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 Bathmanna

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 understice 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 NH₄ 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 depends both on how potential recruits enter the population during the following spring. Therefore, recruitment success depends on 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. 2002a; 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 (Hunley 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 Ciències del Mar (CSIC), Barcelona, Spain
Quetin 1991; Meyer et al. 2002). Larval respiration rates seem to be reduced in winter (Frazer et al. 2002), 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, 2.5°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 Hüsevoyglo 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°S, 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
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 m³ 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 m³ 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).
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 \(-280^\circ C\) 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 \(g\) 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 Titirino (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

\[
f = \frac{N_m}{N_i} \frac{1}{d}
\]

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) and 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):

\[
GI = 100 \left( \frac{L_a - L_m}{L_m} \right)
\]

The change in BL over the intermolt period was determined from a linear regression of BL of uropod length,
samples were collected with a bucket over the,
During the winter expedition, larvae
Figure 4 summarizes the
20.1
0.1
samples

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 whisk, 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 \( \times 200 \) magnification.
Subsequently, common small diatoms and other thecate
flagellates were enumerated on two perpendicular scans
across the whole diameter of the receptacle at \( \times 200 \)
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 Bämstedt 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 \(-20^\circ\)C in the dark
for at least 24 h. Chlorophyll fluorescence was then measured
with a Turner 700D 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 \pm 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 \(-1.4 \pm 0.4°C\). The Chl \( a \) concentration in the upper 5 m of the water column was
highly variable, ranging from very low (0.07 \( \mu \)g Chl \( a \) L\(^{-1}\))
in open-water regions (north of 68°S) to 3.02 \( \mu \)g 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 phyto-
plankton into the ocean.

During the winter cruise, mean seawater temperature in
the upper 50 m was \(-1.8 \pm 0.1°C\). Chl \( a \) concentration was
very low, ranging from 0.01 to 0.04 \( \mu \)g 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%
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

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.
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

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, calyptopy; F, furcilia. n, No. of replicates.

<table>
<thead>
<tr>
<th>Larval stage</th>
<th>Open water</th>
<th>Ice cover</th>
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<tbody>
<tr>
<td></td>
<td>Autumn 2004</td>
<td>Winter 2006</td>
</tr>
<tr>
<td></td>
<td>BL: 3.03 (2.97–3.14)</td>
<td>BL: 3.45 (3.76–4.03)</td>
</tr>
<tr>
<td></td>
<td>DW: 0.06 (0.05–0.06)</td>
<td>DW: 0.08 (0.07–0.09)</td>
</tr>
<tr>
<td>CII</td>
<td>BL: 4.35 (2.97–5.65)</td>
<td>BL: 4.89 (4.55–5.43)</td>
</tr>
<tr>
<td></td>
<td>DW: 0.05 (0.03–0.08)</td>
<td>DW: 0.10 (0.07–0.19)</td>
</tr>
<tr>
<td>FII</td>
<td>BL: 5.87 (5.68–5.99)</td>
<td>BL: 5.50 (5.47–6.01)</td>
</tr>
<tr>
<td></td>
<td>DW: 0.16 (0.12–0.22)</td>
<td>DW: 0.19 (0.17–0.24)</td>
</tr>
<tr>
<td>FIII</td>
<td>BL: 5.78 (5.68–5.99)</td>
<td>BL: 7.00 (5.94–8.30)</td>
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<tr>
<td></td>
<td>DW: 0.16 (0.12–0.22)</td>
<td>DW: 0.35 (0.21–0.52)</td>
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<td></td>
<td>DW: 0.16 (0.12–0.22)</td>
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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 O₂ mg⁻¹ DW h⁻¹) than during winter (0.54 ± 0.19 μL O₂ 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 NH₄ mg⁻¹ DW h⁻¹) compared with autumn (0.03 ± 0.01 μg NH₄ 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 (Carlson and Bämstedt 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, foraminifers, 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 ± 1 × 10⁶ μm³ in autumn and 0.9 ± 1 × 10⁶ μm³ 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 vanhoeoffeni*, *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, furcella. n, No. of replicates.

