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Daily rations and growth of larval krill *Euphausia superba* in the Eastern Bellingshausen Sea during austral autumn

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Abstract

As the German contribution to the Southern Ocean Global Ocean Ecosystems Dynamics Study (SO GLOBEC), RV *Polarstern* visited the Eastern Bellingshausen Sea between 18 April and 1 May 2001. This paper examines in situ feeding cycles, ingestion rates and growth of larval krill *Euphausia superba*. Larval krill were exceptionally numerous, especially over the shelf break and continental slope: mean 8872 larvae m^{-2}, maximum 30 084 larvae m^{-2}. The developmental stage composition of krill larvae over the shelf was advanced compared to that at continental slope stations, which may have resulted from enhanced food availability over the shelf. Despite the season being late autumn, the feeding activity of larval krill was similar to published summer rates. The intermoult period of larval krill ranged from 6 to 17 days, with daily growth rates reaching 2.2% of body length, 8.7% of body wet mass and 5.7% of body carbon. Daily ingestion rates were 8.5–17.6 μg C ind^{-1} d^{-1} for calyptopis 3 to furcilia 2 and 35.1–57.4 μg C ind^{-1} d^{-1} for furcilia 3–5, and were positively correlated with ambient chlorophyll *a* concentrations. Daily rations showed the same tendency, ranging from 21.5 to 44.5% of body C d^{-1} (calyptopis 3 to furcilia 2) and from 17.8 to 29.2% of body C d^{-1} (furcilia 3–5). Comparison of daily rations between open water and sea ice stations supports the notion that larval krill at low pelagic food supply under the sea ice have to exploit ice biota to sustain their metabolic demands.

1. Introduction

Antarctic krill *Euphausia superba* (hereafter "krill") is a keystone species of the Southern Ocean, supporting numerous populations of apex predators, including fish, squid, birds and mammals, as well as a commercial fishery (Knox, 1994). Despite major research efforts starting over a century ago in the Southern Ocean, there are still many gaps in our knowledge of the biology of adult krill and particularly of their larvae (e.g., Miller and Hampton, 1989; Daly, 1990; Ross and Quetin, 1991). Several studies have focused on

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larval and adult krill overwintering strategies (e.g., Daly, 1990; Hagen et al., 2001; Atkinson et al., 2002b). There is growing evidence that, due to differences in ecophysiology and biochemistry, larval and adult krill probably adopt "business as usual" and "compromise" (*sensu* Torres et al., 1994) overwintering strategies, respectively (Daly, 1990; Atkinson et al., 2002b; Meyer et al., 2002). After adult spawning in December–March, krill larvae usually grow to furcilia stage 2–3 by autumn (Fraser, 1936; Makarov et al., 1990; Huntley and Brinton, 1991). If larval krill adopt "business as usual" they have to change from a pelagic to an under the sea-ice habitat between summer and winter for continuous feeding, since a pelagic habitat is unlikely able to sustain sufficient food supply during winter (Daly, 1990; Ross and Quetin, 1991; Meyer et al., 2002). To date, only a few studies have addressed the ecophysiology of larval krill. Daily rations of furcilia have been estimated in only three studies: using gut fluorescence during austral winter in the Scotia Sea (Daly, 1990), in vitro incubations in the southwestern Lazarev Sea (Meyer et al., 2002), and an energetic approach in the western Bransfield Strait region (Huntley and Brinton, 1991). The values ranged widely from 0.4 to 52% of body C d^{-1}.

In a study of Gerlache Strait in 1986–87, Huntley and Brinton (1991) suggested that coastal regions along the Antarctic Peninsula may be significant nursery areas for krill larvae and may act as "focal points in krill recruitment". During April–May 2001, a German Southern Ocean Global Ocean Ecosystems Dynamics (SO GLOBEC) cruise in the Eastern Bellingshausen Sea was conducted. Its main objective was to examine interactions between zooplankton and the physical conditions during the autumn transitional period in this suggested krill "nursery area" (Siegel, 1989, 2000). The main aim of this study was to provide information on feeding dynamics of larval krill using the gut fluorescence technique, and to measure its growth.

2. Material and methods

Data were collected during the expedition ANTARKTIS XVIII/5b to the Eastern Bellingshausen Sea on board RV *Polarstern* conducted between 18 April and 1 May 2001 as the German contribution to the field campaign of the SO GLOBEC (Fig. 1; Bathmann, 2002). At each oceanographic station, seawater temperature, salinity and density were measured using a Sea-Bird Electronics SBE 911 conductivity-temperature-depth (CTD) profiler, which was mounted on a Sea-Bird SBE 32 Carousel holding 24 Niskin bottles of 12 l capacity (Strass et al., 2002). Water samples for total chlorophyll *a* (Chl *a*) were collected at eight standard depths: 0, 10, 25, 50, 75, 100, 150 and 200 m (Brichta and Belem, 2002). Chl *a* was extracted from 1000-ml aliquots in 90% aqueous acetone following filtration through GFF Whatman filters for 12 h in the dark at −18 °C. Concentrations were calculated from fluorescence readings on a Turner Design 10AU fluorometer before and after acidification with HCl (Parsons et al., 1984).

2.1. Larval krill sampling and grazing

Larval krill were collected using a Bongo net (0.5 m^{-2} mouth area, mesh size 300 μm) during vertical tows from 300 m to the surface. Zooplankton samples from one of the net pair were pored through a 300-μm mesh, placed in a plastic bag and immediately transferred to a deep freezer (−80 °C). These samples were used for determination of larval krill abundance and additional measurements of gut fluorescence (see below). Gut pigment content and grazing rates of larval krill were measured from the other net throughout the sampling period at every station. The in situ gut contents were measured either onboard ship by processing from 2 to 6 krill larvae per tube according to developmental stages, including early (calyptopis 3 to furcilia 2) and late stage (3–5) furcilia. In addition, at selected stations gut pigments of different developmental stages were determined using deep-frozen (−80 °C) samples. Deep-frozen samples were thawed in the refrigerator in darkness for several hours, rinsed briefly in deionised water, sorted on ice according to developmental stage and placed (three to five specimens per tube) in 10-ml polypropylene tubes for pigment extraction. The remaining larvae were

