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Physiology, growth, and development of larval krill *Euphausia superba* in autumn and winter in the Lazarev Sea, Antarctica

Bettina Meyer,[a,*] Veronica Fuentes,[b,1] Citlali Guerra,[a] Katrin Schmidt,[c] Angus Atkinson,[c] Susanne Spahic,[a] Boris Cisewski,[d] Ulrich Freier,[a] Alejandro Olariaga,[b,1] and Ulrich Bathmann[a]

[a] Alfred Wegener Institute for Polar and Marine Research, Scientific Division Polar Biological Oceanography, Bremerhaven, Germany
[b] University of Buenos Aires, Department of Biodiversity and Experimental Biology, Buenos Aires, Argentina
[c] British Antarctic Survey, Natural Environment Research Council, Cambridge, United Kingdom
[d] Institute of Environmental Physics, Department of Oceanography, University Bremen, Germany

Abstract

The physiological condition of larval Antarctic krill was investigated during austral autumn 2004 and winter 2006 in the Lazarev Sea. The condition of larvae was quantified in both seasons by determining their body length (BL), dry weight (DW), elemental and biochemical composition, stomach content analysis, and rates of metabolism and growth. Overall the larvae in autumn were in better condition under the ice than in open water, and for those under the ice, condition decreased from autumn to winter. Thus, growth rates of furcilia larvae in open water in autumn were similar to winter values under the ice (mean, 0.008 mm d^{-1}), whereas autumn under-ice values were higher (0.015 mm d^{-1}). Equivalent larval stages in winter had up to 30% shorter BL and 70% lower DW than in autumn. Mean respiration rates of winter larvae were 43% lower than of autumn larvae. However, their ammonium excretion rates doubled in winter from 0.03 to 0.06 μg NH_4 DW^{-1} h^{-1}, resulting in mean O : N ratios of 46 in autumn and 15 in winter. Thus, differing metabolic substrates were used between autumn and winter, which supports a degree of flexibility for overwintering of larval krill. The larvae were eating small copepods (*Oithona* spp.) and protozoans, as well as autotrophic food under the ice. The interplay between under-ice topography, apparent current speed under sea ice, and the swimming ability of larval krill is probably critical to whether larval krill can maintain position and exploit suitable feeding areas under the ice.

Antarctic krill (*Euphausia superba*) play a central role in the Southern Ocean food web, both as grazers and as prey for a wide range of fish, penguins, seals, and whales. The total biomass of krill is enormous, with estimates ranging from 100 to 500 million metric tons (Siegel 2005). The species is important biogeochemically (Le Fèvre et al. 1998) and supports a valuable commercial fishery, an industry poised to expand rapidly in the near future (Kawaguchi et al. 2007). Over the past 30 yr, the abundance of krill across its main population center, the southwest Atlantic sector of the Southern Ocean, has declined (Loeb et al. 1997; Atkinson et al. 2004), but the reasons behind this decline are still unclear. However, a range of correlative studies shows that recruitment success, and hence population size, of krill are linked to winter sea ice cover, with low ice years related to poor recruitment or low abundance the following summer (Loeb et al. 1997; Quetin et al. 2003; Atkinson et al. 2004).

Although overwintering conditions are clearly important for krill, little is yet known about certain phases of the krill life cycle. Larval krill appear during summer, develop during Antarctic winter, and recruit to the postlarval population during the following spring. Therefore, recruitment success depends both on how potential recruits enter winter (reflecting reproductive output and growth and survivorship of larvae during summer and autumn) and on larval growth and survival during their first winter (Siegel 2005; Quetin et al. 2007). The logistical and practical difficulties of working in winter sea ice have enabled only very few studies of larval krill physiology and development in the dark season so far (Frazer et al. 2002*a*; Daly 2004; Ross et al. 2004).

These studies suggest that larval and postlarval krill have different overwintering strategies. Adult krill employ a suite of overwintering mechanisms that provide considerable flexibility in their response to winter conditions. Some studies suggest that they continue to feed but use alternative food sources to phytoplankton (Huntley et al. 1994). They are able to survive for longer than 200 d (i.e., the entire winter) without food by using their lipid reserves and reducing their metabolic rates (Kawagushi et al. 1986; Quetin and Ross 1991; Torres et al. 1994), and it is possible that they shrink during long starvation periods in the field (Quetin and Ross 1991). Adult krill reduce their metabolic rates by up to 50% in autumn and winter compared with summer values (Atkinson et al. 2002), and recently, research has shown that these seasonal physiological changes are triggered by the Antarctic light regime (Teschke et al. 2007).

In contrast to adults, krill larvae have low lipid reserves (Hagen et al. 2001) and cannot tolerate long starvation periods (Meyer and Oettl 2005). Moreover, they are unable to cover their metabolic demands from the autotrophic material available in the water column, making them dependent on the biota associated within and below the sea ice for survival and development (Daly 1990; Ross and

* Corresponding author: bettina.meyer@awi.de

[1] Present address: Institut de Ciéncies del Mar (CSIC), Barcelona, Spain

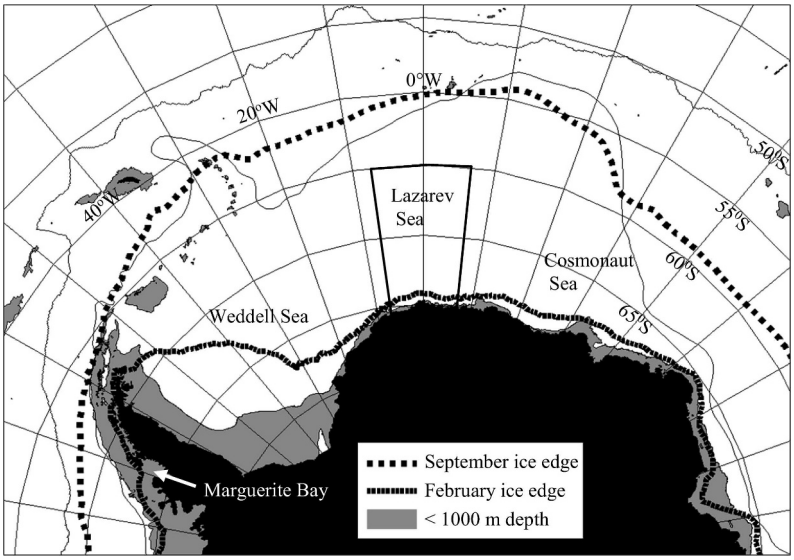

Fig. 1. Study area in the Lazarev Sea (bold box) in relation to the Atlantic and Western Indian sectors, where most other krill larval overwintering studies have been conducted. The summer (February) and winter (September) ice edges are based on the National Oceanic and Atmospheric Administration (NOAA) ice data from 1979 to 2006, having excluded outlying positions because of icebergs and other reasons.

Quetin 1991; Meyer et al. 2002). Larval respiration rates seem to be reduced in winter (Frazer et al. 2002*a*), but not in autumn when compared with summer values (Meyer et al. 2002, 2003). In winter, freshly caught larvae grew more slowly than those caught in autumn (Daly 2004), and even shrinkage is reported during winter (Ross and Quetin 1991; Quetin et al. 2003; Ross et al. 2004).

Most studies on the overwintering of krill larvae have been in the vicinity of the Antarctic Peninsula. The German Lazarev Sea Krill Study (LAKRIS) aimed to broaden the geographical coverage of information about this key life cycle stage (Fig. 1). The Lazarev Sea is located on the eastern fringe of an area of high krill abundance stretching from the western Antarctic Peninsula to the Greenwich Meridian (Marr 1962; Atkinson et al. 2008). It is characterized by Maud Rise, a seamount of more than 200 km in diameter that extends from a depth of 5000 m to 1600 m below the surface, with its top located at 65.1°S, 2.51°E (Muench et al. 2001). This region is typified by warm deep water masses (Schröder and Fahrbach 1999), resulting in a higher productivity than adjacent waters (Spiridonov et al. 1996) and suggesting favorable spawning conditions for krill (Hoffmann and Hüsrevoğlu 2003). The continental shelf is narrow, and the majority of the krill lives in an area of more than 4000 m depth. The westward flow of water masses in the Lazarev Sea (Schröder and Fahrbach 1999) might enable new recruits to enter the Weddell Gyre. It has been hypothesized that the Lazarev Sea could be the seeding ground of the large population observed at the northern outflow of the Weddell Gyre. Only a few historical data on krill exist from this area, and these are mainly on adults (Makarov and Menshenina 1992; Atkinson et al. 2002; Schmidt et al. 2003), with data on larvae almost completely lacking (Meyer et al. 2002).

This study provided the rare opportunity to investigate the physiological state of larval krill in an under-researched but potentially important region for krill in two critical seasons during its ontogenesis: the Antarctic autumn and winter. Such data are needed for better understanding of larval survival in winter and of environmental parameters influencing recruitment success. The LAKRIS project forms the German contribution to the Southern Ocean–Global Ocean Ecosystem Dynamic (SO-GLOBEC) program.

Methods

Surveys—The expeditions in austral autumn (ANTXXI-4, 27 March to 06 May 2004) and winter (ANTXXIII-6, 11 June to 27 August 2006) were carried out on board RV *Polarstern* along four (autumn) and three (winter) parallel meridional transects that extended from the continental coast into the oceanic waters of the Lazarev Sea. The station grids of both cruises are given in Fig. 2a,b. In autumn, the transects were located along 6°, 4°, 2°W, and 0° and from 64° to 70°S (Fig. 2a). During the winter cruise, sampling was performed along 3°E, 0°, 3°W and from 60° to 70°S (Fig. 2b).

Sampling of larval krill—In autumn, larvae were collected with the use of a 200-μm mesh, 0.5-m diameter Bongo net equipped with a 5-liter closed cod end, which was towed vertically from 150 m to the surface at 0.3 m s^{-1}. In addition, a 200-μm mesh net of 0.3 m diameter and a 1-liter cod end was used and towed vertically by hand over the side of the ship from 50 m depth to the surface. The hand net was mainly used in ice-covered regions. In winter, larvae were collected both with the hand net, as above, and by scuba divers. Diving was performed from a zodiac during

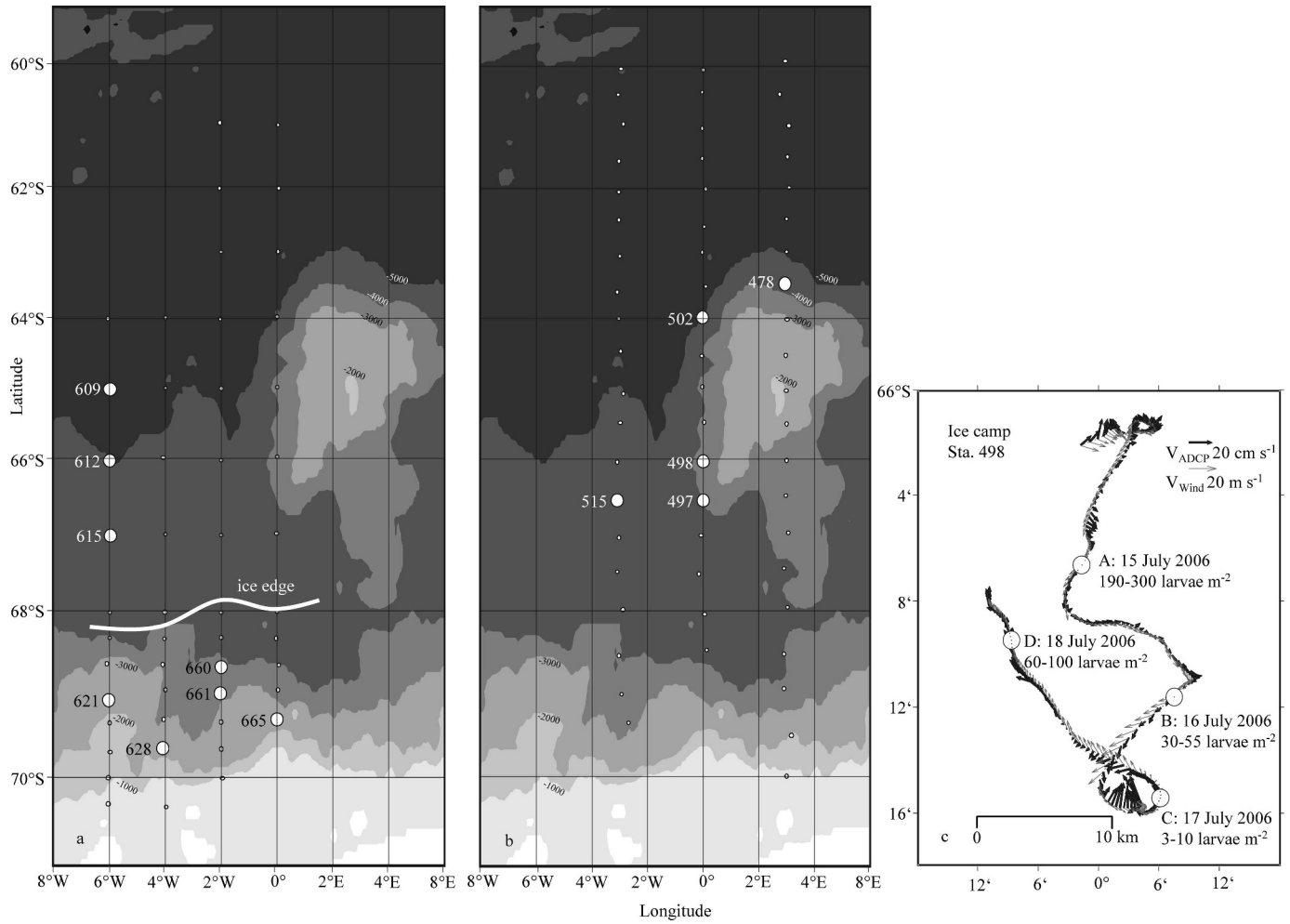

Fig. 2. (a) Study area with station grid and ice edge on the autumn cruise ANTXXI-4 (27 March–06 May 2004). (b) Study area with station grid on the winter cruise ANTXXIII-6 (11 June–27 August 2006). Highlighted stations in panels a and b are the positions at which larvae were caught. (c) Drift of the ice camp at Sta. 498 with sampling positions of larval krill (A–D), day of sampling, and abundance of larvae.

station work and during a 5-d ice camp. The ice camp was set up at 66°06′S and 00°00′W 500 m from the ship on a solid 75-cm-thick ice floe of a few kilometers in diameter. The drift course of the ice floe, sampling dates and positions, and current speed are given in Fig. 2c. Under-ice observations of larval krill by divers were made along 10–40-m transects with an Olympus C 8080 WZ in an Ikelite underwater housing and equipped with an Ikelite flash and a Sony Digital Handycam video system. A detailed description of the dive camp and the general diving procedure is given in Freier et al. (2008).

