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Deep-Sea Research II 51 (2004) 2139–2168

DEEP-SEA RESEARCH
PART II

www.elsevier.com/locate/dsr2

Overwintering growth and development of larval *Euphausia superba*: an interannual comparison under varying environmental conditions west of the Antarctic Peninsula

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Accepted 8 July 2004

Abstract

Growth, molting, and development of larval Antarctic krill were investigated near Marguerite Bay during four cruises in austral autumn and winter 2001 and 2002, as part of the US Southern Ocean GLOBEC program. Overwintering survival of larvae has been linked to annual sea-ice formation and extent, as sea-ice biota may provide food when other sources are scarce in the water column. During autumn 2001, larvae were very abundant (1–19 individuals m^{-3}), with younger stages dominant offshelf and older stages dominant on-shelf. On-shelf larvae were in better condition than offshore larvae. During autumn 2002, larvae again were abundant offshelf (0.01–110 m^{-3}), whereas all stages were scarce on-shelf. Declining diatom and radiolarian blooms were present during autumn in both years. Average chlorophyll concentrations were low (0.10 vs. 0.22 $\mu g\,l^{-1}$) in autumn and an order of magnitude lower in winter. Carbon content of larvae during autumn 2001 and 2002 (41% vs. 38% C of DW) suggested that lipid storage was moderate. The median autumn larval growth rate (0.027 mm d^{-1}) was lower and the intermolt period (19 d) longer than reported summer values. During winter, larvae appeared to be food-limited based on the following observations: (1) the median growth rate decreased (0.00 mm d^{-1}) and the intermolt period increased (40 d), (2) larval length-specific dry weight (DW) and % carbon and nitrogen of DW decreased, and (3) 88% of furcilia 6 did not develop to the juvenile stage, but remained at the same stage after molting. Experimental results demonstrated that some larvae could survive starvation for a month by combusting body reserves (ca. 1% decrease in DW and body C and N d^{-1}), implying that a portion of the population was resilient to the suboptimal food supply. Although sea ice formed up to 2 months earlier in 2002, ice algae at the ice–water interface, where it is accessible to krill, was not an abundant food source in either year (0.05 vs. 0.07 $\mu g\,chl\,l^{-1}$). In winter 2001, furcilia were commonly observed near the undersurface of sea-ice, but only rarely in 2002 until mid-September, when ice algae began to accumulate. Low gut fluorescence values also indicate that little nutrition was derived from autotrophs in winter. Instead, larvae were likely opportunistic scavengers exploiting all available food sources, including microzooplankton, benthic larvae, detritus, scarce phytoplankton and sea-ice biota. In summary, larval krill exhibited several overwintering behaviors: (1) flexible feeding, (2) flexible morphology (i.e., delayed development), (3) flexible physiology (i.e., increased intermolt period, reduced growth), (4) moderate lipid

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0967-0645/$ - see front matter
doi:10.1016/j.dsr2.2004.07.010

storage, and (5) ability to withstand starvation by combusting body C and N. Because most larvae did not shrink in length, this measure may not be a good indicator of the body combustion strategy. At these high latitudes, sea-ice biota may not be a primary source of food during winter, but progressively more important in spring as irradiance levels increase. Winter survivors during 2001 resulted in a significant recruitment to the juvenile size class during spring.