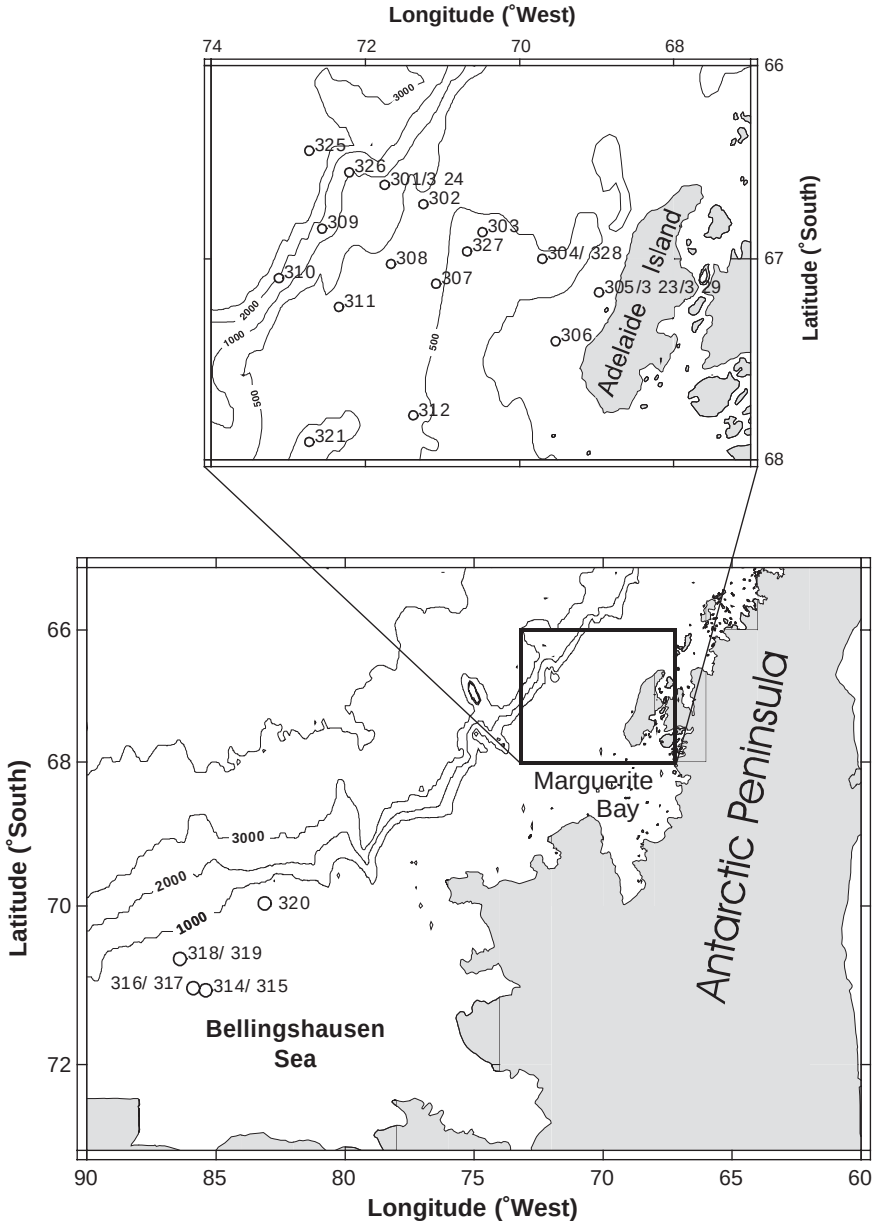

Fig. 1. Location of stations conducted during the ANTARKTIS XVIII/5b cruise to the Eastern Bellingshausen Sea on board RV *Polarstern* between 18 April and 1 May 2001.

counted and their developmental stages were determined.

Gut evacuation rate experiments consisted of in vitro incubations of 70–80 freshly caught specimens in 20-l polyethylene containers filled with surface seawater filtered through 0.2 μm (Milli-Q filtration system) to which non-fluorescent charcoal particles of <100 μm in diameter were added to simulate continuous feeding conditions (Willason and Cox, 1987). The incubations lasted 1.5–2 h, with gut fluorescence measured at 10–15 min intervals for the first hour and at

20–30-min intervals thereafter until the end of the experiment. Prior to each incubation, 5–10 fresh individuals were processed for the measurement of their initial gut pigment content. Gut evacuation rate constants (k, h^{-1}) were then derived from the slope of the regression versus time (Perissinotto and Pakhomov, 1996).

Gut pigment destruction efficiency was estimated using the two-compartment (phytoplankton and grazer) pigment budget approach. For this, freshly caught larvae were first incubated in particle-free seawater for 4–6 h to allow time to empty their guts. 3–5 specimens per jar were then incubated for 1 h in 1-l polyethylene containers containing natural seawater. After 1 h feeding, a comparison of the pigment budgets in the control (without grazers) and experimental containers was carried out. Any significant loss in the pigment budget from the experimental treatment (water + larval krill) was then attributed to gut destruction of phytoplankton pigments (Perissinotto and Pakhomov, 1996). In all experiments, gut pigments were extracted in polyethylene tubes (2–6 individuals per tube, 2–5 replicate tubes) with 10 ml of 90% acetone at –18 °C for 24 h in darkness. After centrifugation at 5000 rpm ($1745 \times g$), the pigment content was measured as for CTD extractions. Pigment contents were then expressed in terms of total pigments (Chl a + phaeopigments) per individual. Where the Chl a:phaeopigment ratio in the gut content was > 0.25, total pigment values were corrected according to Baars and Helling (1985). Background fluorescence was estimated from incubations of krill larvae in filtered seawater for 10–12-h and then subtracted from all gut pigment content data.