Larvae were sampled under the ice by divers with the use of a motor pump system called MAnguera SubMArina (MASMA) designed by Alejandro Olariaga (Fig. 3). During ice camp work, the MASMA was located near the dive hole, whereas it was located on an inflatable boat during station work and towed by the divers' zodiac. The MASMA system consists of a motor-driven centrifugal pump (maximal flow rate 0.4 m^3 min^{-1}) connected to a plankton filtration system. The filtration is carried out through a zooplankton net (200 μm mesh size) with a 2-liter cod end located inside the airtight container and placed upstream of the centrifugal pump (Fig. 3). High volumes of water were transported to the container through a 5-cm-diameter tube (maximum 50 m length). The animals were sampled with a flow rate of 0.1 m^3 min^{-1} and concentrated in the cod end before the water reached the pump. They were in very good condition for physiological experiments. Handling of the plastic tube by the divers was comfortable because it was almost weightless.

Subsampling of freshly caught larvae—One subsample of freshly caught larvae were staged according to Fraser (1936) and measured under the stereomicroscope before being frozen at −80°C for analysis of dry weight (DW), elemental (carbon [C], nitrogen [N]) and biochemical composition (total body lipid and protein), as well as stomach and gut contents. The body length (BL) of larvae was measured from the front of the eyes to the tip of the telson. Another subsample was taken for measurement of larval growth and metabolic rate (oxygen uptake and ammonium production rates).

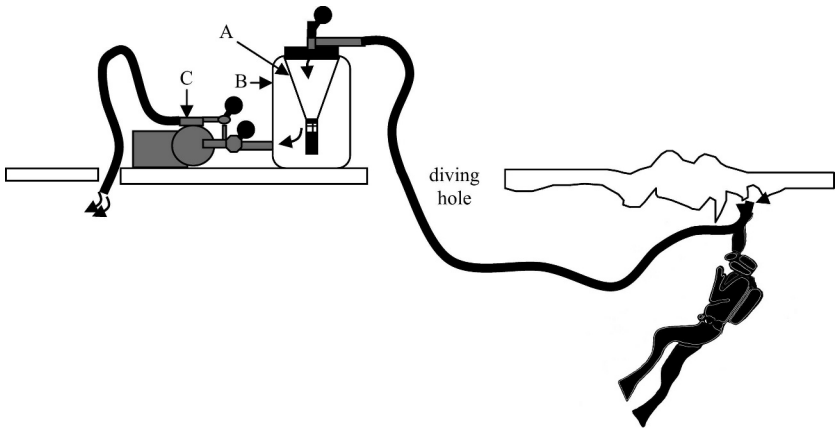

Fig. 3. Zooplankton pump MASMA (MAnguera SubMArina) located on an ice floe. (A) Zooplankton net (200 μm mesh size) with 2-liter cod end, (B) airtight container, and (C) centrifugal pump.

Analysis of DW, body C, N, protein, and lipid content—Individual larvae were freeze dried for 24 h and weighed on a Mettler UM 3 microbalance for determination of individual DW. Elemental (C and N) and biochemical body composition (protein and lipid) were analyzed from bulked samples, comprising at least 10–15 mg DW of krill homogenate. This amount represents a minimum of 70 calyptopis III (CIII) in autumn to 170 CIII in winter; 40 furcilia I (FI, in autumn) to 100 FI (winter); 20 FII (autumn) to 50 FII (winter); 10 FIII (autumn) to 30 FIII (winter); and 25 FIV, 20 FV, and 10 FVI. The individual dried larvae were pooled and homogenized in 1 mL of Milli-Q water by sonication on an ice bath, shock frozen by dipping the tube in liquid nitrogen and then stored at -80°C for further analyses of body C, N, protein, and lipid content.

For C and N analyses, 0.2–0.5 mg of larva powder was used and analyzed as described elsewhere (Meyer et al. 2002, 2003). Total body protein was measured by incubating 0.8–1 mg of larva powder in 1 mL of 1 mol L^{-1} NaOH for 2 h at 60°C. After centrifugation at a relative centrifugal force of 2,000 $\times$ g for 5 min, the supernatant was used for determination of protein according to Lowry et al. (1951), with bovine serum albumin as a standard, in a microplate reader. Lipids were extracted from 10–15 mg of larva powder in dichloromethane and methanol (2 : 1, v/v), from which the content of total lipids was determined gravimetrically (Hagen 2000).

Measurements of metabolic rate—The rates of oxygen consumption and ammonium production were measured by incubating 100 CIII, 40 FI, 15 FIII, 10 FIV, 5 FV, or 5 FVI larvae in 1-liter sealed glass bottles with filtered seawater (0.2 μm pore size). Each experiment comprised three to four bottles with larval krill, and three bottles without krill served as controls. All experimental bottles were incubated for 15–24 h in flow-through tanks at in situ water temperature. After incubation, subsampling was done by rapidly inserting a glass tube attached to a silicon tube and siphoning the mixed contents of the flask into 50-mL Winkler bottles for oxygen determination and into 15-mL Falken tubes for analysis of ammonium. For both oxygen and ammonium determinations, three replicate subsamples were used for each experimental bottle. Oxygen concentration was determined, after immediate fixing for Winkler titrations, with a 716 DWS Titrino (METHROM) as described previously (Meyer et al. 2002). The decrease in oxygen concentration in the experiments was $<10\%$, which is believed not to affect larval respiration (Jonson et al. 1984). Ammonium was analyzed photometrically by the phenol–hypochlorite method according to Solorzano (1969). At each sampling station we performed at least two (autumn) or three (winter) experiments for measuring metabolic rates of larval krill.

Determination of growth rate and intermolt period—Growth rates were measured following the instantaneous growth rate (IGR) method first described by Quetin and Ross (1991) for adult krill and by Ross and Quetin (1991) for larvae. In situ growth rates were determined by randomly sorting 100–400 freshly caught krill larvae and incubating the animals individually in 150-mL jars with natural seawater at in situ sea surface temperature for 3 d. Jars were checked every 12 h for molts and dead animals. Molted larvae and their molts were separated. The daily molting frequency f was calculated as

$$f = N_m / N_i d \quad (1)$$

where d is the duration of the experiment (days), N_m is the number that molted in this time, and N_i is the total number incubated at the start minus the number that died during the experiment. The intermolt period (IMP) is then the inverse of the molting frequency.

The growth increment on molting, GI (% growth IMP^{-1}) was calculated from lengths of the right uropod (when damaged, the left uropod was used) or telson length (when both uropods were damaged) of the newly molted larva, L_a, and the respective premolt length, as measured on the molt L_m (Quetin et al. 2003):

$$GI = 100(L_a - L_m)/L_m \quad (2)$$

The change in BL over the intermolt period was determined from a linear regression of BL of uropod length,

UL (mm), or telson length, TL (mm), of the postmolt krill. Length measurements from all experiments in both years were pooled because of insignificant differences between regressions of seasons and are as follows:

$$\mathrm{BL} = 8.07\mathrm{UL} + 0.81 \quad r^2 = 0.95, \quad n = 137, \quad p < 0.001 \tag{3}$$

$$\mathrm{BL} = 4.82\mathrm{TL} + 0.02 \quad r^2 = 0.94, \quad n = 137, \quad p < 0.001 \tag{4}$$

The growth (mm d^{-1}) was then calculated as the difference between the premolt and postmolt body lengths (BLs) divided by the IMP in days (Daly 2004).

Microscopic analyses of stomach and gut contents—Wet weight and BL of the larvae were measured immediately after removal from the freezer and thawing and blotting dry any excess water. Because of the small size of the larvae, three individuals of the same developmental stage were pooled for each microscopic analysis. The stomach and gut of the larvae were dissected under a stereomicroscope and emptied into a small amount of water. The sample was gently mixed with the use of a whirly-mixer, transferred into an Utermöhl counting receptacle, and allowed to settle for at least 2 h. The sample was analyzed on the same day because no preservative was added. Rare items such as large diatoms, tintinnids, thecate dinoflagellates, or copepod remains were counted first by scanning the complete receptacles at ×200 magnification. Subsequently, common small diatoms and other thecate flagellates were enumerated on two perpendicular scans across the whole diameter of the receptacle at ×200 magnification. The dimensions of different food items were measured for each station, and their biovolumes were calculated following Archer et al. (1996) and Kang et al. (2001) for diatoms and dinoflagellates and according to Buck et al. (1992) and Thompson (2001) for tintinnids. The volumes of copepods were calculated from the relationship between mandible width and prosome length (*see* eq. 1 in Karlson and Båmstedt 1994) and the relationship between prosome length and copepod volume, as in Mauchline (1998).

Analysis of surface Chl a *concentration*—In autumn, in open water areas, surface chlorophyll *a* (Chl *a*) samples were taken at 5 m depth with a rosette sampler fitted with 24 Niskin bottles of 12 liters, whereas in ice-covered regions, Chl *a* samples were collected with a bucket over the side of the ship between ice floes. In winter, Chl *a* samples were taken a few centimeters under sea ice by scuba divers. Two liters of seawater were filtered onto glass microfiber filters (GF/F, Whatman, 25 mm diameter) and passively extracted in 10 mL of 90% acetone at −20°C in the dark for at least 24 h. Chlorophyll fluorescence was then measured with a Turner 7000D fluorometer.

Statistical analysis—Before statistical analyses, data were tested for normality. Nonnormal data were square root–transformed to achieve a normal distribution (Zarr 1999). For testing of significant differences between data groups, a one-way ANOVA (model I) was calculated, and the Holm–Sidak post hoc test was applied for multiple comparisons. These tests were performed by SigmaStat 3.0 (SPSS). A Type I linear regression was used for all correlations presented, and the differences between regression lines were tested according to Zarr (1999) with the use of GraphPad Prism 4. Michaelis–Menten kinetics were calculated with SigmaPlot 8.0 (SPSS). The significance level for all tests was set at $p < 0.05$. Data are presented two ways: Data not normally distributed are expressed as median with minimum and maximum values. Normally distributed data are expressed as mean ± standard deviation.

Results

Environmental conditions—During the autumn cruise, sea ice formation had already started, and the ice edge was located at 68°S (Fig. 2a). Mean seawater temperature in the upper 50 m of the study area was −1.4 ± 0.4°C. The Chl *a* concentration in the upper 5 m of the water column was highly variable, ranging from very low (0.07 μg Chl *a* L^{-1}) in open-water regions (north of 68°S) to 3.02 μg Chl *a* L^{-1} at some locations in the ice-covered regions (south of 68°S). At such high Chl *a* concentrations, larval krill can reach maximum carbon ration and growth (Ross et al. 2000; Meyer et al. 2002). Numerous dark brown-colored ice floes were observed in the ice-covered region. The high pelagic Chl *a* concentrations could have resulted from continuous movements and rubbing of these ice floes caused by the wind and currents, which abraded and released phytoplankton into the ocean.

During the winter cruise, mean seawater temperature in the upper 50 m was −1.8 ± 0.1°C. Chl *a* concentration was very low, ranging from 0.01 to 0.04 μg L^{-1}, and the whole study area, from 60°S to the Antarctic continent at 70°S, was covered by sea ice.

Stage composition and BL—Figure 4 summarizes the stage and length frequency distributions between seasons and regions (according to open water vs. ice in autumn, and among the various ice conditions in winter). In autumn, in areas of open water (stations 609, 612, 615), stage composition ranged from CII to FII, whereas the stage composition at stations in the ice-covered region of the Lazarev Sea (south of 68°S) ranged from CIII to FIII (Fig. 4). The BLs of equivalent larval stages in ice-covered areas were significantly larger ($p < 0.001$) than those from open-water stations. Also, between seasons, the BLs of equivalent larval stages were significantly higher ($p < 0.05$) in autumn than in winter (Table 1; Fig. 4).