<table>
<thead>
<tr>
<th>Larval stage</th>
<th>% body C</th>
<th>% body N</th>
<th>C : N ratio</th>
<th>% body lipid</th>
<th>% body protein</th>
</tr>
</thead>
<tbody>
<tr>
<td>CIII</td>
<td>37.8 (31.7–42.5)</td>
<td>29.4 (25.6–32.0)</td>
<td>9.0 (7.4–10.4)</td>
<td>10.0 (9.5–10.2)</td>
<td>4.2 (3.5–4.8)</td>
</tr>
<tr>
<td>n</td>
<td>40</td>
<td>10</td>
<td>40</td>
<td>10</td>
<td>40</td>
</tr>
<tr>
<td>FI</td>
<td>39.3 (23.9–48.1)</td>
<td>29.5 (28.4–31.7)</td>
<td>9.0 (6.1–15.1)</td>
<td>9.5 (9.1–10.2)</td>
<td>4.4 (2.8–3.1)</td>
</tr>
<tr>
<td>n</td>
<td>150</td>
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<tr>
<td>FII</td>
<td>44.3 (33.9–51.9)</td>
<td>31.0 (30.1–31.8)</td>
<td>9.5 (7.1–12.2)</td>
<td>9.3 (9.0–10.1)</td>
<td>4.5 (3.3–5.5)</td>
</tr>
<tr>
<td>n</td>
<td>24</td>
<td>12</td>
<td>24</td>
<td>12</td>
<td>24</td>
</tr>
<tr>
<td>FIII</td>
<td>44.2 (40.9–46.7)</td>
<td>34.8 (32.8–40.3)</td>
<td>9.3 (8.3–10.3)</td>
<td>9.6 (8.9–11.0)</td>
<td>4.7 (3.9–5.4)</td>
</tr>
<tr>
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<td>43</td>
<td>24</td>
<td>43</td>
<td>24</td>
<td>43</td>
</tr>
<tr>
<td>FIV</td>
<td>—</td>
<td>31.6 (30.0–37.5)</td>
<td>—</td>
<td>8.9 (8.6–10.6)</td>
<td>—</td>
</tr>
<tr>
<td>n</td>
<td>13</td>
<td>17</td>
<td>13</td>
<td>17</td>
<td>13</td>
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<tr>
<td>FV</td>
<td>—</td>
<td>33.1 (31.1–38.4)</td>
<td>—</td>
<td>9.1 (8.0–10.2)</td>
<td>—</td>
</tr>
<tr>
<td>n</td>
<td>24</td>
<td>24</td>
<td>24</td>
<td>24</td>
<td>24</td>
</tr>
<tr>
<td>FVI</td>
<td>—</td>
<td>37.5 (33.2–39.8)</td>
<td>—</td>
<td>8.6 (8.3–9.1)</td>
<td>—</td>
</tr>
<tr>
<td>n</td>
<td>13</td>
<td>13</td>
<td>13</td>
<td>13</td>
<td>13</td>
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</tbody>
</table>
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...
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.
During autumn, the physiological condition of larval krill (Euphausia superba) 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, 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.

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, 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.

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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 \(\alpha\) (Chl \(\alpha\)) 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.