Daily ingestion rates (I, ng pigm ind^{-1} d^{-1}) were estimated from the relationship of Perissinotto (1992): $I = kG/(1-b')$, where G is an integrated value over 24 h period of gut pigments (ng pigm ind^{-1} d^{-1}), k is the gut evacuation rate constant (h^{-1}) and b' is efficiency of gut pigment destruction. To convert pigment concentrations into autotrophic carbon (C), we used a mean POC: pigment (Chl a + phaeopigments) ratio of 37.5, obtained at Stations 303 and 320 in the top 100-m water layer (M. Brichta and A. Belem, unpublished).

2.2. Moulting experiments

Three moulting experiments were conducted using larval krill collected gently with a hand-hauled Apstein net in the top 30-m water layer during darkness. One hundred and sixty-four to 174 furcilia (stages 1–6) were immediately transferred to 250- or 500-ml bottles (depending on size, one furcilia per jar) filled with surface seawater. Experiments were run for 2 days in darkness at ambient (0 °C) seawater temperature. At the end of each experiment, each jar was examined and all animals and moults were frozen at –80 °C. The intermoult period was calculated as the inverse of the fraction of the population that moulted per day (Nicol et al., 1992). To determine growth increments, the exopodite of the right uropod was measured on both the moult and the moulted animal using a microscope ocular micrometer. To calculate growth rates, 30 furcilia ranging from stage 1 to 5 were selected from the moulting experiments. Uropod- and total length (from the base of the eye to the tip of telson) were measured for these individuals before determination of their wet mass, dry mass and C and N masses. For dry mass, individual larvae were oven-dried for 36 h at 60 °C in pre-weighed tin capsules and then used for C and N mass measurements in a Carlo Erba 1500 analyser. Growth rates were expressed as the percentage change in uropod length between the postmoult krill and its moult. The percentage change in mass (wet, dry, carbon and nitrogen) was determined using uropod length–body mass regressions. The daily growth rates (d^{-1}) were calculated as the difference between the premoult and postmoult length/mass parameters divided by the intermoult period.

3. Results

3.1. Larval distribution, abundance and composition

Total larval density varied between 4 and 30 084 ind m^{-2} (Table 1). The highest concentrations (> 10 000 ind m^{-2}) were observed near the shelf break and over the continental slope, while

Table 1
E. superba larval abundance estimated using Bongo net during April and May 2001 in the Eastern Bellingshausen Sea

Area, station number	Date, 2001	Sampling depth (m)	Sampling time (local)	Chl-*a* biomass ($mg\,m^{-2}$)	Total larval density ($ind\,m^{-2}$)
Near shelf break, over continental slope					
309	20 Apr	0–300	06:40	110.7	18 984
324	28 Apr	0–300	20:42	44.0	30 084
325	29 Apr	0–300	08:00	16.5	14 164
326	29 Apr	0–300	21:23	15.1	14 544
Mean (±SD)					19 444±7423
Shelf region					
302	18 Apr	0–400	14:28	51.1	1004
304	19 Apr	0–100	01:37	30.3	26 516
305	19 Apr	0–300	06:49	86.2	188
306	19 Apr	0–200	11:00	59.9	4
312	21 Apr	0–300	12:37	130.9	44
323	28 Apr	0–200	06:55	89.9	60
327	30 Apr	0–300	16:21	53.8	1308
328	1 May	0–300	06:26	44.8	7760
329	1 May	0–300	12:45	99.6	680
Mean (±SD)					4174±8730

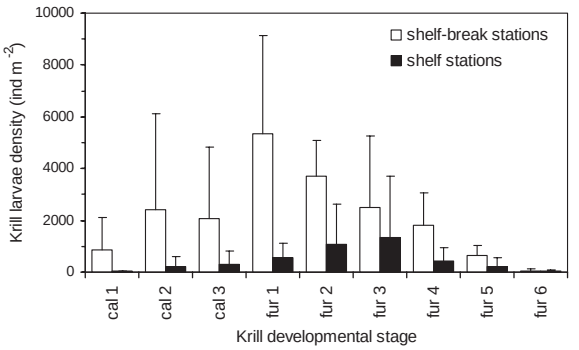

Fig. 2. Larval krill *E. superba* developmental composition in the Eastern Bellingshausen Sea during 18 April to 1 May 2001 according to Bongo net tows. Cal: calyptopis; fur: furcilia. Error bars represent 95% confidence limits.

over the shelf, with the exception of Station 304, larval concentrations did not exceed $8000\,ind\,m^{-2}$ (Table 1). Average larval densities were 4174 and $19\,444\,ind\,m^{-2}$ over the shelf area and near the shelf break, respectively. Krill larvae ranged from calyptopis 1 to furcilia 6. Although the larval composition was not significantly different (Spearman's rank test, $r=0.642$, $n=9$, $P>0.05$) between the shelf and near the shelf break regions, there was a clear tendency toward advanced larval composition over the shelf (Fig. 2). At stations near the shelf break and over the continental slope, furcilia 1 and 2 predominated, accounting on average for 47% of total larvae. Calyptopis 2 and 3 stages contributed on average 23% to total abundance. On stations over the shelf, furcilia 2 and 3 comprised ~60% of total larval abundance (Fig. 2).

3.2. Larval krill feeding dynamics

Individual gut pigment contents of krill larvae ranged widely between and within open-water and ice stations and between different stages (Fig. 3). Daytime gut pigment values were generally lower (occasionally significantly) than nighttime values. Furthermore, 57 and 26% of the variation in gut pigments in the open-ocean stations of early (calyptopis 3 to furcilia 2) and late (furcilia 3–5) furcilia was accounted for by variability in Chl *a* standing stock (Fig. 4). Thus for further analysis all larvae were separated into two age groups (early and late furcilia) and further according to ambient Chl *a* stock (lower or higher than $50\,mg\,m^{-2}$). However, for the ice stations all furcilia were pooled due to small differences in gut pigments among larval stages and the limited number of observations (Fig. 3).