Dive observations—During the winter expedition, larvae were caught at eight stations (478, 497, 498A, 498B, 498C, 498D; and at the ice camp, 502 and 515). Young stages (<FII) were present only at one station (478). The stage compositions at station (Sta.) 478 ranged from CIII to FV, but larvae of stages CIII and FI were in extremely weak condition, as judged from their slow movement and high mortality. In these stages, the mortality rate was 87%

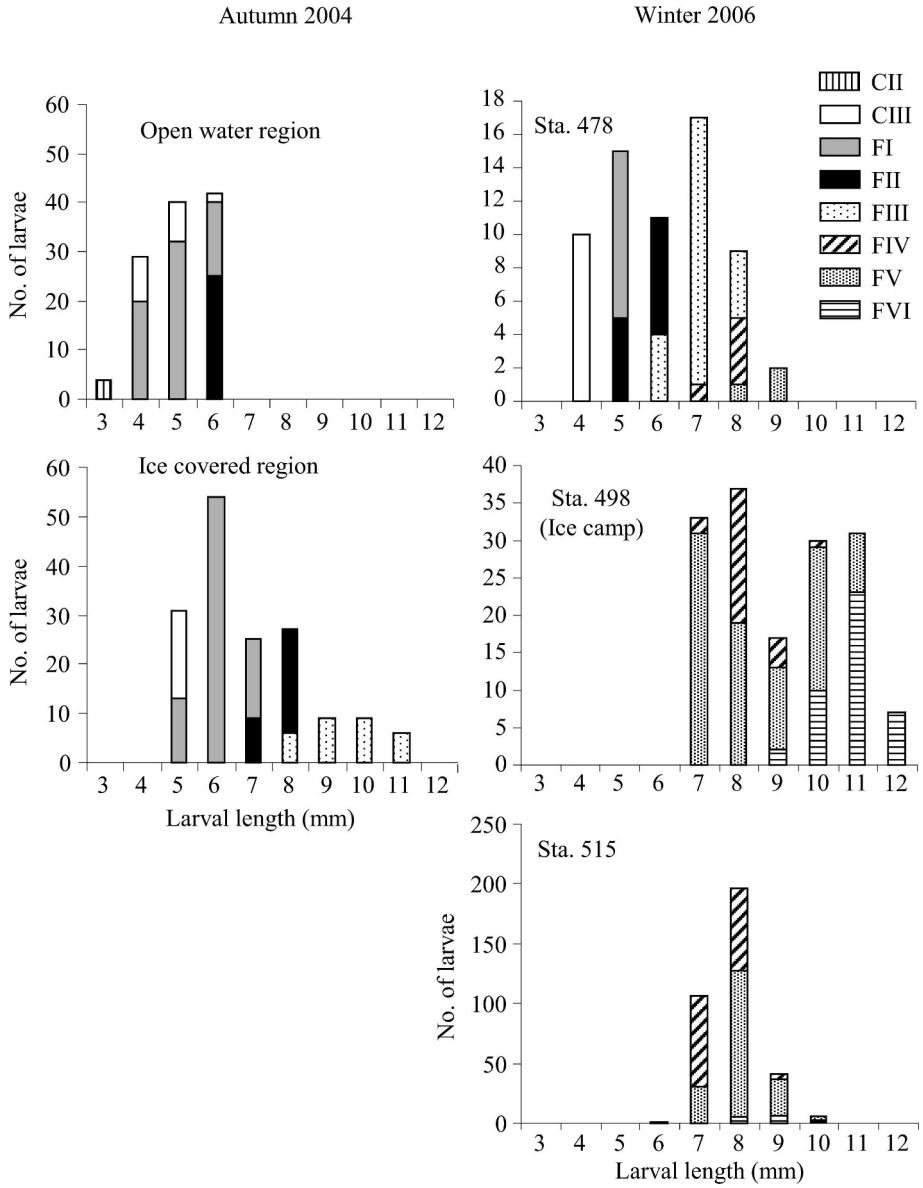

Fig. 4. *Euphausia superba.* Stage composition and length frequency of randomly sampled larval krill from open-water and ice-covered regions during autumn and from various stations during winter in the Lazarev Sea.

during the first 24 h of the IGR experiment. Sufficient numbers of larvae to perform a complete set of analyses for a comprehensive comparison of larval condition between locations were only found during ice camp work (Stas. 498A, B, D) and at Sta. 515. The stage compositions of larvae from both stations were comparable and ranged from FIV to FVI (Fig. 4). Equivalent larval stages at Sta. 515 showed a significantly ($p < 0.001$) lower BL than larvae from the ice camp (Fig. 4).

During ice camp work, abundance of larvae varied by two orders of magnitude. The highest number of individuals (ind.) occurred during the first diving day (A: 190–300 ind. m^{-2}; Fig. 2c), with much fewer on the second day (B: 30–55 ind. m^{-2}). The lowest abundance was estimated on the third day (C: 3–10 ind. m^{-2}), after which numbers increased again on the last day (D: 60–100 ind. m^{-2}). The under-ice topography of the ice floe around the dive hole was mainly smooth, with some hollows, ice dents, and 2-m-long ridges. Larval krill were observed on all dives close to the undersurface of sea ice in areas sheltered from the current (hollows, dents, and ridges; Fig. 5a). In the upper water column, from the undersurface of sea ice down to 10–15 m depth, the larvae were drifting passively with the current as shown schematically in Fig. 5a. The highest measured current speed in the water column was 27.5 cm s^{-1} (mean, 8.1 cm s^{-1}), with no apparent vertical gradient in the current speed in the upper 15 m. In the sheltered refuges, larvae held their positions against the current by pleopod movement and were located a few centimeters from the overlying sea ice. They were never

Table 1. *Euphausia superba*. Body length (BL, mm) and dry weight (DW, mg) of larval stages from stations in open water and with ice in autumn and in the Lazarev Sea in winter. Data are given as median with the range in parentheses. Larval stage: C, calyptopis; F, furcilia. *n,* No. of replicates.

Larval stage	Open water		Ice cover	
		Autumn 2004		
CII	BL: 3.03 (2.97–3.14)	n=3		
	DW: 0.06 (0.05–0.06)	n=3		
CIII	BL: 4.35 (2.97–5.65)	n=23	BL: 4.80 (4.54–5.12)	n=18
	DW: 0.05 (0.03–0.08)	n=23	DW: 0.21 (0.18–0.28)	n=18
FI	BL: 4.88 (4.04–5.98)	n=67	BL: 6.17 (4.81–6.79)	n=83
	DW: 0.15 (0.08–0.25)	n=67	DW: 0.35 (0.17–0.90)	n=83
FII	BL: 5.78 (5.68–5.99)	n=25	BL: 7.73 (6.54–8.36)	n=30
	DW: 0.16 (0.12–0.22)	n=25	DW 0.61 (0.43–0.83)	n=30
FIII			BL: 9.07 (7.97–10.62)	n=30
			DW: 0.87 (0.38–1.19)	n=30
		Winter 2006		
CIII			BL: 3.84 (3.59–4.38)	n=10
			DW: 0.06 (0.04–0.07)	n=10
FI			BL: 4.89 (4.55–5.43)	n=10
			DW: 0.10 (0.07–0.19)	n=10
FII			BL: 5.50 (4.57–6.01)	n=12
			DW: 0.19 (0.17–0.24)	n=12
FIII			BL: 7.00 (5.94–8.30)	n=24
			DW: 0.35 (0.21–0.52)	n=24
FIV			BL: 7.50 (6.00–9.85)	n=177
			DW: 0.39 (0.24–0.85),	n=177
FV			BL: 8.00 (6.70–11.23)	n=243
			DW: 0.45 (0.26–1.39)	n=243
FVI			BL: 10.77 (8.00–12.31)	n=52
			DW: 1.16 (0.44–2.00)	n=52

directly attached to the undersurfaces of sea ice (Fig. 5a) and changed their positions in the refuges according to the direction of the current, suggesting that they were not feeding at the under-ice surface. During darkness, the larvae remained in their protected refuges. They were lured out of their protective areas by the head torches of divers, however, with the consequence that the current moved them away. Numerous ctenophores of the species *Callianira antarctica* were also present in the water column and near the undersurface of sea ice. There was no obvious coloration of the ice. Despite that, melted ice pieces from the larvae's location contained a rich ice community of large diatoms, such as *Fragilariopsis cylindrus, Rhizosolenia* sp., *Corethron* sp., *Chaetoceros* sp., and tintinnids.

At Sta. 515, where diving was done from the zodiac, large aggregations of larvae (>1000 m^{-2}) were found between over-rafted ice floes, where they were sheltered from the current in the open water. The current speed measured by the ship's acoustic Doppler current profiler (ADCP) in the open water here ranged from 8 to 13 cm s^{-1}. The majority of krill larvae were located in these refuges a few centimeters above the upward-facing ice floes (Fig. 5b). They maintained their positions by pleopod movement, and only a few larvae were swimming actively in the center of these refuges (Fig. 5b), suggesting a much lower current speed compared with the outside of these sea ice refuges. At this dive station too, coloration of the ice was not visible, but a high number of small zooplankton

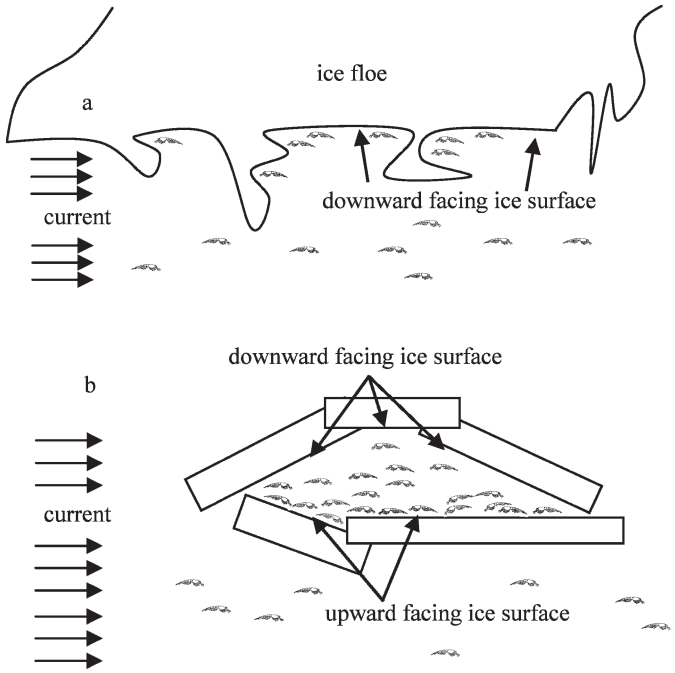

Fig. 5. Topography of the underside of sea ice during the winter cruise (a) at the ice camp (Sta. 498) and (b) in regions with over-rafted ice floes (Sta. 515) with location of larvae, sheltered from the current in the open water. The depth range shown below the sea ice is ~10–15 m.

organisms such as *Oithona* spp. were caught (up to 15 *Oithona* spp. L^{-1} with 8 ind. L^{-1} on average).

DW, body C, N, and lipid and protein content—During autumn in the Lazarev Sea, DWs of comparable larval stages were significantly higher ($p < 0.001$) in individuals collected under the ice compared with those collected in open water (Table 1). Also, the relative body C, lipid, and protein contents in advanced larval stages during winter (FIV–FVI) were much lower than those of younger furcilia in autumn (Table 2). In winter, the larvae varied substantially between stations in their elemental and biochemical body compositions. Likewise, equivalent larval stages from the ice camp (Sta. 498) and over-rafted sea ice refuges (Sta. 515) varied greatly in their physiological states. Larvae from Sta. 515 were significantly smaller ($p < 0.001$) with less body DW than larvae from the ice camp (Fig. 6), and their elemental and biochemical compositions differed markedly, with lower values at Sta. 515 (Table 3).

Seasonal variations in the amount of body C and N are simple indices of which energy sources (lipid, protein, or both) were being used by the larvae, because the quantities of C and N are highly correlated with the amounts of total lipid and protein. Between seasons, the regressions between BL and DW as well as between DW and C of larval krill differ significantly ($p < 0.05$), whereas no difference was found between DW and N (Figs. 7, 8a,b). However, the percentages of body lipid and protein on a DW basis demonstrate that proteins were used in addition to body lipids by the larvae in winter, with a high variability in the lipid fraction (Figs. 8c,d; Table 2). In both seasons, body C and N were highly correlated with the amounts of body lipid and protein, respectively (Fig. 8e,f). But between seasons, the relationships between C and lipid varied slightly (Fig. 8e), whereas the relationships between N and protein were markedly different between seasons (Fig. 8f; Table 4).

Metabolic and growth rates—Oxygen uptake rates of freshly caught krill were significantly higher during autumn (0.95 ± 0.28 μL O_2 mg^{-1} DW h^{-1}) than during winter (0.54 ± 0.19 μL O_2 mg^{-1} DW h^{-1}, $p < 0.001$; Table 5). Ammonium production, however, showed the reverse trend, with significantly higher values in winter (0.06 ± 0.02 μg NH_4 mg^{-1} DW h^{-1}) compared with autumn (0.03 ± 0.01 μg NH_4 mg^{-1} DW h^{-1}, $p < 0.05$; Table 5). The corresponding O : N ratio was more than twofold higher in autumn than in winter, suggesting a more pronounced use of nitrogenous compounds during winter (46 ± 14 and 15 ± 4, respectively, $p < 0.01$; Table 5).

In general, growth was much higher in autumn than in winter ($p < 0.001$; Fig. 9a,b). During autumn, however, larval growth was significantly lower in larvae from open-water areas compared with individuals from ice-covered regions ($p < 0.001$; Fig. 9a). During winter, the median growth rate was positive; only a few larvae from Sta. 515 (26%) had negative growth (Fig 9b; Table 6). At all other stations and in both seasons, larvae showed an increase in uropod length upon molting (Fig. 9a,b; Table 6). The percent growth increment on molting (GI) was significantly higher in autumn than in winter ($p < 0.001$), whereas IMP was longer, in most cases, in winter than in autumn (Table 6). Increasing Chl *a* concentration in the water column was associated with an increasing GI (Fig. 10a) and decreasing IMP (Fig. 10c), and in combination, this led to much higher growth rates in autumn than in winter.