1. Introduction

High concentrations of Antarctic krill, *Euphausia superba*, occur along the western side of the Antarctic Peninsula and eastward into the Scotia Sea (Marr, 1962). The suite of environmental and biological factors that sustain this persistent stock and the processes that lead to its considerable interannual variability remain poorly known. One critical period in the krill life cycle is during the first autumn and winter. Young larvae must survive a long period when much of the Southern Ocean is covered by sea-ice and primary production in the water column is extremely low. Observations and field experiments within the pack ice zone during the 1980s led to the hypothesis that the overwintering survival and recruitment of young krill are related to the timing and extent of sea-ice and its associated biota (Guzman, 1983; Daly and Macaulay, 1988; Marschall, 1988; Daly, 1990; Smetacek et al., 1990). Sea-ice biota, which is composed of ice algae (often dominated by pennate diatoms), bacteria, protozoans, and small metazoans, can have relatively high concentrations from late autumn to spring (Hoshiai, 1985; Garrison and Close, 1993). Sea-ice primary production is estimated to be ca. 66 Tg C per year, which is about 5% of the total annual primary production in the Southern Ocean (Lizotte, 2001). Much of that production, however, occurs in late autumn or spring when phytoplankton production in the water column is negligible. Hence, extensive sea-ice coverage in winter may act to dampen the strong seasonal oscillation in food supply and promote ecosystem stability.

Subsequent studies reported correlations between recruitment indices of krill and sea-ice conditions (Kawaguchi and Satake, 1994; Siegel and Loeb, 1995), where years with extensive ice cover were often followed by higher recruitment of larvae to the juvenile class than during years with little or no ice cover. Because females reproduce over several years, Siegel and Loeb (1995) noted that on average the krill stock appeared to remain relatively stable despite 1–2 years of poor recruitment. However, they predicted that reduced ice cover for 3 or more years would significantly impact densities. The implication being that larval survival or mortality overwinter was more important than reproductive success in determining recruitment success or failure.

High-latitude zooplankton have evolved life history strategies to accommodate the large seasonal oscillation in environmental conditions. In the last two decades, *E. superba* was reported as having a suite of overwintering behaviors, including feeding on sea-ice biota (Daly and Macaulay, 1988; Marschall, 1988), carnivory (Hopkins et al., 1993), utilizing sequestered lipids to support metabolism (Hagen et al., 1996), body shrinkage (combustion of body carbon and nitrogen to support metabolism, Ikeda and Dixon, 1982), and reduced metabolism (Quetin et al., 1994; Torres et al., 1994). Recent findings suggest that behavior in larval krill may vary. For example, Meyer et al. (2002a) did not observe a decrease in respiration rate and enzyme activity between summer and autumn in furcilia stage 3 (F3). Frazer et al. (2002a), however, measured decreased respiration rates for F4–F6 during winter, which appeared to be sensitive to decreasing temperature and food supply. Due to the limited number of investigations on larval krill physiology, the relative importance of different behaviors under varying environmental conditions remains poorly known.

The strategy of body shrinkage, in particular, has received considerable attention. Euphausiids are obligate molters; molting throughout their lifespan and during all seasons. The results from several laboratory and field studies suggest that

E. superba larvae (Ross and Quetin, 1991) and juveniles and adults (Ikeda and Dixon, 1982; Sun et al., 1995; McGaffin et al., 2002) shrink in length at molting when food limited, which would confound estimates of growth and longevity based on net sample length–frequency data. The extent to which body shrinkage occurs in the field is currently being debated (Buchholz, 1991; Nicol, 2000). Nicol (2000) recommended integrating field sampling with short-term shipboard experiments to measure instantaneous or finite growth rates, and noted that standardization of growth rate measurements was needed to improve confidence in the interpretation of morphometric relationships and to compare results among different investigations. Variations in larval growth, development, and nutritional condition are the result of an integration of genetic, physiology, and environmental effects, with temperature and food quality and quantity being the primary environmental factors influencing larval physiology. Thus, growth (or shrinkage) is a measure of the net integration of overwintering strategies that larvae may employ to mitigate unfavorable winter conditions. A mechanistic understanding of larval krill behavior in relation to individual variability in growth (or shrinkage) and development is necessary to understand population size structure, secondary production, as well as fluctuations in recruitment.