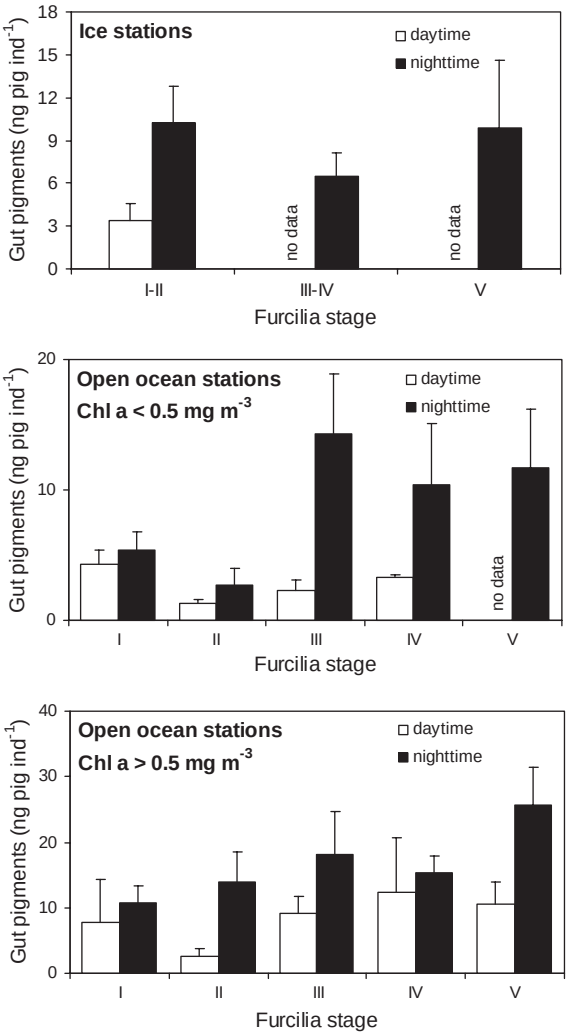

Fig. 3. Gut pigment levels of different developmental stages of larval krill on open water and ice stations. Error bars represent 95% confidence limits.

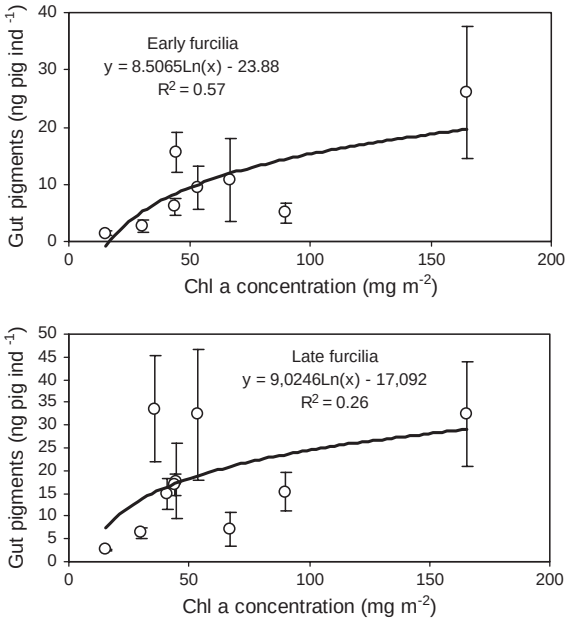

Fig. 4. Relationship between gut pigment contents and ambient chlorophyll *a* concentration in early and late furcilia of *E. superba* at nighttime stations in the Eastern Bellingshausen Sea during 18 April to 1 May 2001. *Y*: gut pigments (ng(pig) ind^{-1}); *X*: Chl *a* concentration ($mg\,m^{-2}$); Ln: natural logarithm. Error bars represent 95% confidence limits.

No dedicated 24-h stations were conducted during the cruise, so the diel series of in situ gut pigment contents of krill larvae are expressed simply as a composite of all stations separated according to Chl *a* ambient stock (Fig. 5). All data sets show elevated feeding rates at night (Fig. 5). There were approximately 2-fold differences in mean gut pigment contents of each larval group between stations with low and high Chl *a* stock (Fig. 5). Gut clearance rates of larval krill ranged from 0.65 to 1.72 h^{-1}, equivalent to gut passage times of 0.6–1.5 h (Table 2). Gut pigment destruction rates determined on two occasions ranged from 63 to 86% in early furcilia and from 60 to 89% in late furcilia (Table 3).

Daily ingestion rates of larval krill at ice stations were 612 ng pig $ind^{-1}\,d^{-1}$ or 23 μg C $ind^{-1}\,d^{-1}$, equivalent to 16.5% of body C d^{-1}. In open waters, daily ingestion rates of krill furcilia ranged from 226 to 1531 ng pig $ind^{-1}\,d^{-1}$, equivalent to 8.5–57 μg C $ind^{-1}\,d^{-1}$ or 18–45% of body C d^{-1} (Table 4).

3.3. Larval krill morphometrics, moulting and growth rates

Morphometric relationships obtained for the three moulting rate stations are presented in Fig. 6. The biometric parameters of krill furcilia 1–5 are summarised for comparative purposes in Table 5.