At Sta. 478, all larvae that molted developed successfully into the next stage. Most of the larvae (40%) developed from FIV to FV, and 20% developed from FII to FIII, FIII to FIV, and FV to FVI, respectively. At the ice camp (Sta. 498A–D), 70% of larvae molted from FV to FVI and 10% from FIV to FV, and 20% of FVI larvae molted to the same stage, whereas at Sta. 515, the majority of larvae molted from FIV to FV (70%) and then from FV to FVI (7%). Thirty percent of FIV and FVI larvae and 20% of FV larvae molted to the same stage. With the use of the regressions shown in Table 4 and an average daily growth rate of 0.01 mm d^{-1} for autumn larvae and 0.0014 mm d^{-1} for winter larvae, the estimated daily increases in DW, C, and N for an 8-mm furcilia larva are, in autumn, 2.2 μg DW d^{-1}, 1.0 μg C d^{-1}, and 0.2 μg N d^{-1} and, in winter, only 0.23 μg DW d^{-1}, 0.1 μg C d^{-1}, and 0.02 μg N d^{-1}.

In the Lazarev Sea, the measured growth and respiration rates of furcilia in autumn corresponded to a C allocation of 2.5% of body C d^{-1} into growth (1.2% in winter) and 3.3% body C d^{-1} to fuel respiration (1.6% in winter), with a respiratory quotient of 0.97 (Ikeda et al. 2000).

Stomach and gut contents—Of the items with identifiable hard parts seen in the stomach and gut, these were dominated by autotrophic flagellates and diatoms, various protozoan groups, plus fragments of cnidaria, copepods, and krill (Table 7). The smallest discoid diatoms were about 10 μm in diameter, whereas the largest copepod mandibles had a width of ~50 μm, suggesting a copepod prosome length of about 600 μm (Karlson and Båmstedt 1994). Some samples contained large numbers of krill setae and loose setulae, but never eye fragments or feeding appendages, which suggests that they were derived from molts rather than living animals. Heterotrophic food sources such as tintinnids, foraminiferans, copepods, and krill debris were much more prominent in stomachs in winter than in autumn (Table 7). Diatoms accounted for at least 80% of the estimated volume of identifiable food items in autumn but only 7–60% in winter (Fig. 11). However, across stations, the average diatom volume per stomach was similar in both seasons ($0.8 \pm 1 \times 10^6$ μm^3 in autumn and $0.9 \pm 1 \times 10^6$ μm^3 in winter). Thus, the total volumes of identifiable items were clearly higher in most winter samples than in the two samples from autumn (Table 7). In autumn, for instance, most of the diatoms in the stomach were intact, medium to large *Fragilariopsis* spp. cells, whereas in winter, discoid diatoms were dominant (except Sta. 502) and *Fragilariopsis* spp. cells were crushed into small bits. Even though we never found more than six copepods per sample (of three pooled furcilia), mainly the small cyclopoid *Oithona* spp., copepods accounted for most of the identified volumes in the winter samples (Stas. 515 and 497). At other stations, identifiable hard parts of the stomach contents were dominated by tintinnids, which were either numerous (*Codonellopsis* spp., Sta. 498) or of large volume (*Cymatocylis vanhoeffeni*, *Cymatocylis calyciformis*; Sta.

Table 2. *Euphausia superba*. Percentage of carbon (C), nitrogen (N), total lipid, and protein per dry weight and C : N ratio of different larval stages that came from all stations sampled in autumn and winter in the Lazarev Sea. Data are given as the median with the range in parentheses. Larval stage: C, calyptopis; F, furcilia. *n,* No. of replicates.

	% body C		% body N		C : N ratio		% body lipid		% body protein	
Larval stage	Autumn 2004	Winter 2006	Autumn 2004	Winter 2006	Autumn 2004	Winter 2006	Autumn 2004	Winter 2006	Autumn 2004	Winter 2006
CIII	37.8 (31.7–42.5) *n*=40	29.4 (25.6–32.0) *n*=10	9.0 (7.4–10.4) *n*=40	10.0 (9.5–10.2) *n*=10	4.2 (3.5–4.8) *n*=40	2.9 (2.7–3.2) *n*=10	6.6 (6.5–6.7) *n*=4	—	31.5 (28.2–34.9) *n*=4	—
FI	39.3 (23.9–48.1) *n*=150	29.5 (28.4–31.7) *n*=10	9.0 (6.1–15.1) *n*=150	9.5 (9.1–10.2) *n*=10	4.4 (2.8–5.1) *n*=150	3.2 (2.8–3.5) *n*=10	10.1 (9.4–11.4) *n*=4	—	39.7 (37.1–42.8) *n*=4	—
FII	44.3 (33.9–51.9) *n*=26	31.0 (30.1–31.8) *n*=12	9.5 (7.1–12.2) *n*=26	9.3 (9.0–10.1) *n*=12	4.5 (3.3–5.5) *n*=26	3.4 (3.0–3.5) *n*=12	13.8 (9.4–15.1) *n*=7	—	40.9 (38.5–45.6) *n*=7	—
FIII	44.2 (40.9–46.7) *n*=43	34.8 (32.8–40.3) *n*=24	9.3 (8.3–10.3) *n*=43	9.6 (8.9–11.0) *n*=24	4.7 (3.9–5.4) *n*=43	3.6 (3.4–3.9) *n*=24	14.4 (9.7–15.1) *n*=4	—	44.2 (42.6–45.6) *n*=4	—
FIV	—	31.6 (30.0–37.5) *n*=17	—	8.9 (8.6–10.6) *n*=17	—	3.5 (3.4–3.8) *n*=17	—	5.2 (2.4–5.7) *n*=6	—	35.8 (31.8–38.0) *n*=6
FV	—	33.1 (31.1–38.4) *n*=24	—	9.1 (8.0–10.2) *n*=24	—	3.6 (3.4–4.1) *n*=24	—	5.1 (3.5–11.8) *n*=7	—	35.1 (29.8–38.5) *n*=7
FVI	—	37.5 (33.2–39.8) *n*=13	—	8.6 (8.3–9.1) *n*=13	—	4.3 (3.7–4.7) *n*=13	—	10.8 (7.3–16.4) *n*=6	—	30.9 (30.3–38.0) *n*=6

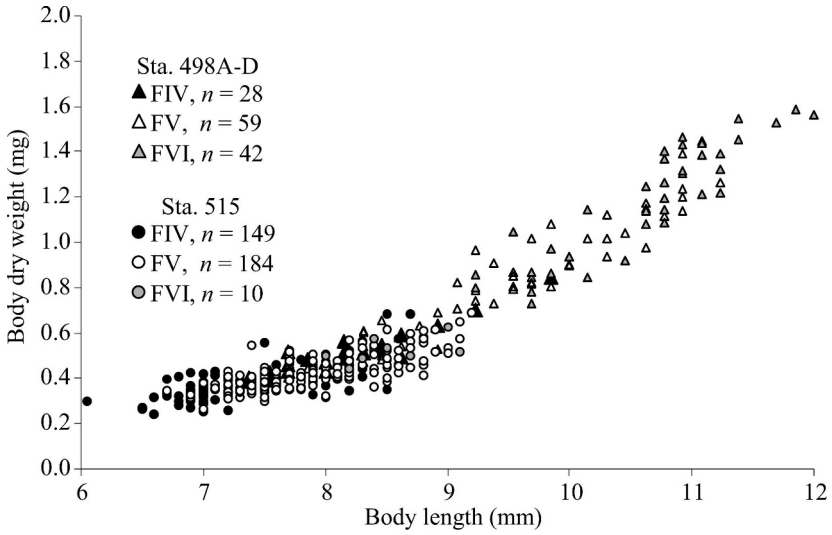

Fig. 6. *Euphausia superba.* Relationship of dry weight to length of furcilia (F) IV–VI larvae from two dive stations during the winter cruise in the Lazarev Sea: the ice camp (Stas. 498A–D) and Sta. 515 (n = number of larvae per stage).

497). The highest amount of identifiable items per stomach was found at Sta. 502 (Table 7) and comprised a mixture of diatoms, copepods, and tintinnids. Thecate dinoflagellates and foraminifera were usually of minor importance in the diet of krill.

Discussion

The Lazarev Sea, located in the High Antarctic Zone, is characterized by a long season of pack ice cover. With regard to ice cover, bathymetry, and current system, it differs significantly from the western Antarctic Peninsula region, where most previous studies on overwintering of larval krill have been undertaken (Fig. 1). This study is also novel in that it incorporates, for the first time, all relevant parameters (e.g., morphometrics, biochemical composition, physiology, feeding, and growth) for autumn and winter larvae (Table 8). Our major conclusions are: (1) In autumn, the larvae from within the ice were in better physiological condition than those from open water. (2) Within the ice, autumn larvae were in a better physiological state than winter larvae. (3) Different metabolic substrates were used in autumn and winter, suggesting flexible survival mechanisms for winter. (4) Heterotrophic organisms (small copepods, protozoans, or both) are important food items for winter larvae. (5) Physics (current speed and under-ice

Table 3. *Euphausia superba*. Percentage of carbon (C), nitrogen (N), total lipid, and protein per dry weight and C : N ratio of similar larval stages from two dive stations (ice camp 498A–D and 515) in the austral winter 2006 in the Lazarev Sea. Data are given as a median with the range in parentheses. *n,* No. of replicate samples. Each sample comprised 10–25 furcilia (*see* Methods).

	Larval stage								
	FIV			FV			FVI		
% body C									
498A–D	33.6	(33.0–34.0)	n=3	36.3	(32.9–36.8)	n=3	38.5	(36.3–38.9)	n=3
515	30.5	(30.2–31.0)	n=3	32.5	(32.1–32.9)	n=4	33.6	(32.9–33.9)	n=3
% body N									
498A–D	9.2	(9.0–9.4)	n=3	8.9	(8.3–9.4)	n=3	8.5	(8.4–8.9)	n=3
515	8.8	(8.7–8.8)	n=3	9.1	(9.1–9.3)	n=4	8.9	(8.8–9.4)	n=3
C : N ratio									
498A–D	3.6	(3.5–5.7)	n=3	4.0	(3.9–4.1)	n=3	4.3	(4.3–4.6)	n=3
515	3.5	(3.4–3.5)	n=3	3.5	(3.5–3.6)	n=4	3.8	(7.3–9.2)	n=3
% body lipid									
498A–D	5.3	(5.2–5.7)	n=3	9.9	(8.1–11.8)	n=3	12.5	(9.0–16.4)	n=3
515	4.3	(2.4–5.3)	n=4	4.0	(3.5–5.1)	n=4	9.0	(7.3–9.2)	n=3
% body protein									
498A–D	37.8	(37.0–38.0)	n=3	33.2	(29.8–35.1)	n=3	30.6	(30.3–30.7)	n=3
515	32.8	(31.8–34.7)	n=3	35.8	(34.7–38.5)	n=4	31.8	(31.0–38.0)	n=3

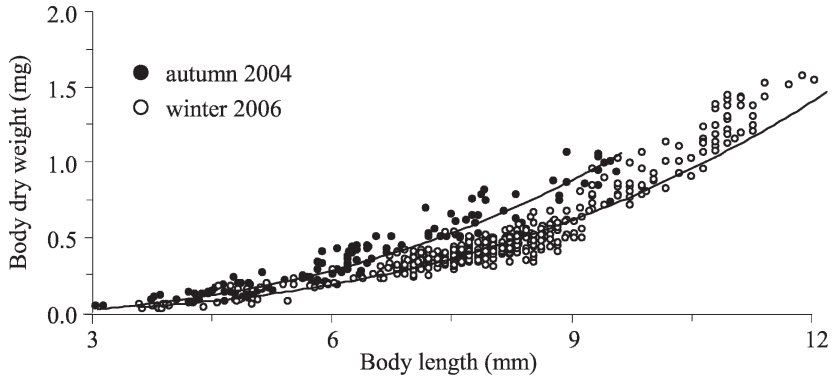

Fig. 7. *Euphausia superba.* Relationships of dry weight to body length of larval krill from autumn and winter in the Lazarev Sea. The equations of the regressions are given in Table 4.