As part of the US Southern Ocean GLOBEC program, the overwintering behaviors of larval *E. superba* were investigated along the western Antarctic Peninsula in the vicinity of Marguerite Bay. One objective of this program was to test the hypothesis that early and long-lasting ice cover provides a dependable food supply and enhanced survival of larvae. Here I report the development and growth of larval krill in relation to sea-ice dynamics during austral autumn and winter in 2001 and 2002. Two methods to experimentally measure growth rates are compared, as well as growth rates in terms of length and biomass (dry weight and body carbon and nitrogen) based on short-term shipboard experiments and field samples to determine whether larval growth or shrinkage occurs during winter in this region of the Southern Ocean.

2. Methods

Larval and Year 0 (Y0) juvenile *Euphausia superba* were collected during austral autumn and winter on four cruises between April 2001 and September 2002 in the vicinity of Marguerite Bay west of the Antarctic Peninsula as part of the US Southern Ocean GLOBEC Program (Figs. 1 and 2). This program had two ships operating simultaneously, one for process studies (Fig. 2A) and the other for surveys (Fig. 2B) of the study area. The observations reported here were obtained aboard the process ship on the autumn cruises and aboard the survey vessel during winter, hence the different station patterns. In the first year, field observations were made aboard the R.V. *Lawrence M. Gould* between 23 April and 6 June 2001 and aboard the R.V.I.B. *Nathaniel B. Palmer* between 24 July and 31 August 2001. In the second year, field observations were made aboard the R.V. *L. M. Gould* between 7 April and 20 May 2002 and aboard the R.V.I.B. *N. B. Palmer* between 31 July and 18 September 2002.

Surface chlorophyll samples were collected from the ship's flow-through seawater system, which have seawater intake between 5 and 7 m depth on both ships. Water-column chlorophyll was collected during CTD casts using 10-l Niskin bottles mounted on a rosette. Sea-ice biota were collected from the undersurface of ice floes at the ice–water interface by divers using a suction sampler. About 175 cm^2 of the under-ice surface area were simultaneously scraped and suctioned into a 1-l container. A variety of ice types were sampled, including where krill were observed feeding, such as surface ice slush, under first and second year ice, and new grease ice. Phytoplankton or sea-ice biota were filtered into GF/F filters, passively extracted in 7 ml of 90% acetone at −20 °C in the dark for at least 24 h, then chlorophyll fluorescence was measured on a Turner Design Digital 10-AU-05 fluorometer calibrated prior to the cruise. Particulate organic carbon (POC) and nitrogen (PON) samples collected by Niskin bottles and by the under-ice sampler were filtered through combusted (450 °C for 2 h) GF/F filters under low vacuum and frozen at −80 °C. Samples were analyzed at the University of California Santa Barbara,