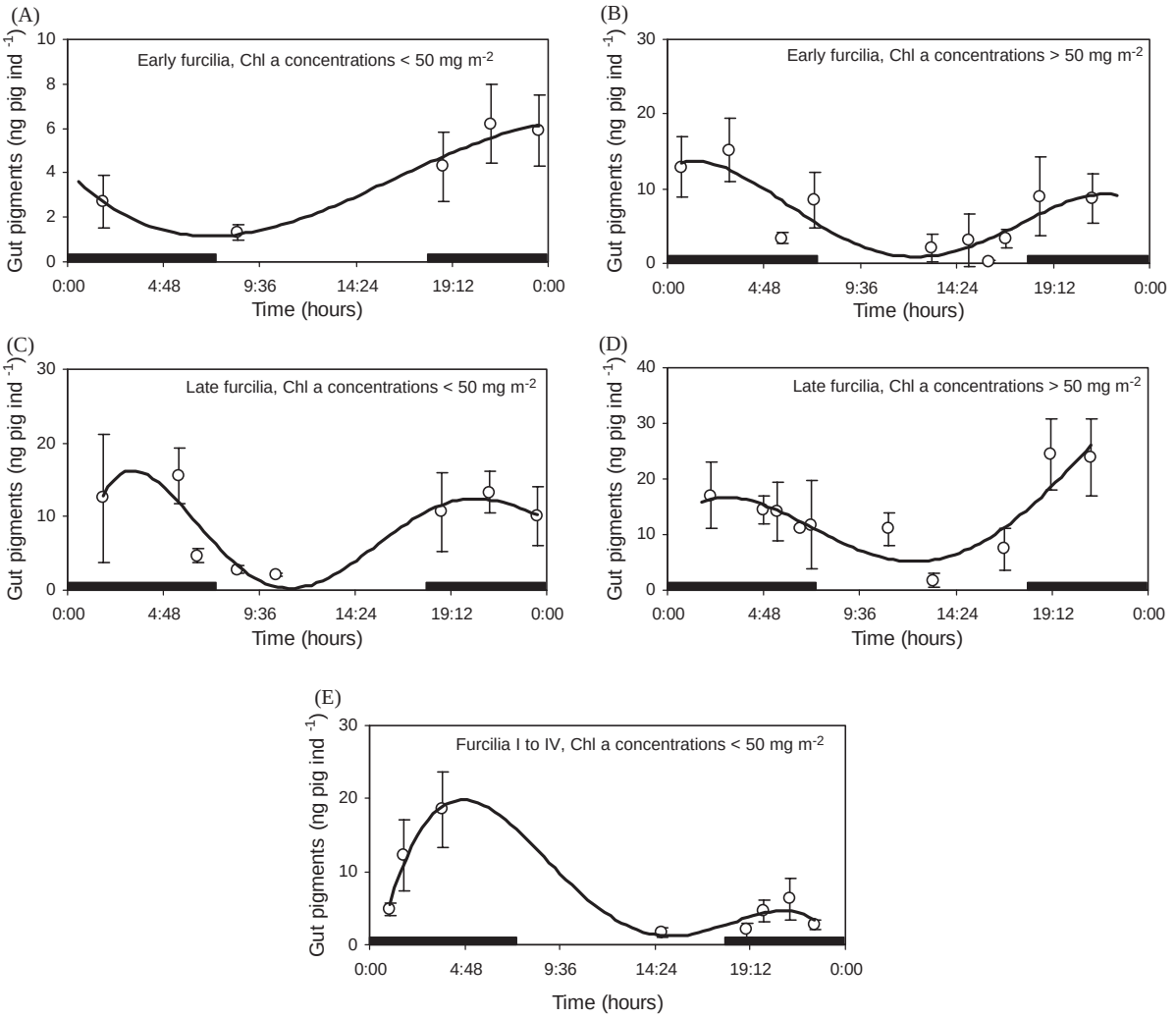

Fig. 5. Diel dynamics in gut pigment contents of larval krill *E. superba* at open water (A–D) and sea ice (E) stations for early and late furcilia at different ambient chlorophyll *a* concentrations in the Eastern Bellingshausen Sea during 18 April to 1 May 2001. Error bars represent 95% confidence limits. Thickening of the horizontal axis indicates the period of darkness.

We stress that variability of mass within each particular stage was high, often reaching one order of magnitude (Table 5).

The intermoult period increased with the developmental stage and was 6–8, 8–15 and 16–17 days for furcilia 3, 4 and 5, respectively (Table 6). The daily growth increments decreased with developmental stage (Table 6). For example, between furcilia 3 and 5 growth increments consistently decreased: from 2–2.2% d^{-1} to 0.7–1.1% d^{-1} based on uropod length, from 7.4–8.7% d^{-1} to 2.4–4.2% d^{-1} for wet mass and from 4.9–5.7% d^{-1} to 1.6–2.7% d^{-1} for carbon mass (Table 6).

4. Discussion

Huntley and Brinton (1991) proposed that certain areas at the Antarctic Peninsula, such as Gerlache Strait, may be hotspots for recruitment

Table 2
E. superba larvae gut clearance parameters and their relationships with ambient Chl *a* concentration (0–200 m) and initial gut pigment content (IGPC)

Station number	Local time (hours)	IGPC (±SD) (ng pig ind^{-1})	Chl-*a* conc. (mg m^{-2})	k (h^{-1})	$1/k$ (h)	R^2 (%)
Early furcilia						
318 (ice)	14:00	3.4±0.4	22.1	0.6564	1.523	39.4
319 (ice)	01:00	12.9±4.9	22.1	1.7255	0.579	69.7
324	20:00	3.4±1.5	44.0	1.1330	0.883	53.8
Late furcilia						
301	01:30	18.5±3.6	40.9	0.7391	1.353	48.7
308	01:00	47.8±4.9	35.8	1.2213	0.819	65.0
316 (ice)	18:50	8.0±0.8	22.7	0.8760	1.141	87.1
324	20:00	17.7±5.0	44.0	1.6750	0.597	54.8
325	08:30	2.0±0.3	16.5	1.4326	0.698	68.0

Table 3
E. superba furcilia: estimation of pigment destruction

Station number	Initial pigment concentration (ng pig l^{-1})	Incubation time (hour)	Pigment ingested (ng pig ind.$^{-1}$)	Pigment recovered (ng pig ind.$^{-1}$)	Destruction efficiency (%)	
					Mean	Range
Early furcilia						
303	2250±825	1	80.8±42.7	18.9±9.4	74.8±9.8	63.5–85.6
Late furcilia						
303	2834±11	1	74.6±35.2	12.3±2.0	80.7±11.8	72.4–89.1
308	2579±30	1	117.5±14.8	40.6±2.2	65.1±6.3	60.6–69.5

of Antarctic krill. The Marguerite Bay area is also a potential hotspot, but with the paucity of studies this far south along the peninsula, this has been conjectural. Therefore, SO GLOBEC targeted this area to study overwintering of krill. Only modest numbers of krill postlarvae were encountered in this area during April and May 2001, either with acoustics or with nets (Atkinson et al., 2002a). However, the abundance of krill larvae was exceptional, with numbers reaching 30 000 ind m^{-2}. Comparable larval krill densities have been observed previously only in Gerlache Strait, Scotia Sea and Prydz Bay region (e.g., Brinton et al., 1986; Huntley and Brinton, 1991; Pakhomov and Karpenko, 1992), while the abundances in the Bransfield Strait and Drake Passage are much lower (Fraser, 1936; Brinton and Townsend, 1984; Brinton et al., 1986; Siegel, 1989; Huntley and Brinton, 1991). Furthermore, this area should clearly be recognised as another "hotspot" in Antarctic krill recruitment along the Antarctic Peninsula. Krill larvae comprised a large proportion of both the abundance and total biomass of the mesozooplankton (S. Schiel, unpublished data), so these early stages of krill may play a major role in the shelf ecosystem of the eastern Bellingshausen Sea.