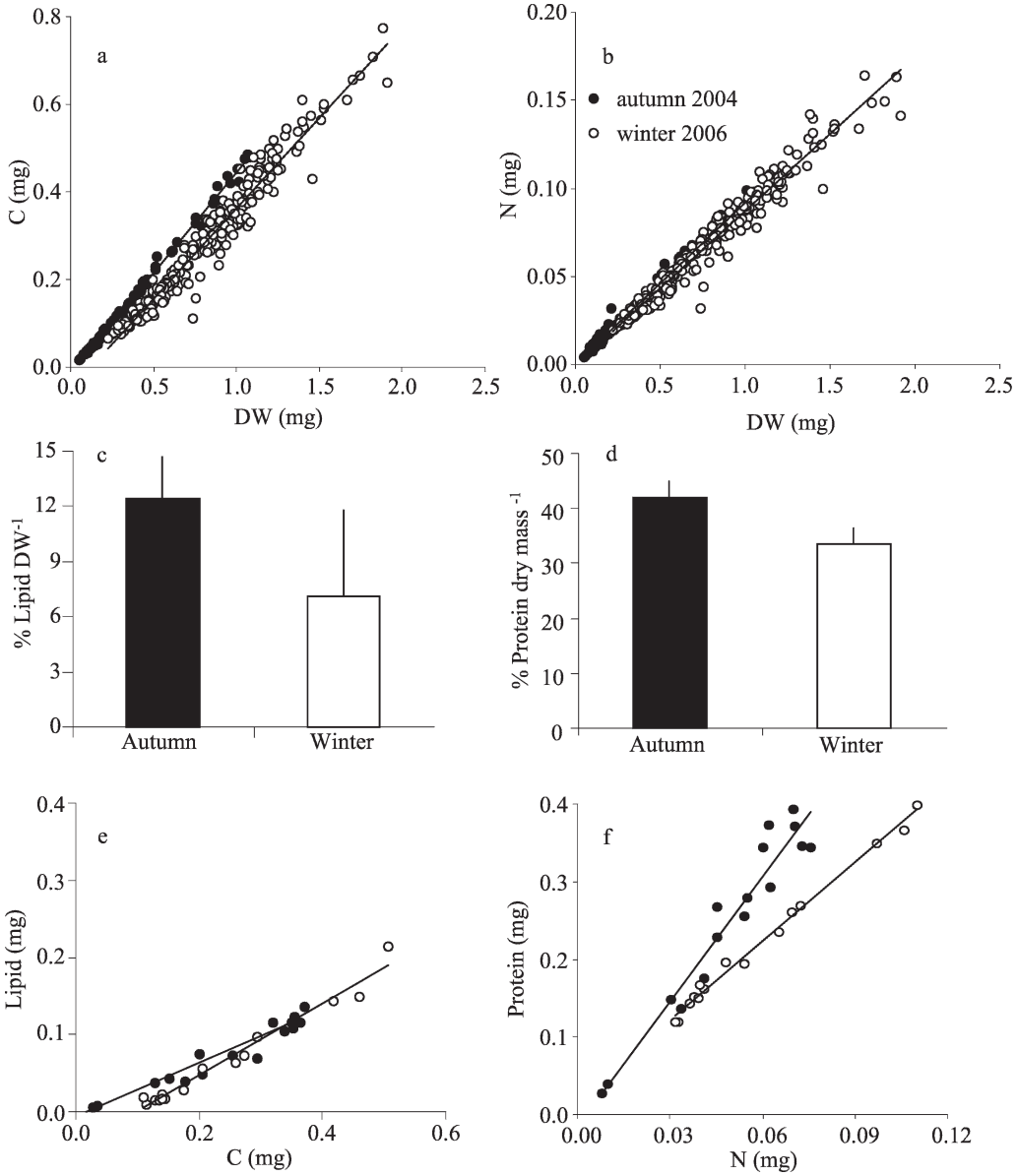

Fig. 8. *Euphausia superba.* Relationships of (a) dry weight (DW) to carbon (C), (b) DW to nitrogen (N), (c) percentage of total body lipid per DW, (d) percentage of total body protein per DW, (e) C to total lipid, and (f) N to total body protein of larval krill from autumn and winter in the Lazarev Sea. Regressions are given in Table 4.

Table 4. *Euphausia superba*. Seasonal relationship between body length (BL) and dry weight (DW), DW and carbon (C), DW and nitrogen (N), C and lipid (mg), N and protein (mg), C : N ratio, and percent body lipid of larval stages from the Lazarev Sea (CIII–FIII) in austral autumn 2004 and (CIII–FVI) in austral winter 2006.

Season	Equation	r^2	n
Autumn 2004	$DW = 2.6 \times 10^{-3}\ L^{2.67}$	0.91	279
	$C = 0.45\ DW - 0.01$	0.99	107
	$N = 0.091\ DW$	0.99	107
	$Lipid = 0.35\ C - 0.01$	0.93	16
	$Protein = 5.34\ N - 0.01$	0.94	16
	$\%\ lipid = 3.66\ C:N - 5.67$	0.81	16
Winter 2006	$DW = 1.3 \times 10^{-3}\ L^{2.83}$	0.93	527
	$C = 0.41\ DW - 0.05$	0.96	345
	$N = 0.088\ DW$	0.96	345
	$Lipid = 0.46\ C - 0.05$	0.97	16
	$Protein = 3.37\ N + 0.02$	0.99	16
	$\%\ lipid = 11.24\ C:N - 35.36$	0.93	16

topography) might dictate whether larval krill can exploit the food associated with sea ice or are advected away from suitable feeding habitats. Whereas the first two findings resemble those from previous research on krill larvae, all others were rather unexpected. Taking previous results from other areas into account, we discuss below (1) the large-scale seasonal and regional differences in the physiological conditions of the larvae, (2) the potential mechanisms for overwintering, and (3) the role of the physical habitat in promoting suitable environmental conditions.

Large-scale seasonal and regional differences in larval condition—During autumn, the physiological condition of larvae was better in the ice-covered region south of 68°S of the Lazarev Sea than in open water. This is most likely the result of a broadly latitudinal or onshelf-to-offshelf gradient in Chl *a*, with highest Chl *a* values in the south (i.e., in areas that are covered by ice earlier than further north). The advance of the ice edge from March (Fig. 12a) to April (Fig. 12b) increasingly covers water with declining and often low Chl *a* concentrations. We predicted, therefore, that in autumn, the southern region of the Lazarev Sea provides more favorable feeding habitats for krill since there is not enough ice to block out the light. As a result, high Chl *a* concentrations are scavenged. In winter,

Table 5. *Euphausia superba*. Mean values ± SD of oxygen uptake (O_2) and ammonium (NH_4) production rate (mg dry weight [DW] h^{-1}) and the atomic oxygen (O) to nitrogen (N) ratio of furcilia larvae in the Antarctic autumn 2004 and winter 2006 in the Lazarev Sea; *n*, No. of experiments.

	Autumn 2004 (n=11)	Winter 2006 (n=14)
$\mu L\ O_2$ (mg DW h^{-1})	0.95±0.28	0.54±0.19
$\mu g\ NH_4$ (mg DW h^{-1})	0.03±0.01	0.06±0.02
O : N ratio	46±14	15±4

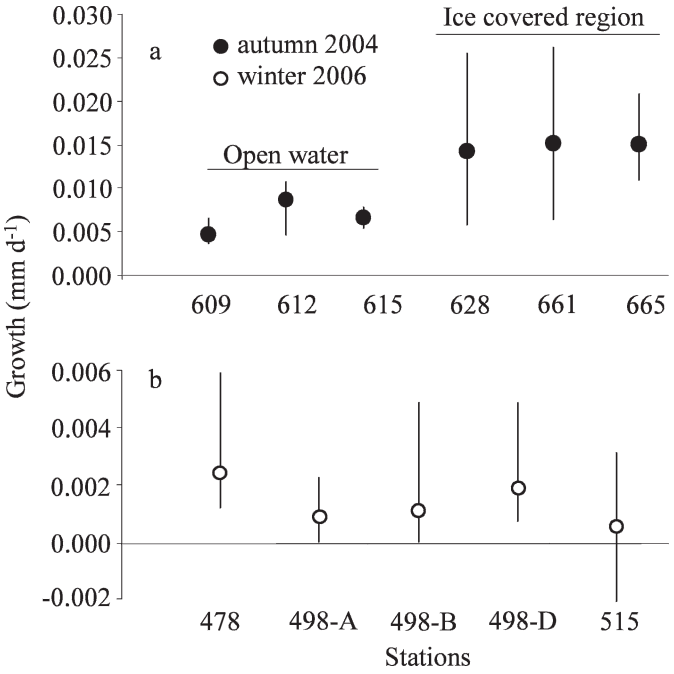

Fig. 9. *Euphausia superba.* Median growth rate for larval krill (mm d^{-1}) during (a) autumn and (b) winter in the Lazarev Sea. In autumn, Stas. 609, 612, and 615 were located in open-water areas, whereas the other stations were in ice-covered regions.

however, the northern latitudes of the Southern Ocean might provide a more dependable food source for overwintering larvae: the ice is thinner and more incident radiation is available for photosynthesis. This proposed regional gradient is outlined schematically in Fig. 13.

A similar prediction concerning the disadvantage for overwintering of larval krill in southern latitudes was made previously (Daly 2004; Quetin et al. 2007) from studies in the Weddell–Scotia Sea (60°S) and Marguerite Bay (66–69°S). There was no evidence of food limitation in furcilia from the northern region (60°S) in contrast to larvae from Marguerite Bay, which were food-limited in winter. Although any such schematic is clearly a gross generalization for any sector, it provides a testable conceptual model of how ice habitats could change throughout the dark season.

Physiological overwintering mechanism of larval krill—The studies in the Lazarev Sea were not performed within a single year, being in autumn 2004 and winter 2006; so the differences observed might reflect interannual as well as seasonal variability. Indeed, west of the Antarctic Peninsula, the interannual sea ice dynamics and microalgal biomass in winter pack ice can be highly variable (Fritsen et al. 2008), and this affects the condition of larval krill (Ross and Quetin 1991; Quetin et al. 2003). Instead of potentially overinterpreting so-called seasonal differences within this Lazarev Sea study, we will instead evaluate it alongside autumn and winter findings from the West Antarctic Peninsula (WAP) to obtain a wider perspective.

Despite the fact that interannual variability in the sea ice biota can have a large effect on the condition of larval krill,

Table 6. *Euphausia superba.* Growth and intermolt period (IMP) for larval krill. Growth is given as the median GI (% change in uropod length on molting) and as the median daily growth rate (mm d^{-1}). The range of both growth measurements is given in Figs. 9a,b and 10a. The range of sea surface temperature (SST) and surface chlorophyll *a* (Chl *a*) concentration at specific stations in austral autumn 2004 and winter 2006 in the Lazarev Sea are shown. Larval stage: C, calyptopis; F, furcilia. *n,* No. of molted individuals.

Station	Larval stages	Growth		*n*	IMP (d)	SST (°C)	Chl *a* (μg L^{-1})
		GI (%)	mm d^{-1}				
			Autumn 2004				
609	CIII–FI	11.1	0.0060	16	31	−0.61	0.17
612	CIII–FI	10.8	0.0100	12	25	−0.92	0.22
615	CIII–FII	7.1	0.0080	11	28	−0.90	0.17
628	FI–FII	11.1	0.0142	24	14	−1.84	0.35
661	FII–FIV	13.2	0.0152	21	17	−1.71	0.48
665	FI–FIII	12.8	0.0151	27	16	−1.78	0.59
			Winter 2006				
478	FII–FV	3.6	0.0025	15	24	−1.69	0.050
498A	FIV–FVI	1.4	0.0008	13	36	−1.79	0.032
498B	FIV–FVI	1.9	0.0011	17	37	−1.84	0.030
498D	FIV–FVI	4.1	0.0019	8	41	−1.83	0.040
515	FIV–FVI	1.3	0.0005	32	39	−1.75	0.036

our results of the seasonal differences of BL and DW are in line with previous studies from the western Antarctic Peninsula (Fig. 14), demonstrating that larvae of similar length had lower DW in winter compared with autumn. Comparable regressions exist between BL and DW as well as between DW and C and N (Daly 2004; Table 4). Growth rates measured in autumn and winter in this study are almost exclusively positive and in the range of those estimated for other regions during the same seasons, as well as during late summer (Fig. 15a–c; Quetin et al. 2003). However, Quetin et al. (2003) and Ross et al. (2004) have shown that in situ growth rates of larval krill in winter west of the Antarctic Peninsula can be extremely variable between years, as are their body lipid contents (Ross and Quetin 1991). The authors hypothesized that such variations were dependent on the quality of the pack ice, determined by the interaction of the timing of sea ice advance and autumn phytoplankton stocks (Quetin et al. 2007).

Our main results are that winter larvae had low growth, consumed heterotrophic food items, utilized mainly body lipids and, to a moderate extent, body protein for energy provision, and had reduced oxygen uptake rates. However, it has to be taken into account that growth and respiration rates are mainly controlled by temperature and food availability (Brinton and Townsend 1984). In our study, the mean temperatures did not differ much between seasons (−1.4°C in autumn, −1.8°C in winter). However, when comparing autumn and winter Chl *a* concentrations from the surface layer or ice–water interface, this index of food is a surprisingly good overall predictor of larval growth (Fig. 15). This basic relationship seems to hold because winter Chl *a* concentrations and larval growth rates are much lower than those during autumn (Table 6). The use of water column Chl *a* concentration as a food proxy to predict growth is most robust in autumn, being less reliable in winter when growth varies greatly from 1% to 4% GI^{-1} (Table 6), despite very low Chl *a* concentrations. Thus, some other food source and body substrates, such as heterotrophic diet, body lipids, and proteins, are needed during winter to support larval metabolism and growth.