<table>
<thead>
<tr>
<th>Station</th>
<th>Larval stages</th>
<th>Growth</th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>GI (%)</td>
<td>mm d(^{-1})</td>
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<tr>
<td></td>
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<tr>
<td></td>
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<td></td>
</tr>
<tr>
<td>609</td>
<td>CIII–FI</td>
<td>11.1</td>
<td>0.0060</td>
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<tr>
<td>612</td>
<td>CIII–FI</td>
<td>10.8</td>
<td>0.0100</td>
</tr>
<tr>
<td>615</td>
<td>CIII–FIII</td>
<td>7.1</td>
<td>0.0080</td>
</tr>
<tr>
<td>628</td>
<td>FI–FIII</td>
<td>11.1</td>
<td>0.0142</td>
</tr>
<tr>
<td>661</td>
<td>FII–FIV</td>
<td>13.2</td>
<td>0.0152</td>
</tr>
<tr>
<td>665</td>
<td>FI–FIII</td>
<td>12.8</td>
<td>0.0151</td>
</tr>
<tr>
<td>478</td>
<td>FII–FV</td>
<td>3.6</td>
<td>0.0025</td>
</tr>
<tr>
<td>498A</td>
<td>FIV–FVI</td>
<td>1.4</td>
<td>0.0008</td>
</tr>
<tr>
<td>498B</td>
<td>FIV–FVI</td>
<td>1.9</td>
<td>0.0011</td>
</tr>
<tr>
<td>498D</td>
<td>FIV–FVI</td>
<td>4.1</td>
<td>0.0019</td>
</tr>
<tr>
<td>515</td>
<td>FIV–FVI</td>
<td>1.3</td>
<td>0.0005</td>
</tr>
</tbody>
</table>

Our results show 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). 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 \(\alpha\) 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 \(\alpha\) concentrations and larval growth rates are much lower than those during autumn (Table 6). The use of water column Chl \(\alpha\) 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 \(\alpha\) 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 protein. Amino acids would become available for energy production after their release from hydrolyzed dietary and protein availability (Brinton and Townsend 1984). 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 \(\alpha\) 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 \(\alpha\) concentrations and larval growth rates are much lower than those during autumn (Table 6). The use of water column Chl \(\alpha\) 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 \(\alpha\) concentrations. Thus, some other food source and body substrates, such as
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). The low respiration rates in winter are comparable to rates of starved furcilia (Frazer et al. 2002; 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).

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Fig. 10. *Euphausia superba*. Relationship of surface chlorophyll $a$ (Chl $a$) concentration (see Table 6) to growth $\pm$ 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.

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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
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; Rosset 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

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 (μm³ stomach⁻¹) and per dry weight (μm³ 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.

<table>
<thead>
<tr>
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<th>Autumn</th>
<th>Winter</th>
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<tbody>
<tr>
<td></td>
<td>Sta. 621</td>
<td>Sta. 660</td>
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<td>FI (n=3)</td>
<td>FIII (n=4)</td>
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<tr>
<td>Silicoflagellates (items sample⁻¹)</td>
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<td>2</td>
</tr>
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<td>Diatoms</td>
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<td></td>
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<tr>
<td>Discoid (broken)</td>
<td>91</td>
<td>8</td>
</tr>
<tr>
<td>Discoid (small, complete)</td>
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<tr>
<td>Discoid (medium, complete)</td>
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<td>15</td>
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<tr>
<td>Fragilaria spp. (small)</td>
<td>1231</td>
<td>104</td>
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<td>Fragilaria spp. (medium)</td>
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<td>856</td>
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<td>Pennate (medium)</td>
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<td>Codonellopsis spp.</td>
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</tr>
<tr>
<td>Cymatocylis spp.</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Foraminifera</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Cnidaria</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nematocysts</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Copepods</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mandibles</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>Appendages</td>
<td>26</td>
<td>2</td>
</tr>
<tr>
<td>Krill</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Setae</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>Setulae</td>
<td>5</td>
<td>167</td>
</tr>
<tr>
<td>Furcilia DW (mg ind⁻¹)</td>
<td>0.47</td>
<td>0.8</td>
</tr>
<tr>
<td>Volume of items (×10⁶ μm³ stomach⁻¹)</td>
<td>1.3</td>
<td>0.7</td>
</tr>
<tr>
<td>Volume of items (×10⁶ μm³ mg⁻¹ DW)</td>
<td>2.8</td>
<td>0.9</td>
</tr>
</tbody>
</table>

Fig. 11. Euphausia superba. Contribution of different plankton groups to the total estimated volume of identifiable stomach items (×10⁶ μm³ mg⁻¹ DW) in furcilia I–VI larvae (FI–FVI) from the Lazarev Sea in the Antarctic autumn and winter.
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 \( \text{\text{8c ms}^{-2}} \), 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, 2002b), 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. 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.
This simplified conceptual model is based on literature observations, as well as those reported here, and reflects the general latitudinal gradient in Chl α 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.