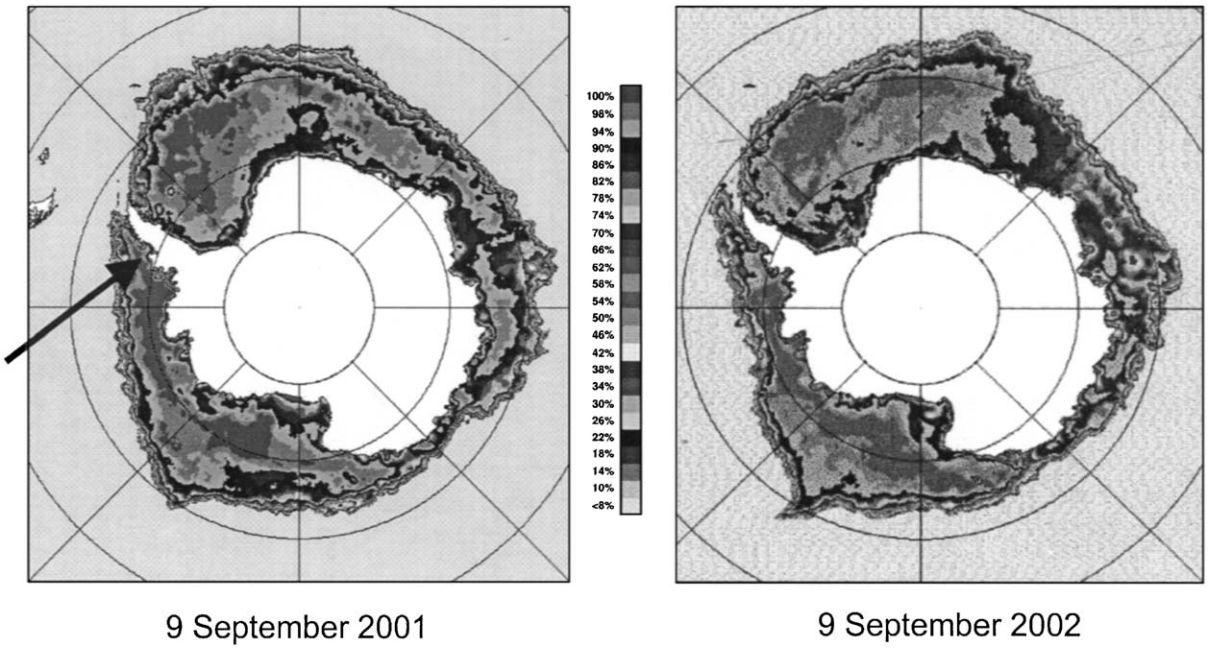


Fig. 1. Sea-ice concentration maps during winter maximum of the sea-ice extent in 2001 (left) and 2002 (right). Arrow shows location of the study area. Satellite images courtesy of J. Comiso.

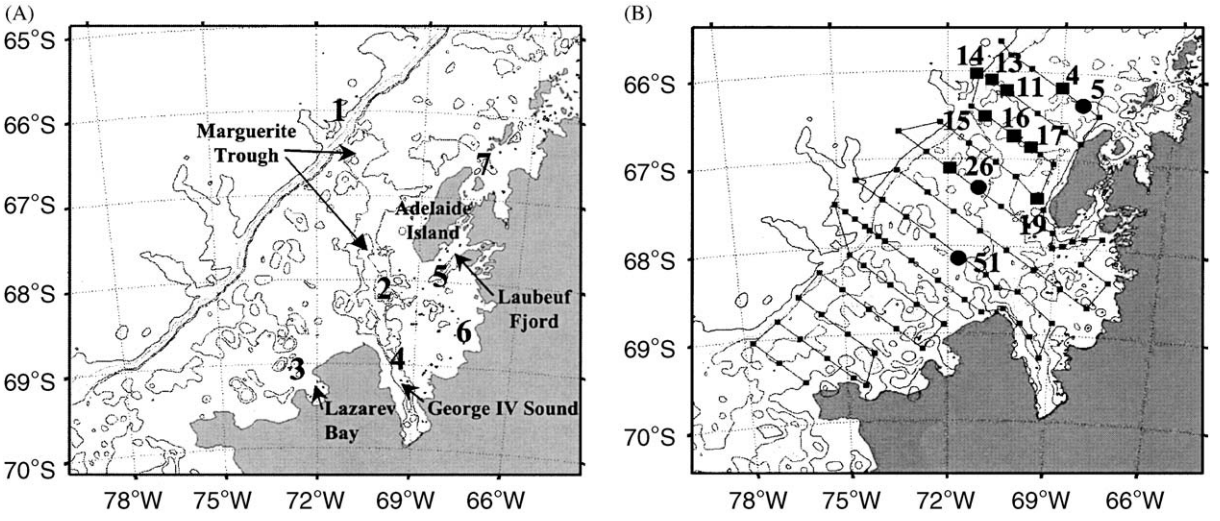


Fig. 2. Station locations during the austral autumn (A) and winter (B) cruises. Autumn stations are designated by numbers. The small dots on the grid in (B) show the survey sampling scheme; circles designate the 2001 stations and squares the 2002 stations mentioned in the text.

Marine Science Institute Analytical Laboratory using the high-temperature combustion Dumas method and an organic elemental analyzer.