5. Feeding dynamics

Within the study area, the shelf was greatly affected by Circumpolar Deep Water (Strass et al., 2002; Klinck et al., 2004). Almost all shelf stations

Table 4
Daily consumption rates of larval krill *E. superba* in the Eastern Bellingshausen Sea during late autumn 2001

Region	Chl *a* stock ($mg\,m^{-2}$)	Group	Consumption rates ng (pig) $ind^{-1}\,d^{-1}$	$\mu g\,C\,ind^{-1}\,d^{-1}$	% body $C\,d^{-1}$
Sea ice stations	< 50	All furcilia	619.9	22.9	16.5
Open ocean stations	< 50	Early furcilia	225.7	8.5	21.5
Open ocean stations	< 50	Late furcilia	936.9	35.1	17.8
Open ocean stations	>50	Early furcilia	470.4	17.6	44.5
Open ocean stations	>50	Late furcilia	1531.1	57.4	29.2

All furcilia: furcilia 1 to 5; Early furcilia: calyptopis 3 to furcilia 2; Late furcilia: furcilia 3–5.

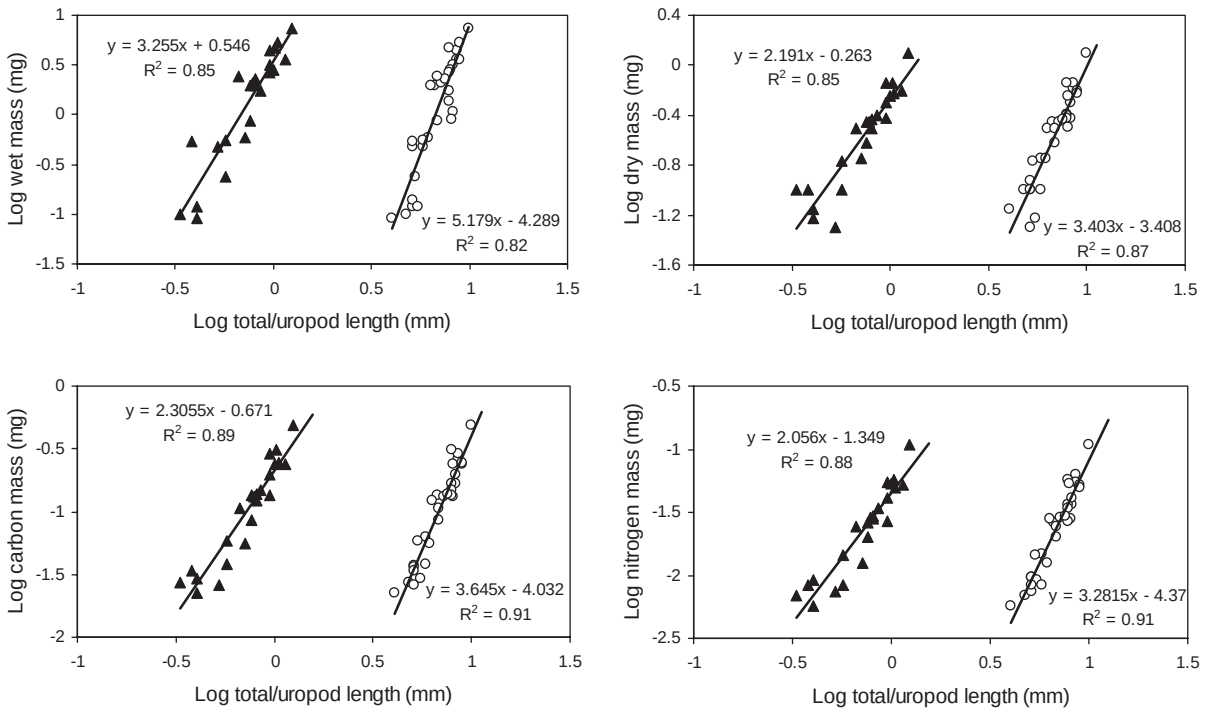

Fig. 6. Relationships between total (open circles) and uropod (filled triangles) lengths and wet, dry, carbon and nitrogen mass of larval krill in the Eastern Bellingshausen Sea during 18 April to 1 May 2001. *Y*: log-transformed wet, dry, carbon or nitrogen furcilia mass (mg); *X*: log-transformed total (open circles) or uropod (filled triangles) furcilia length (mm).

Table 5
Biometrical parameters of *E. superba* furcilia in the Eastern Bellingshausen Sea during late autumn 2001

Stage	Total length (mm)		Wet mass (mg)		Dry mass (mg)		Carbon (μg)		Nitrogen (μg)	
	Mean	Range (*N*)	Mean	Range (*N*)	Mean	Range (*N*)	Mean	Range (*N*)	Mean	Range (*N*)
1	5.04	4.1–5.8 (9)	0.27	0.09–0.55 (8)	0.09	0.05–0.1 (8)	31.2	22.5–37.6 (8)	8.2	5.7–9.8 (8)
2	5.88	5.3–7.2 (13)	0.44	0.24–0.59 (3)	0.18	0.17–0.19 (3)	58.7	55.3–63.1 (3)	13.9	12.6–14.8 (3)
3	7.21	7.2–8.2 (28)	1.76	0.86–2.45 (8)	0.34	0.24–0.41 (8)	132	86.4–168 (8)	28.8	20.2–36.5 (8)
4	8.10	7.9–8.6 (25)	2.35	0.89–3.64 (5)	0.46	0.32–0.65 (5)	183	131–266 (5)	41.0	28.1–62.5 (5)
5	8.77	7.9–10 (16)	4.77	3.15–7.38 (6)	0.74	0.5–1.24 (6)	295	197–494 (6)	60.8	41.4–109 (6)