<table>
<thead>
<tr>
<th>Parameter measured</th>
<th>Region</th>
<th>Season</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>O₂ consumption, NH₄⁺ excretion, O: N</td>
<td>Weddell–Scotia Sea</td>
<td>January–March</td>
<td>Ikeda 1981</td>
</tr>
<tr>
<td>BL, growth</td>
<td>Scotia Sea</td>
<td>Mid and late summer 1981</td>
<td>Brinton and Townsend 1984</td>
</tr>
<tr>
<td>Stomach gut content</td>
<td>Western Weddell Sea</td>
<td>Autumn 1986</td>
<td>Hopkins and Torres 1989</td>
</tr>
<tr>
<td>BL, WW, gut evacuation, ingestion, clearance rate, growth, stomach content</td>
<td>Weddell–Scotia Sea</td>
<td>Winter</td>
<td>Daly 1990</td>
</tr>
<tr>
<td>O₂ consumption, NH₄⁺ excretion, O: N</td>
<td>Western Antarctic Peninsula</td>
<td>Winter 1991, 1993</td>
<td>Frazer et al. 2002b</td>
</tr>
<tr>
<td>O₂ consumption, NH₄⁺ excretion, O: N</td>
<td>Lazarev Sea</td>
<td>Autumn 1999</td>
<td>Meyer et al. 2002</td>
</tr>
<tr>
<td>BL, DW, C, N, total lipid, protein, carbohydrates, O₂ consumption, ingestion, clearance rate, assimilation efficiency</td>
<td>Rothera Time Series monitoring station</td>
<td>Late summer 2000</td>
<td>Meyer et al. 2003</td>
</tr>
<tr>
<td>BL, WW, DW, C, N, gut evacuation, ingestion rate, growth</td>
<td>Bellinghausen Sea</td>
<td>Autumn 2001</td>
<td>Pakhomov et al. 2004</td>
</tr>
<tr>
<td>BL, WW, DW, C, growth</td>
<td>West of Adelaide Island, Marguerite Bay</td>
<td>July and August 2001</td>
<td>Ross et al. 2004</td>
</tr>
<tr>
<td>DW, C, N, O₂ consumption, NH₄⁺ excretion, O: N, total lipid, protein</td>
<td>Bellinghausen Sea</td>
<td>Autumn 2001</td>
<td>Meyer and Oettl 2005</td>
</tr>
</tbody>
</table>
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

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O. 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: \( y = 0.0013x^{2.84}, r^2 = 0.91, n = 14, p < 0.001. \)

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E. 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[Chl \( a \)/(0.30 + 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.

Acknowledgments

We thank the captain and crew of RV Polarstern for their professional support on both cruises. We are especially grateful to the diving team and the help of numerous cruise participants who contributed to the success of the first diving activities of the Alfred-Wegener Institute (AWI) in Antarctic winter. We also thank Lutz Auerswald and two anonymous referees for their constructive improvements on the manuscript. We are grateful to the National Aeronautics and Space Administration (NASA) and the National Oceanic and Atmospheric Administration (NOAA) for the use of satellite-derived Chl a and sea ice data.

This work was supported by funding from the German Ministry of Education and Science through project 03F0400A, Subproject 4, of the Lazarev Sea Krill Study (LAKRIS) Project, and the Natural Environment Research Council (United Kingdom, AFI 5/09). The LAKRIS Project is the German contribution to the Southern Ocean–Global Ocean Ecosystem Dynamics (SO-GLOBE) program. The data of the publication are available at: doi:10.1594/PANGAEA.707193.

References


Associate editor: Michael R. Landry

Received: 02 November 2008
Accepted: 03 April 2009
Amended: 12 May 2009