From several parameters determined (stomach and gut content, ammonium production rates, O : N ratio, relationship between N and protein and DW and N), we conclude a high importance of heterotrophic diet for winter larvae. The relationships between N and protein were remarkably different between seasons, suggesting that different nitrogenous fractions were used by larvae (Anger 2001). In autumn larvae, a slope parameter of 5.3 indicates that most of the N is bound in the muscle protein fraction (Anger 2001). In winter larvae, the relationship of N to protein shows a higher N content and a lower content of muscle proteins compared with autumn larvae. This is an indication that a high amount of N was bound in nitrogenous fractions other than muscle proteins (e.g., free amino acids) in winter larvae. Free amino acids were not measured, however, by the Lowry method used in this study. A possible increase in the free amino acid pool in winter larvae might result from the digestion of a heterotrophic diet but also from the utilization of body protein. Amino acids would become available for energy production after their release from hydrolyzed dietary and body proteins (Rosa and Lunes 2005), which results in increasing excretion rates (Ming 1985). Higher ammonium excretion rates and lower O : N ratios in winter larvae compared with autumn larvae support this hypothesis (Frazer et al. 2002*a*). The ammonium excretion was the only physiological parameter that increased from autumn to winter (Table 5). Krill larvae with O : N ratios lower than 24 are thought to be feeding on animal matter (e.g., copepods) or starving, whereas larvae with an O : N ratio greater than 24 are primarily herbivorous, feeding on phytoplankton or ice algae (Frazer et al. 2002*a*). The relationship between DW and N in winter larvae, which was not significantly different from those from autumn (Fig. 8b), might indicate the utilization of a protein-rich diet rather than of body protein. The results depicted in

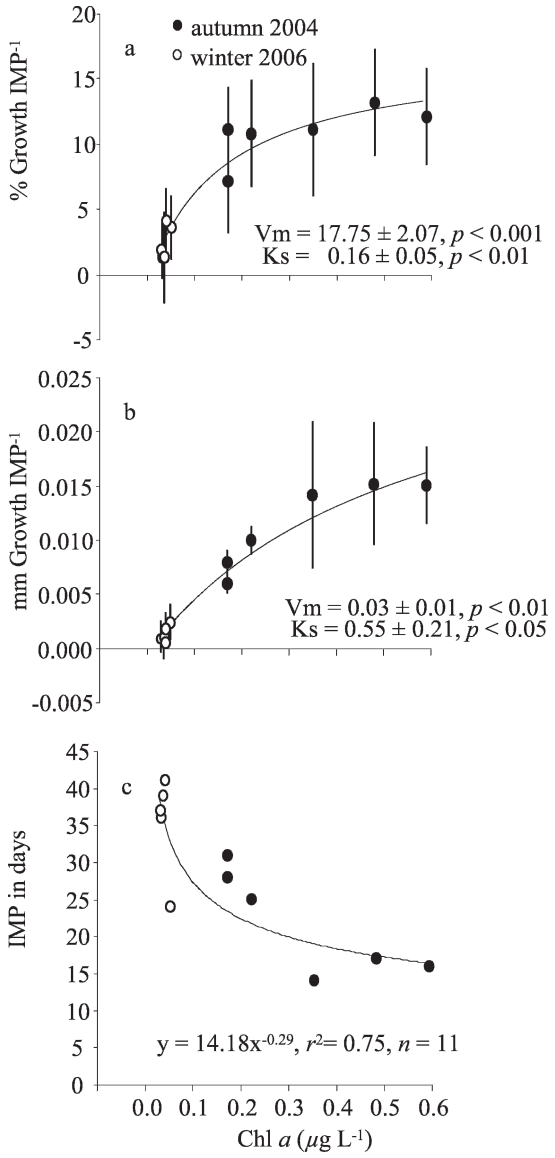

Fig. 10. *Euphausia superba.* Relationship of surface chlorophyll *a* (Chl *a*) concentration (*see* Table 6) to growth ± SD as (a) % growth per intermolt period (GI), (b) mm growth d^{-1}, and (c) intermolt period (IMP^{-1}). Panels a and b are expressed as a Michaelis–Menten uptake function as follows: (a) % growth $IMP^{-1} = 17.75[\text{Chl } a/(0.16 + \text{Chl } a)]$, $r^2 = 0.93$, $n = 11$; (b) mm growth $IMP^{-1} = 0.03[\text{Chl } a/(0.55 + \text{Chl } a)]$, $r^2 = 0.96$, $n = 11$. Vm and Ks are constants representing, respectively, maximum growth and the Chl *a* concentration at which growth is half the maximum. Ks reflect the ability to grow at low food concentration.

Fig. 8d, however, imply that body protein was used in winter by the larvae. Therefore, the high excretion rates and low O : N ratio in winter might indicate a high flexibility of larval krill in the source used for energy production.

There are caveats attached to the use of any feeding method in isolation for krill (Schmidt et al. 2006), but nevertheless, the stomach and gut content analyses yielded slightly surprising results. For the larvae under the ice, heterotrophic foods appeared to play a greater role in winter than in autumn. The reasons are unclear because the ambient food composition could not be determined, but one explanation is that in autumn, the FI and FIII are smaller and less able to capture the larger moving animals. Alternatively, the heterotrophic organisms are available at a higher proportion under sea ice in winter than in autumn (Garrison and Close 1993; Schnack-Schiel et al. 2001) so that larvae change to carnivory during winter. The similar diatom volumes in the stomachs and guts of larval krill in both seasons demonstrate that these heterotrophic compounds were not ingested as a replacement of diatoms but rather in addition to them (Fig. 11).

The observation that the total volume of identifiable items in stomachs and guts of winter larvae is generally higher than in autumn (Fig. 11) is not easy to explain. This was unexpected given the seasonal decrease in growth rates under ice cover. It has to be stressed here that the items with hard parts that we counted in the stomach are only a subset of the total krill diet (Schmidt et al. 2006). Soft-bodied organisms such as flagellates, ciliates, and turbellarians are common members of the sea ice microbial community. They are easily digested and hence not visible in the stomachs and guts of the larvae. In Antarctic autumn, ciliates can contribute more than 75% of total cell numbers (Fiala et al. 2006), whereas the biomass of turbellarians and the autotrophic flagellate *Phaeocystis* sp. can provide 45% (Schnack-Schiel et al. 2001) and 25% (Garrison et al. 2005), respectively, of the sea ice microbial community. Therefore, the discrepancy between lower growth rates but higher volumes of identifiable food items in stomachs and guts of larvae in winter compared with autumn could have different causes: First, unidentified soft-body autotrophs, such as *Phaeocystis* sp., might have been an important component of the larval diet in autumn but not in winter. This would also explain why Chl *a* concentration in the water column represented a good prediction for growth in autumn, despite the low volume of identifiable items in the larvae. Second, the discrepancy could also be explained by a longer gut passage time in winter larvae compared with larvae from autumn. During our winter study, a single experiment yielded a value of 2.7 h, whereas Daly (1990) determined in winter a duration of 1.6 h. This compares with values of 1 h measured in autumn (Pakhomov et al. 2004). The seasonal differences in gut passage time is reflected by the fact that in winter most *Fragilariopsis* spp. cells in the stomach were broken into fragments but were intact in autumn (Table 7). Finally, it has to be taken into account that stomach contents represent snapshots—food ingested during the last few hours—whereas growth rates integrate feeding conditions over 1–2 weeks.

The reduced respiration rates of winter larvae from the Lazarev Sea, which were also found in previous studies from the western Antarctic Peninsula, seem to be a result of low food availability during winter (Torres pers. com in Daly and Macaulay 1991 and in Daly 2004; Frazer et al. 2002*a*;). The low respiration rates in winter are comparable to rates of starved furcilia (Frazer et al. 2002*a*; Meyer et al. 2002) and winter larvae from the open water west of the Antarctic Peninsula, which is supposed to be an unfavorable feeding ground for krill larvae in winter (Quetin et al. 2003).

Table 7. *Euphausia superba.* Stomach content of furcilia larvae from different stations in ice-covered areas of the Lazarev Sea. The number of identifiable items is given per sample (items sample^{-1}), which comprised three or four larvae, whereas the total volume of items is given per individual (μm^3 stomach^{-1}) and per dry weight (μm^3 mg^{-1} DW). Discoid diatoms include species such as *Coscinodiscus* spp., *Thalassiosira* spp., and *Asteromphalus* spp. Small pennate diatoms are complete or broken *Thalassionema* sp. and *Pseudonitzschia* spp. Medium pennate diatoms include bits of species such as *Thalassiothrix* sp., *Chaetoceros* spp., and *Rhizosolenia* spp.

	Autumn		Winter						
	Sta. 621 FI (n=3)	Sta. 660 FIII (n=4)	Sta. 497 FV (n=3)	Sta. 497 FVI (n=3)	Sta. 498 FV (n=3)	Sta. 502 FV (n=3)	Sta. 502 FVI (n=3)	Sta. 515 FIV (n=3)	Sta. 515 FV (n=3)
Silicoflagellates (items sample^{-1})	1		2	2		1	4	2	3
Diatoms									
Discoid (broken)	91	8	340	26	19	272	248	23	171
Discoid (small, complete)	52	1	85	18	118	90	37	42	
Discoid (medium, complete)		1	15	6	17	21	18	5	11
Fragilariopsis spp. (small)			1231	104	1062	4539	7871	258	990
Fragilariopsis spp. (medium)	2376	856	99	67	207	225	382	38	46
Fragilariopsis spp. (large)	166	21							
Pennate (small)	1956	4104	5094	1306	2076	10,406	5601	827	1618
Pennate (medium)	270	355	148	84	11	33	269	9	32
Eucampia sp.	21			1					
Dinoflagellates									
Prorocentrum spp.			2	1	17	1			
Dinophysis spp.						1	4		
Protoperidinium spp.	1	7	3			3	5		2
Tintinnids									
Codonellopsis spp.	3			1	61	7	21	2	4
Cymatocylis spp.			5	2	4	3	4		
Foraminifera			2	1	1	7	10	6	10
Cnidaria									
Nematocysts			6	5	1	7		1	5
Copepods									
Mandibles				6		4	12	4	2
Appendages				26	2	40	129	104	64
Krill									
Setae		2	10	32	13	12	31	6	15
Setulae		5	167	263	268	97	4056	359	483
Furcilia DW (mg ind^{-1})	0.47	0.8	0.59	0.83	0.59	0.65	1.15	0.42	0.32
Volume of items ($\times 10^6$ μm^3 stomach^{-1})	1.3	0.7	2.5	2.2	2.3	2.6	8.2	1.3	3.4
Volume of items ($\times 10^6$ μm^3 mg^{-1} DW)	2.8	0.9	4.2	2.6	3.9	4.0	7.1	3.1	10.6

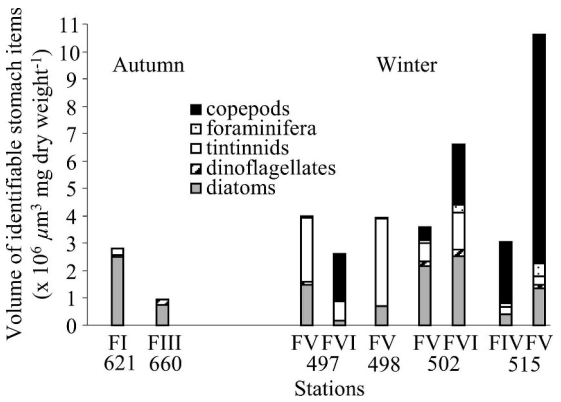

Fig. 11. *Euphausia superba*. Contribution of different plankton groups to the total estimated volume of identifiable stomach items ($\times 10^6$ μm^3 mg^{-1} DW) in furcilia I–VI larvae (FI–FVI) from the Lazarev Sea in the Antarctic autumn and winter.

The role of under-ice topography and current speed—The observations by divers during our winter survey, combined with our analytical results, demonstrate that the current speed and ice texture might play a critical part in the ability of larval krill to exploit food associated with sea ice. Previous research revealed that winter larvae were generally found in areas in which (1) plant pigment was rarely visible to the naked eye and (2) sea ice was over-rafted, eroded, or both, and aggregations of larvae occurred more often above upward-facing ice surfaces and structurally complex microhabitats (i.e., areas with two or more adjacent ice surfaces) than smooth downward-facing ice surfaces. In addition, former studies observed that large-scale movements of larval krill in the ice are restricted to periods of darkness or extremely low light (Frazer et al. 1997, 2002*b*; Ross et al. 2004).