Table 6
Summary of growth rate experiments (GRE) conducted using larval *E. superba* during April and May 2001 in the Eastern Bellingshausen Sea

Station Number	Date, 2001	Ambient Chl *a* ($mg\,m^{-2}$)	Chl-*a* in containers ($\mu g\,l^{-1}$)	Larval stages	No moulting	IMP (days)	% Change in uropod length	Growth increments during IMP (%, mean ±SD)			
								Wet mass	Dry mass	Carbon	Nitrogen
303	19/04	151.2	2.3	F2-F4 (mostly F4)	17	14	14.4±5.3	56.1±23.1	34.7±13.6	36.8±14.5	32.2±12.5
324	28/04	44.0	1.2*	F1–F2	1	(64)**	11.1	40.9	26.0	27.5	38.7
				F2–F3	1	(32)**	12.0	44.6	28.2	29.9	49.9
				F3–F4	11	8	17.5±3.6	69.7±17.0	42.6±9.7	45.3±10.74	36.7±16.6
				F4–F5	6	15	18.5±7.9	75.9±40.2	45.7±21.9	48.7±23.6	43.4±8.3
				F5–F6	3	17	18.0±5.3	72.1±24.9	43.9±14.1	46.7±15.1	29.5±3.0
328	1/05	44.8	0.65	F3–F4	5	6	11.7±5.6	44.4±23.4	27.7±14.0	29.4±14.9	30.5±9.0
				F4–F5	12	8	10.2±2.7	37.5±11.3	23.8±6.8	25.2±7.2	17.2±8.1
				F5–F6	12	16	10.4±5.5	39.0±22.1	24.5±13.5	25.9±14.3	26.7±9.4

IMP: intermoult period; F1–F2: furcilia 1 to furcilia 2. *Water in the incubation container was enriched from $0.4\,\mu g\,l^{-1}$ ambient Chl *a* concentration by net phytoplankton collected using the Apstein net in the top 25 m. **In brackets are preliminary values due to the limited number of moulted furcilia: data are presented but not discussed.

displayed the typical oceanic vertical water structure, with temperature > 0.5 °C below 100 m depth. A relatively warm and fresh upper mixed layer induced a sharp shallow picnocline, creating favourable conditions (increased vertical stability) for phytoplankton bloom development (Brichta and Belem, 2002). At open-water stations, Chl *a* concentrations in the upper layer ranged from 0.2 to $2.43\,mg\,m^{-3}$ (mean $0.9\,mg\,m^{-3}$) and decreased sharply below 60 m depth. Depth-integrated Chl *a* stocks (0–200 m) varied between 15 and $165\,mg\,m^{-2}$ (Brichta and Belem, 2002). Although no clear pattern in Chl *a* distribution was found, the highest Chl *a* values ($>1\,mg\,m^{-3}$ and $>50\,mg\,m^{-2}$) were observed over the shelf. At the ice stations (Stations 314–318), Chl *a* concentrations were low and never exceeded $0.3\,mg\,m^{-3}$ and $25\,mg\,m^{-2}$ (Brichta and Belem, 2002). Further, the Sea Wide Field Viewing Sensor (SeaWiFS) data confirmed that bloom conditions had persisted here since March 2001 (Belem, 2002). Hence, feeding conditions had probably been good for larval krill in the Eastern Bellingshausen Sea during late summer—autumn 2001.

Larval *E. superba* were feeding actively on the autumn bloom. Their feeding rates were equivalent to those found in summer along the Antarctic Peninsula or in winter under the sea ice in the Scotia-Weddell Seas (Daly, 1990; Huntley and Brinton, 1991). The gut evacuation rates in this study were generally higher than the values of Daly (1990) during winter, but lower than those for *E. crystallorophias* larvae during spring/early summer (Pakhomov and Perissinotto, 1996). A previous study (Perissinotto and Pakhomov, 1996) suggested that gut passage time might co-vary with the initial gut pigment content of krill. This, however, was not observed in this study (see Table 2). There are no gut pigment destruction rates available for larval krill, but our values are broadly similar to those for juvenile krill (Daly, 1998) and for northern hemisphere copepods (Head and Harris, 1992, 1996) but generally lower than values for adult krill (58–98%, Perissinotto and Pakhomov, 1996).

Daily ingestion rates during April and May 2001 in the Eastern Bellingshausen Sea varied between 8.5 and $57.4\,\mu g\,C\,ind^{-1}\,d^{-1}$ and were within the

range (2–67 μg C ind^{-1} d^{-1}) previously reported for furcilia 3–6 (Daly, 1990; Huntley and Brinton, 1991; Meyer et al., 2002). The daily rations estimated in this study were in the higher range of values (<1–52% of body carbon) reported in the literature and similar to the value (28% of body carbon) estimated from in vitro incubations with high food concentrations (Meyer et al., 2002, 2003).

During our study, the particulate organic carbon (POC) concentration within the top 50 m of the open-water stations was often ~200 μg C l^{-1} (Brichta and Belem, unpublished data). Based on the relationship between the daily ration and food concentration published by Meyer et al. (2002), the average food intake of larval krill would then be equivalent to ~20% of body carbon, similar to our own measured values. In comparison, POC concentrations in the top 50 m water layer at the ice stations generally did not exceed 50 μg C l^{-1} (Brichta and Belem, unpublished data). The calculated daily ration at such carbon concentrations using the same equation will not exceed 2% of body carbon, which is ~8-fold lower than we found using the gut fluorescence method. This suggests that larval krill under the sea ice were either exploiting dense localised food patches or, likely, may have been feeding on ice algae (Meyer et al., 2002).

