 2) to study the diet and condition of krill collected within the sea-ice zone at this time of year; and 3) to investigate to capacity of krill to withstand long-term food deprivation.

The study used a combination of instantaneous growth rate measurements, morphological measurements and microscopy, as well as complementary biochemical methods such as signature lipids. Biochemical methods offer the advantage of providing sample resolution where conventional methods are unable to provide specific information.

2. Materials and methods

2.1. Sampling

Sampling was conducted as part of the Sea Ice Physics and Ecosystems eXperiment (SIPEX) in September-October 2007 off East Antarctica (110–130°E). Ice core samples were collected from a number of stations within the sea-ice zone, beginning at 64° 13.78′S 127° 56.82′E for station 1 on 11 September 2007 and continuing in a westerly direction until station 14, at 64° 19.00′S 116° 49.00′E on 6 October 2007 (Table 1). Ice-core samples were collected using a 0.09 m-diameter SIPRE corer. An umbrella net was deployed below the ice at each station to collect mesozooplankton for use in other studies, and a Surface and Under-Ice Trawl (SUIT; developed by the Dutch research team of Dr. Jan van Franeker at IMARES (Wageningen UR)) was used to collect krill from below the ice (van Franeker et al., 2009). In open-water areas, krill were collected using a Rectangular Midwater Trawl (RMT 8+1) from the upper 200 m of the water column. Krill furciliae V and VI larvae were collected from directly under the ice as ice cores were retrieved at station 1. Postlarval krill were collected from an open-water area using the RMT 8 on 20 September 2007 (65° 28′S, 124° 40′E). Samples of one of the dominant copepods in the area, *Calanus propinquus*, were collected opportunistically throughout the survey.

Table 1
Dates and positions of ice stations sampled during the SIPEX survey.

Ice Station Number	Date (UTC)	Latitude	Longitude
1	11/09/2007	64° 13.78′S	127° 06.82′E
2	12/09/2007	64° 29.00′S	128° 05.00′E
3	14/09/2007	64° 24.00′S	127° 07.00′E
5	18/09/2007	65° 31.47′S	124° 45.12′E
7	22/09/2007	65° 34.00′S	121° 31.00′E
8	25/09/2007	65° 33.00′S	118° 52.00′E
10	29/09/2007	64° 57.00′S	119° 08.00′E
11	03/10/2007	65° 01.00′S	117° 32.00′E
13	06/10/2007	64° 44.00′S	116° 49.00′E
14	06/10/2007	64° 19.00′S	116° 49.00′E

2.2. Microscopy

Several ice core and umbrella net samples were microscopically examined to provide a qualitative indication of species composition of the under-ice community. Several krill stomachs were also examined to determine which food items were being utilised.

2.3. Digestive gland size

At each sampling site the digestive gland, carapace length and total length (Standard length 1 (Mauchline, 1980) measured from the anterior tip of the rostrum to the distal end of the telson) of krill were measured using digital callipers. The size of the digestive gland (relative to carapace length) was calculated for each individual to provide an indication of its recent feeding history. Digestive gland data collected during this voyage were compared with data for samples collected in January-February 2006 as part of the Baseline Research on Oceanography, Krill and the Environment – West (BROKE-West) voyage (30-80°E) (Virtue et al., 2010).

2.4. Instantaneous growth rates

Postlarval (juvenile to adult; n=882) and larval (n=43) krill were used for a series of onboard growth experiments using the instantaneous growth rate (IGR) method (as first described by Quetin and Ross (1991)). Immediately after capture, live krill were placed in individual 250 ml jars within a large flow-through tank supplied with surface seawater. The tanks were located in a cold (0.5 °C) and mostly darkened room. Jars were checked for moults at 24 hour intervals over a period of five days. Each day, any animals found to have moulted were collected and frozen in liquid nitrogen along with their discarded moults.

Growth increments (% growth per moult) were calculated by measuring the length of both left and right uropod exopodites on the fresh and discarded exoskeletons using a Leica DFC 400 digital microscope camera and LAC Version 3.1 image analysis software. Growth increments (GI) were calculated using the formula:

$$GI = 100 \times \frac{((LU-LM)/LM)+((RU-RM)/RM)}{2}$$

where LU is the total length of the animal's left uropod, LM is the length of the moulted left uropod, RU is the length of the animal's right uropod, and RM is the length of the moulted right uropod. Where one uropod was damaged, GI was calculated based on the undamaged side only. If both left and right uropods were damaged, the animal was excluded from the study.

2.5. Starvation experiments

A number of larval and postlarval (subadult and/or adult stage) krill were maintained under low-nutrient conditions to study their capacity to withstand long-term food deprivation. Krill were maintained using a surface water flow-through system as used for the IGR experiments, with no additional food provided. Very low nutrient levels, as determined by chlorophyll *a* levels, were found in the surface waters at this time of year.

On passing the polar front on the return trip to Hobart, the flow-through system was turned off and water was manually changed twice daily with chilled seawater (below 2.5 °C). All seawater collected after this point was treated using a biofiltration system with foam-fractionator to remove organic materials and ammonia. On arrival in Hobart after 27 days, krill were transferred to facilities at the Australian Antarctic Division krill aquarium in Kingston, Tasmania.

Three krill were sampled on each of days 5, 12, 20, 26 and 47, and the remaining 14 krill were collected on day 207 when the