In the Lazarev Sea, the largest aggregations of larvae were also found in a region with over-rafted ice floes. In these refuges, the animals were mainly located a few

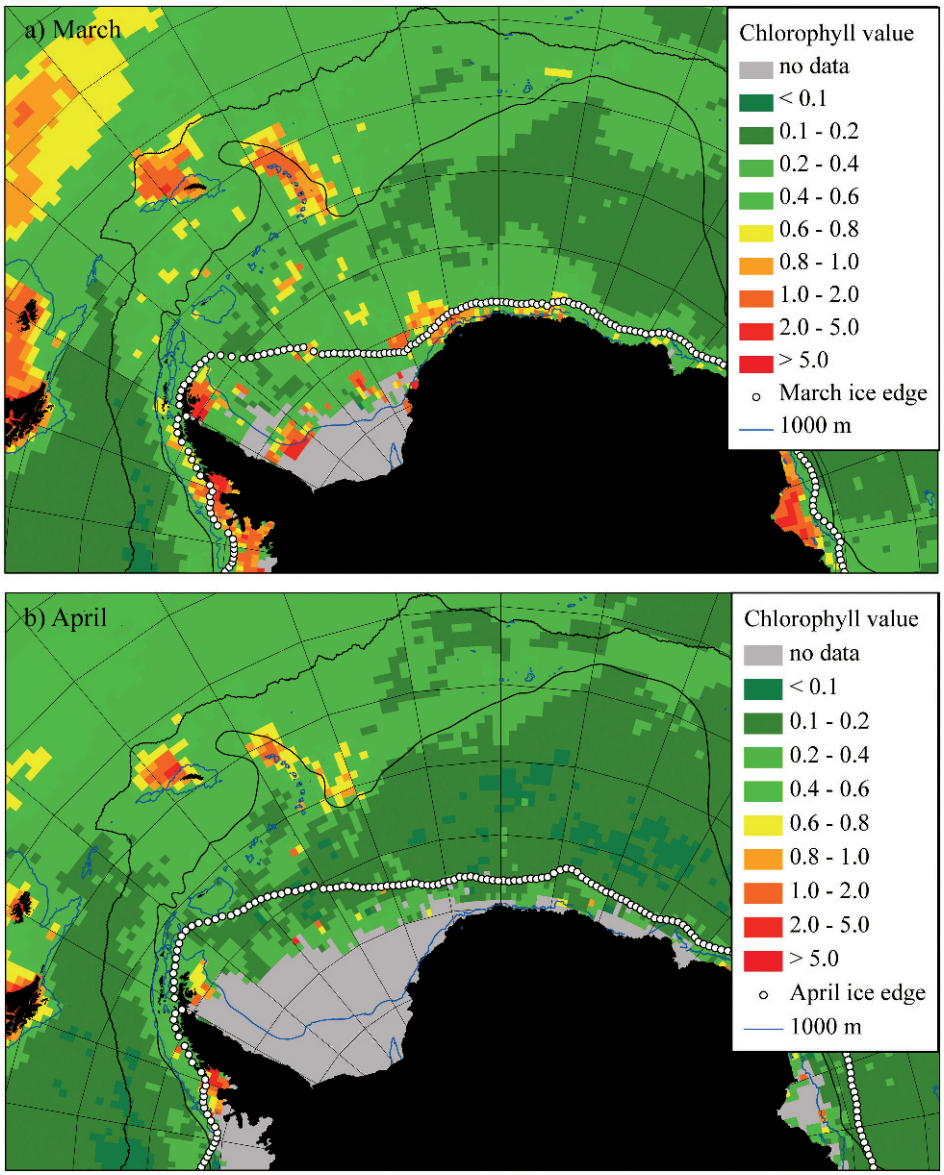

Fig. 12. Autumn progression of physical and biological conditions for krill larvae in Atlantic and Western Indian sectors, showing climatological mean conditions for March and April. Chlorophyll values are mean values (mg m^{-3}) for (a) March and (b) April of the years 1998–2004, and ice edges for the respective months are based on northern extent of 15% ice concentration for the years 1979–2006. This illustrates the advance of the sea ice in autumn, covering declining Chl *a* concentrations everywhere, albeit with higher values at highest latitudes closest to the Antarctic continent.

centimeters above the upward-facing ice floes (Fig. 5b). However, the movement of larvae in the Lazarev Sea was never restricted to specific light conditions (e.g., day vs. night) but was rather driven by the current speed in the open water. Locations where we found a high number of larvae (ice camp and Sta. 515) had similar mean current speeds in the upper 20 m of ~8 cm s^{-1}, and the larvae drifted passively with the current in the open water. Large-scale active migrations by larvae in the water column, as described for the western Antarctic Peninsula (Frazer et al. 1997, 2002*b*), were therefore impossible. The large over-rafted ice refuges (Sta. 515) seemed to be more sheltered from the current than the small hollows and dents we found at the ice camp (Fig. 5a,b), because the larvae were actively swimming from one position to another, which was not the case in the refuges at the ice camp. Because of physical factors (under-ice topography and its influence on current speed), larvae can aggregate and rest in these over-rafted ice refuges and might find, in addition, favorable feeding conditions resulting from these physical factors. These irregularities in the under-ice topography might also allow aggregation of other plankton organisms that passively drift in the current, plus any ice biota released by ice movements. At Sta. 515, for instance, a high abundance of

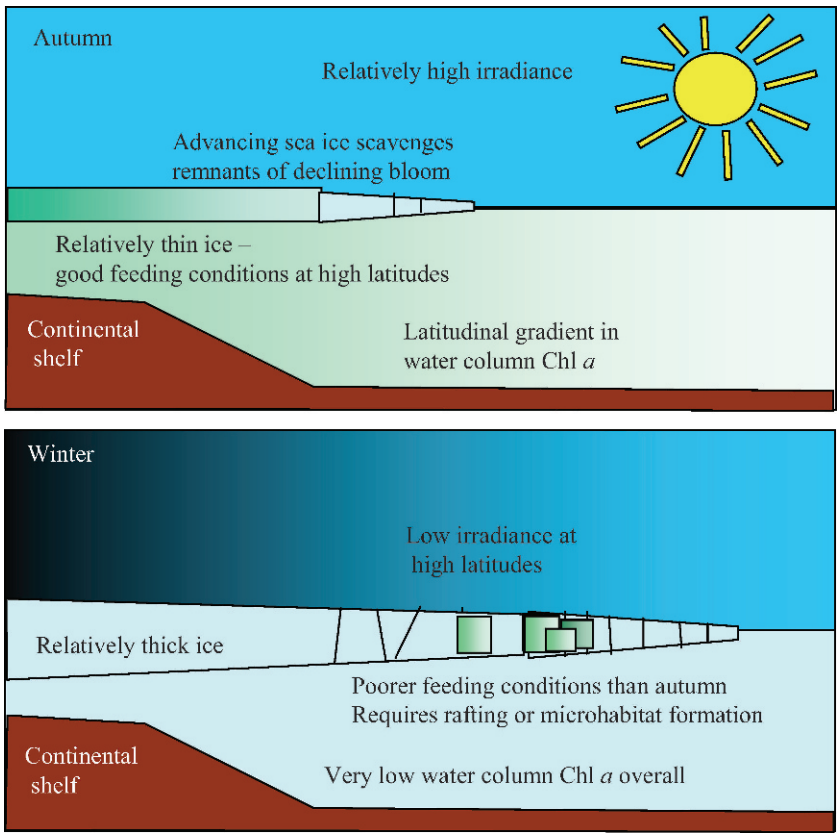

Fig. 13. Schematic of physical and biological conditions for larval krill overwintering. This simplified conceptual model is based on literature observations, as well as those reported here, and reflects the general latitudinal gradient in Chl *a* conditions during the autumn period of ice advance shown in Fig. 12.

Table 8. Parameter measured in larval krill from previous field studies in the Southern Ocean. WW, wet weight.

Parameter measured	Region	Season	Reference
O_2 consumption, NH_4^+ excretion, O : N	Weddell–Scotia Sea	January–March	Ikeda 1981
BL, growth	Scotia Sea	Mid and late summer 1981	Brinton and Townsend 1984
Stomach gut content	Western Weddell Sea	Autumn 1986	Hopkins and Torres 1989
BL, WW, gut evacuation, ingestion, clearance rate, growth, stomach content	Weddell–Scotia Sea	Winter	Daly 1990
Growth, C, total lipid	Western Antarctic Peninsula	Winter 1987, 1989	Ross and Quetin 1991
O_2 consumption, NH_4^+ excretion, O : N	Western Antarctic Peninsula	Winter 1997, 1993, 1994	Frazer et al. 2002*a*
BL	Western Antarctic Peninsula	Winter 1991, 1993	Frazer et al. 2002*b*
DW, C, N, lipid, protein, carbohydrates, O_2 consumption, NH_4^+ excretion, O : N, stomach-gut content, ingestion, clearance rate	Lazarev Sea	Autumn 1999	Meyer et al. 2002
BL, growth	Bransfield Strait to south of Marguerite Bay	Winter 1987, 1989, 1991, 1993, 1994, 1999, autumn 1991, 1993	Quetin et al. 2003
BL, DW, C, N, total lipid, protein, carbohydrates, O_2 consumption, ingestion, clearance rate, assimilation efficiency	Rothera Time Series monitoring station	Late summer 2000	Meyer et al. 2003
BL, DW, C, N; growth, stomach-gut content	Marguerite Bay	Autumn, winter 2001, 2002,	Daly 2004
BL, WW, DW, C, N, gut evacuation, ingestion rate, growth	Bellingshausen Sea	Autumn 2001	Pakhomov et al. 2004
BL, WW, DW, C, growth	West of Adelaide Island, Marguerite Bay	July and August 2001	Ross et al. 2004
DW, C, N, O_2 consumption, NH_4^+ excretion, O : N, total lipid, protein	Bellingshausen Sea	Autumn 2001	Meyer and Oettl 2005

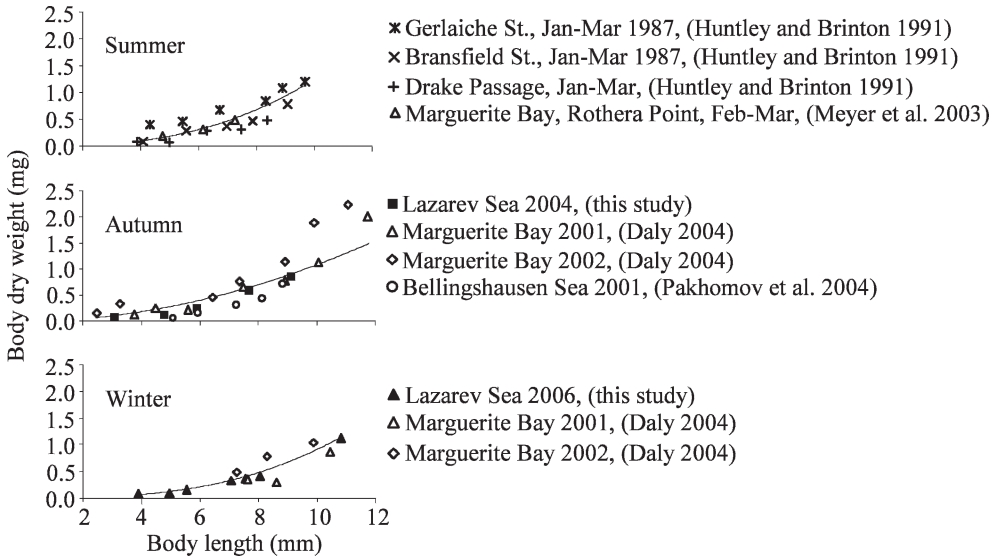

Fig. 14. *Euphausia superba*. Relationship between body length and dry weight of larval krill from the Lazarev Sea compared with previous studies. The equations demonstrate the best fit of all data. Summer: $y = 0.0027x^{2.65}$, $r^2 = 0.68$, $n = 19$, $p < 0.01$; autumn: $y = 0.0123x^{1.93}$, $r^2 = 0.71$, $n = 24$, $p < 0.001$; winter: $y = 0.0013x^{2.84}$, $r^2 = 0.91$, $n = 14$, $p < 0.001$.

Oithona spp. (mean, 8 ind. L^{-1}) was found. In an advective environment, ice refuges might therefore be essential for resting and feeding of krill larvae. According to Quetin et al. (2007), the timing of ice formation plays an important part in dictating habitat quality and hence survival of larval krill. Our results suggest that in addition to timing of formation, the local under-ice topography is also important. The condition of similar larval stages from Sta. 515 and the ice camp indicate that variable local conditions could be important. Larvae from Sta. 515 had much lower DW and BL and showed a high variability in their lipid content, despite seemingly better environmental conditions than at the ice camp. On their way within the current to Sta. 515 the larvae possibly encountered (1) a lack of refuges to rest and feed, (2) a lack of favorable feeding conditions in the refuges they found, or (3) both. Hence, when they reached Sta. 515, it was, according the condition parameters measured (Fig. 7; Table 3), too late for numerous larvae to survive. By then, the lipid content had fallen below the 3.5% DW^{-1} that is thought to be essential for survival (Hagen et al. 2001).

The differences observed in larval krill from the Lazarev Sea might reflect interannual as well as seasonal variability because the studies are not performed in a single year. Taken together, all of the above results point to a high potential of larval krill to survive Antarctic winter. During winter in the Lazarev Sea, larval krill utilized body lipids and nitrogenous compounds from a heterotrophic diet and, to some extent, from body protein for energy provision. The low oxygen uptake and growth rates seem to be a result of the low food availability during winter, rather than the result of an external trigger, such as light, as proposed for adult krill (Teschke et al. 2007). Moreover, we suggest that the physics under the sea ice (under-ice topography and current speed) could have a critical part to play in whether larval krill can exploit food associated with the sea ice or whether they drift within the current. Additional winter studies in areas with different under-ice topography, ice

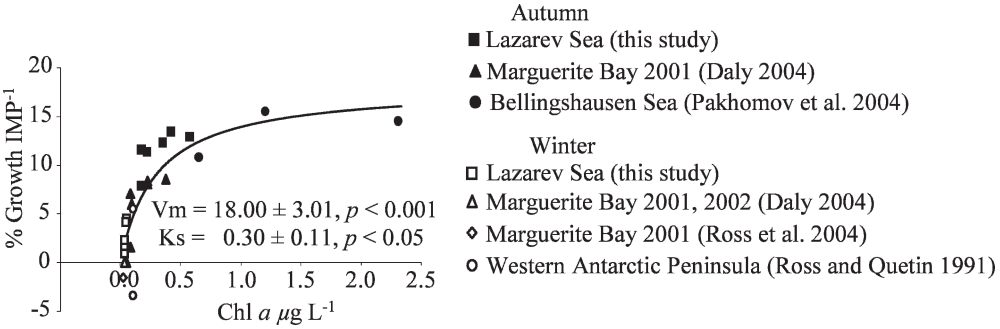

Fig. 15. *Euphausia superba*. Relationship between mean chlorophyll *a* (Chl *a*) concentration and percent growth per intermolt period (IMP^{-1}) of larval krill from autumn and winter in the Lazarev Sea compared with previous studies. Data are expressed as a Michaelis–Menten uptake function as follows: % growth $IMP^{-1} = 18.00[\text{Chl } a/(0.30 + \text{Chl } a)]$, $r^2 = 0.68$, $n = 25$.

texture, and oceanographic condition are necessary to evaluate of effects of these physical factors on the development of larval krill during winter.