Physiological measures such as respiration, excretion and growth are useful indicators of the minimum metabolic demands of individuals. During the same cruise, larval krill respiration and ammonia excretion rates also were measured and will be published elsewhere. Preliminary calculations indicate that C and N losses of freshly caught krill furcilia 3–5 were approximately 2% of body C and 1% of body N per day (Meyer and Oettl, 2002), which are close to those obtained for furcilia 3 in the southwestern Lazarev Sea (Meyer et al., 2002). Combining these values with maximal growth rates from Table 6 and assuming an average assimilation efficiency of 0.7 (Conover, 1978), the minimal daily ration would be ~9% (furcilia 3–12%, furcilia 5–7%) of body C and 7% (furcilia 3–10%, furcilia 5–5%) of body N. Daly (1990) reported daily rations ranging from 3 to 52% of body C based on the gut fluorescence method and suggested that a daily ration of 10% was realistic. Our preliminary calculations using the energy budget support this suggestion. However, in this study the gut fluorescence method showed substantially higher (up to 44% of body C d^{-1}) ingestion rates. This may be a result of drawbacks associated with the gut fluorescence technique (Perissinotto and Pakhomov, 1996) but could also imply a decreased assimilation efficiency at high food concentrations. A decrease in assimilation efficiency at high food concentrations is well documented for copepods (Gaudy, 1974). Nevertheless, our findings demonstrate that the feeding rates of larval krill obtained using the gut fluorescence method during autumn in the Eastern Bellingshausen Sea appeared to be close to the maximal reported in in vitro studies in the Lazarev Sea and at Rothera Station (25–30% of body carbon d^{-1}, Meyer et al., 2002, 2003). These values, therefore, are probably a realistic assessment of maximal, food-saturated larval ingestion rates.

Estimating grazing impact of krill larvae was not an aim of this study. However, using average densities of larval krill (Table 1) and pigment ingestion rates (Table 4), the grazing impact exerted by krill larvae alone in the Eastern Bellingshausen Sea during austral autumn of 2001 could be either negligible ($\ll$0.1 of Chl *a* stock d^{-1}) or as high as 25% of Chl *a* stock d^{-1}. This clearly places larval krill among the most important players in carbon cycling of the Eastern Bellingshausen Sea and may explain the general negative correlation between the Chl *a* stock and larval krill densities in the study region.

6. Larval composition, growth and development

The favourable feeding conditions, particularly over the shelf, could be reflected in the larval krill average body length and mass as well as in the developmental composition (Huntley and Brinton, 1991). Indeed, larval lengths (furcilia 3–5) in this study were comparable with those obtained during several summer studies (Fraser, 1936; Brinton and Townsend, 1984; Brinton et al., 1986; Huntley and Brinton, 1991). However, they were 8–17%

smaller than those measured in Gerlache Strait and in laboratory-raised furcilia (Huntley and Brinton, 1991; Ikeda, 1984, respectively). In both of the latter studies, food concentrations were substantially higher than in our study. Our furcilia stages 3–4 were ~6–17% longer than equivalent stages in winter in the Scotia-Weddell area (Daly, 1990). Further, the average dry mass of furcilia in our study is in the upper range of values reported for the Southern Ocean (e.g., Brinton and Townsend, 1984; Daly, 1990; Meyer et al., 2002).

Larval growth and development rates respond to food availability over different timescales (Brinton and Townsend, 1984; Ikeda, 1984). The age structure of larval krill over the shelf during our April–May 2001 study was similar to that in mid-March 1987 in Gerlache Strait (Huntley and Brinton, 1991). A slower seasonal development rate and slightly smaller larvae in our study may be explained by the exceptionally abundant food in Gerlache Strait. On the other hand, their age structure in our study was similar to that in June 1988 (Daly, 1990), so the Marguerite Bay populations were probably intermediate in development between the 1987 Gerlache Strait and the 1988 Weddell-Scotia populations.

Differences in developmental stage composition between slope and shelf stations during April and May 2001 may be a result of the prolonged spawning period (Siegel, 2000) but likely are due to differences in food concentrations between the open-ocean and shelf realms (Brichta and Belem, 2002). Consequently, larvae hatching at the same time but at different places would be exposed to different food concentrations (Huntley and Brinton, 1991). This may explain a discrepancy in larval abundance and composition between the shelf and open-ocean stations in the Eastern Bellingshausen Sea. Although it is not quantified, it is important to note that earlier larval stages (late calyptopis–early furcilia) of krill had higher mortality rates than later stages in all three moulting experiments. Two other research teams working with larval krill independently observed a similar phenomenon during the same cruise. We speculate that the open-ocean "cohort", exposed to lower food concentrations in the past, despite good feeding conditions during the study, was in poorer condition and appeared to have naturally higher mortality rates than their counterparts found over the shelf region. Although very limited, our results on furcilia 1 and 2 intermoult period and intermoult growth increments presented in Table 6 support this suggestion.

The intermoult periods obtained during this study in the Eastern Bellingshausen Sea were in the range of those previously measured in the laboratory, near Palmer Station and in Gerlache Strait during summer (range 8–17 days, Murano et al., 1979; Ikeda, 1984; Huntley and Brinton, 1991; Ross et al., 2000) and substantially lower than observed under the sea ice during winter and in the Bransfield Strait during late summer (range 20–28 days, Daly, 1990; Huntley and Brinton, 1991). The growth rates estimated in this study were somewhat greater than previously reported (Ikeda, 1984; Ross and Quetin, 1991) and are comparable to values obtained in Gerlache Strait during late summer, near Palmer Station in spring/early summer and in the Scotia-Weddell Seas under the sea ice during winter (~5% of wet mass per day, Daly, 1990; Huntley and Brinton, 1991; Ross et al., 2000). The long-term study near Palmer Station has supported the hypothesis that the secondary production of larval and juvenile Antarctic krill are limited by both food quantity and quality most of the time and only maximal during diatom blooms (Ross et al., 2000). Our study shows that favourable conditions in the Eastern Bellingshausen Sea in late summer/autumn 2001 resulted in an abundant and advanced larval krill population. Furthermore, it appears that feeding and growth rates of larval krill at that time of year were more comparable to summer maximum rates rather than to late summer or winter rates, suggesting that a "business as usual" strategy, with continuous feeding and growth, has been adopted by larval krill (Meyer et al., 2002).

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