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References

Anger, K. 2001. The biology of decapod crustacean larvae, p. 183–211. *In* R. Vonk [ed.], Crustacean. A. Balkema.

Archer, S. D., R. J. G. Leakey, P. H. Burkill, and M. A. Sleigh. 1996. Microbial dynamics in coastal waters of East Antarctica: Herbivory by heterotrophic dinoflagellates. Mar. Ecol. Prog. Ser **139:** 239–255.

Atkinson, A., B. Meyer, D. Stübing, W. Hagen, and U. V. Bathmann. 2002. Feeding and energy budgets of Antarctic krill *Euphausia superba* at the onset of winter—II. Juveniles and adults. Limnol. Oceanogr. **47:** 953–966.

———, V. Siegel, E. Pakhomov, and P. Rothery. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature **432:** 100–103.

———, and others. 2008. Oceanic circumpolar habitats of Antarctic krill. Mar. Ecol. Prog. Ser. **362:** 1–23.

Brinton, E., and A. W. Townsend. 1984. Regional relationships between development and growth in larvae of Antarctic krill, *Euphausia superba*, from field samples. J. Crustac. Biol. **4:** 224–246.

Buck, K. R., D. L. Garrison, and L. Hopkins. 1992. Abundance and distribution of tintinnid ciliates in an ice edge zone during the austral autumn. Antarct. Sci. **4:** 3–8.

Daly, K. L. 1990. Overwintering development, growth, and feeding of larval *Euphausia superba* in the Antarctic marginal ice zone. Limnol. Oceanogr. **35:** 1564–1576.

———. 2004. Overwintering growth and development of larval *Euphausia superba* an interannual comparison under varying environmental conditions west of the Antarctic Peninsula. Deep-Sea Res. II. **51:** 2139–2168.

———, and M. C. Macaulay. 1991. Influence of physical and biological mesoscale dynamics on the seasonal distribution and behaviour of *Euphausia superba* in the Antarctic marginal ice zone. Mar. Ecol. Prog. Ser. **79:** 37–66.

Fiala, M., H. Kuosa, E. E. Kopczyńska, L. Oiriol, and D. Delille. 2006. Spatial and seasonal heterogeneity of sea ice microbial communities in the first-year ice of Terre Adélie area (Antarctica). Aquat. Microb. Ecol. **43:** 95–106.

Fraser, F. C. 1936. On the development and distribution of young stages of krill (*Euphausia superba*). Discov. Rep. **24:** 1–192.

Frazer, T. K., L. B. Quetin, and R. M. Ross. 1997. Abundance and distribution of larval krill, *Euphausia superba*, associated with annual sea ice in winter, p. 107–111. *In* B. Battaglia, J. Valencia and D. W. H. Walton [eds.], Antarctic communities: Species, structure and survival. Cambridge Univ. Press.

———, ———, and ———. 2002*a*. Energetic demands of larval krill, *Euphausia superba*, in winter. J. Exp. Mar. Biol. Ecol. **277:** 157–171.

———, ———, and ———. 2002*b*. Abundance, sizes and developmental stages of larval krill, *Euphausia superba,* during winter in ice-covered seas, west of the Antarctic Peninsula. J. Plankton Res. **24:** 1067–1077.

Freier, U., M. S. Yasseri, S. Spahic, C. Pape, H. Flores, A. Olariaga, and L. Auerswald. 2008. Scientific diving under Antarctic winter conditions during ANT-XXIII/6, p. 122–129. *In* U. Bathmann [ed.], Reports on polar and marine research 580, Alfred-Wegener Institut, http://hdl.handle.net/10013/epic.30948.

Fritsen, C. H., J. Memmott, and F. J. Stewart. 2008. Interannual sea-ice dynamics and micro-algal biomass in winter pack ice of Marguerite Bay, Antarctica. Deep-Sea Res. II **55:** 2059–2067.

Garrison, D. L., and A. R. Close. 1993. Winter ecology of the sea ice biota in Weddell Sea pack ice. Mar. Ecol. Prog. Ser. **96:** 17–31.

———, A. Gibson, S. L. Coale, M. M. Gowing, Y. B. Okolodkov, C. H. Fritsen, and M. O. Jeffries. 2005. Sea-ice microbial communities in the Ross Sea: Autumn and summer biota. Mar. Ecol. Prog. Ser. **39:** 39–52.

Hagen, W. 2000. Lipids, p. 113–147. *In* R. P. Harris, P. H. Wiebe, J. Lenz, H. R. Skjoldal and M. Huntley [eds.], I.C.E.S. zooplankton methodology manual. Academic.

———, G. Kattner, A. Terbrüggen, and E. S. Van Vleet. 2001. Lipid metabolism of the Antarctic krill *Euphausia superba* and its ecological implications. Mar. Biol. **139:** 95–104.

Hoffmann, E. E., and Y. S. Hüsrevoğlu. 2003. A circumpolarmodeling study of habitat control of Antarctic krill (*Euphausia superba)* reproductive success. Deep-Sea Res. II **51:** 1323–1331.

Hopkins, T. L., and J. J. Torres. 1989. Midwater food web in the vicinity of a marginal ice zone in the western Weddell Sea. Deep-Sea Res. **36:** 543–560.

Huntley, M., and E. Brinton. 1991. Mesoscale variation in growth and early development of *Euphausia superba* Dana in the western Bransfield Strait region. Deep-Sea Res. **38:** 1213–1240.

———, W. Nordhausen, and M. D. G. Lopez. 1994. Elemental composition, metabolic activity and growth of Antarctic krill *Euphausia superba* during winter. Mar. Ecol. Prog. Ser. **107:** 23–40.

Ikeda, T. 1981. Metabolic activity of larval stages of Antarctic krill. Antarct. J. US **16:** 161–162.

———, J. J. Torres, S. Hernandez-Leon, and S. P. Geiger. 2000. Metabolism, p. 455–532. *In* R. Harris, P. H. Wiebe, J. Lenz, H. R. Skjoldal and M. Huntley [eds.], I.C.E.S. zooplankton methodolgy manual. Academic.

Johnson, M. A., M. C. Macaulay, and D. C. Biggs. 1984. Respiration and excretion within a mass aggregation of *Euphausia superba*: Implications for krill distribution. J. Crust. Biol. **4:** 174–184.

Kang, S.-H., J.-S. Kang, S. Lee, K. H. Chung, D. Kim, and M. G. Park. 2001. Antarctic phytoplankton assemblages in the marginal ice zone of the northwestern Weddell Sea. J. Plankton Res. **4:** 333–352.

Karlson, K., and U. Båmstedt. 1994. Planktivorous predation on copepods. Evaluation of mandible remains in predator guts as a quantitative estimate of predation. Mar. Ecol. Prog. Ser. **108:** 79–89.

Kawaguchi, K., S. Ishikawa, and O. Matsuda. 1986. The overwintering strategy of Antarctic krill (*Euphausia superba* Dana) under the coastal fast ice off the Ongul Islands in Lützow-Holm Bay, Antarctica. Mem. Nat. Inst. Polar Res. **44:** 67–85.

Kawaguchi, S., and S. Nicol. 2007. Learning about Antarctic krill from the fishery. Antarct. Sci. **19:** 219–230.

Le Fèvre, J., L. Legendre, and R. B. Rivkin. 1998. Fluxes of biogenic carbon in the Southern Ocean: Roles of large microphagous zooplankton. J. Mar. Syst. **17:** 325–345.

Loeb, V., V. Siegel, O. Holm-Hansen, R. Hewitt, W. Fraser, W. Trivelpiece, and S. Trivelpiece. 1997. Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. Nature **387:** 897–900.

Lowry, O. H., N. J. Rosebrough, A. L. Farr, and R. J. Randall. 1951. Protein measurement with the Folin Phenol reagent. J. Biol. Chem. **193:** 265–275.

Makarov, R. R., and L. L. Menshenina. 1992. Larvae of euphausiids of Queen Maud Land. Polar Biol. **11:** 525–523.

Marr, J. W. S. 1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). Discov. Rep. **32:** 33–464.

Mauchline, J. 1998. The biology of calanoid copepods. Adv. Mar. Biol. **33:** 1–710.

Meyer, B., A. Atkinson, B. Blume, and U. V. Bathmann. 2003. Feeding and energy budgets of larval Antarctic krill, *Euphausia superba*, in summer. Mar. Ecol. Prog. Ser. **257:** 167–178.

———, ———, D. Stübing, B. Oettl, W. Hagen, and U. V. Bathmann. 2002. Feeding and energy budgets of Antarctic krill *Euphausia superba* at the onset of winter—I. Furcilia III larvae. Limnol. Oceanogr. **47:** 943–952.

———, and B. Oettl. 2005. Effects of short term starvation on composition and metabolism of larval Antarctic krill, *Euphausia superba* 2005. Mar. Ecol. Prog. Ser. **292:** 263–270.

Ming, F. W. 1985. Ammonia excretion rate as an index for comparing efficiency of dietary protein utilization among Rainbow Trout (*Salmo gairdneri*) of different strains. Aquaculture **46:** 27–35.

Muench, R. D., J. H. Morison, L. Padman, D. Martinson, P. Schlosser, B. Huber, and R. Hohmann. 2001. Maud Rise revisited. J. Geophys. Res. **106:** 2423–2440.

Pakhomov, E., A. Atkinson, B. Meyer, B. Oettl, and U. V. Bathmann. 2004. Daily rations and growth of larval krill *Euphausia superba* in the Eastern Bellingshausen Sea during austral autumn. Deep-Sea Res. II **51:** 2185–2198.

Quetin, L. B., and R. M. Ross. 1991. Behavioural and physiological characteristics of the Antarctic krill, *Euphausia superba*. Am. Zool. **31:** 49–63.

———, ———, C. H. Fritsen, and M. Vernet. 2007. Ecological responses of Antarctic krill to environmental variability: Can we predict the future? Antarct. Sci. **19:** 253–266.

———, ———, T. K. Frazer, M. O. Amsler, C. Wyatt-Evens, and S. A. Oakes. 2003. Growth of larval krill, *Euphausia superba*, in fall and winter west of the Antarctic Peninsula. Mar. Biol. **143:** 833–843.

Rosa, R., and M. L. Lunes. 2005. Seasonal patterns of nucleic acid concentrations and amino acid profiles of *Parapenaeus longirostris* (Crustacea, Decapoda): Relation to growth and nutritional condition. Hydrobiologia **537:** 207–216.

Ross, R. M., and L. B. Quetin. 1991. Ecological physiology of larval euphausiids, *Euphausia superba* (Euphausiacea). Mem. Qld. Mus. **31:** 321–333.

———, ———, K. S. Baker, M. Vernet, and R. S. Smith. 2000. Growth limitation in young *Euphausia superba* under field conditions. Limnol. Oceanogr. **45:** 31–43.

———, ———, T. Newberger, and S. A. Oakes. 2004. Growth and behaviour of larval krill (*Euphausia superba*) under the ice in late winter 2001 west of the Antarctic Peninsula. Deep-Sea Res. II **51:** 2169–2184.

Schmidt, K., A. Atkinson, K.-J. Petzke, M. Voss, and D. W. Pond. 2006. Protozoans as a food source for Antarctic krill, *Euphausia superba*: Complementary insights from stomach content, fatty acids, and stable isotopes. Limnol. Oceanogr. **51:** 2409–2427.

———, ———, J. W. McClelland, J. P. Montoya, and M. Voss. 2003. Trophic relationships among Southern Ocean copepods and krill. Some uses and limitations of a stable isotope approach. Limnol. Oceanogr. **48:** 277–289.

Schnack-Schiel, S. B., G. S. Dieckmann, R. Gradinger, L. A. Melnikov, N. Spindler, and D. N. Thomas. 2001. Meiofauna in sea ice of the Weddell Sea (Antarctica). Polar Biol. **24:** 724–728.

Schröder, M., and E. Fahrbach. 1999. On the structure and the transport of the eastern Weddell Gyre. Deep-Sea Res. II **46:** 501–527.

Siegel, V. 2005. Distribution and population dynamics of *Euphausia superba*: Summary of recent findings. Polar Biol. **29:** 1–22.

Solorzano, L. 1969. Determination of ammonia in natural waters by the phenolhypochlorite method. Limnol. Ocenogr. **14:** 799–801.

Spiridonov, V. A., E.-M. Nöthig, M. Schröder, and A. Wisotzki. 1996. The onset of biological winter in the eastern Weddell Gyre (Antarctica) planctonic community. J. Mar. Syst. **9:** 211–230.

Teschke, M., S. Kawaguchi, and B. Meyer. 2007. Simulated light regimes affect feeding and metabolism of Antarctic krill, *Euphausia superba*. Limnol. Oceanogr. **52:** 1046–1054.

Thompson, G. A. 2001. Distribution and abundance of microzooplankton from the Atlantic sector of the Southern Ocean with emphasis of the biogeography of Tintinnida (Protozoa: Ciliata). Ph.D. thesis. Univ. of Buenos Aires.

Torres, J. J., J. Donnelly, T. L. Hopkins, T. M. Lancraft, A. V. Aarset, and D. G. Ainley. 1994. Proximate composition and overwintering strategies of Antarctic micronektonic Crustacea. Mar. Ecol. Prog. Ser. **113:** 221–232.

Zarr, J. H. 1999. Biostatistical analysis. Prentice-Hall.

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