For physiology experiments, larval krill were collected either from the upper 100 m of the water column using a 1.5-m^2 Tucker Trawl, having a

1/4 in mesh graded down to a 707 μm mesh with a protected cod-end, or larvae were collected under sea-ice by divers. On the second winter cruise, larvae were collected primarily using a 1-m diameter Reeve Net with a 333 μm mesh net having a 20 l protected cod end, in tandem with a 1-m diameter Ring Net (333 μm mesh). The heavy Reeve net cod-end was kept afloat using Syntactic foam. The Reeve Net was hung about 3–5 m below the Ring Net, and both were deployed off the stern at about 10 and 15 m in depth, respectively. The propellers were run at 15–25% to keep water circulating into the nets, but with little to no forward ship movement or ice sweep-down under the hull. This method collected larvae in excellent shape. In addition larvae were collected at discrete depth intervals to assess their distribution in the water column during autumn using a 1-m^2 MOCNESS net with 333 μm mesh.

Larvae were identified to life history stage (Calyptopis I–III, Furcilia I-IV, or juvenile) after Makarov (1980). Direct or indirect development determinations were based on variant forms of telson morphology following Fraser (1936). Individuals were then measured for length from the base of the eye to the tip of the telson, excluding setae. Freshly collected and undamaged individuals also were measured for dry weight and carbon and nitrogen content. These larvae were rinsed briefly with distilled water to remove salts, blotted dry, then placed either individually, or in small groups for the younger stages, on a weighed combusted GF/F filter and dried in a combusted shell vial at 60 °C. Dry weights were measured on a Mettler UMX2 microbalance. A subset of these larvae was analyzed for carbon (C) and nitrogen (N) content by the UCSB Analytical Laboratory.

The effect of food limitation on dry weight and body C and N content of winter larvae was examined in 2001. Several hundred F4–F6 larvae, 6.5–14 mm in length, were collected from under sea-ice at Sta. 5 on July 28 and held in filtered (0.1 μm) seawater in two 20 l containers at about −1.0 °C. Container water was changed regularly and unhealthy-looking or dead individuals were removed. About every 3–5 days, 20 active individuals were removed and frozen, until August 24 when all remaining larvae were frozen. In the laboratory, slightly thawed larvae were measured for length and for dry weight. Larvae for CN measurements were placed directly on weighed, combusted GF/F filters to avoid any loss of material such as lipids. They were then dried, weighed, and analyzed for CN.

Gut fluorescence was measured by placing 1–30 larvae immediately upon collection in vials containing 90% acetone. Gut pigments were passively extracted in the dark at −20 °C for at least 24 h, then measured for fluorescence (Daly, 1990). Pigment content is expressed as total pigment (chlorophyll a + phaeopigments), with no correction factor for an unknown degradation loss. Larval stages for gut fluorescence included F4–F6 during autumn and primarily F6 during winter.

In situ molting rates were assessed using about 100 individuals in each experiment. Immediately after collection larvae were sorted into separate 28–129 ml jars containing filtered (1 μm) seawater and held in a water bath or large flow-through aquaria at in situ sea surface temperature (−0.59 to −1.82 °C) for 4–5 days. Water was changed every 1–2 days. Individuals were checked for molts every 12 h and dead, damaged, or molted individuals were removed. Larvae must be checked at least at that frequency and then separated from their molts if they are not measured immediately, as they often ingest their molts. For each experiment, the intermolt period (IMP) in days was calculated as the inverse of the average of the proportion of individuals molting each day of the experiment:

$$\mathrm{IMP} = \frac{1}{\frac{\sum (M_i/K_i)}{n}}$$

where M_i is the number of individuals molted per day, K_i is the number of individuals available to molt each day, and n is the number of days.

Growth rates were measured following the methods of Poleck and Denys (1982) as updated by Nicol (2000). Individuals that molted in the above experiments were removed and measured within a few hours for total length, then the length of the telson (Fig. 3A) and the exopodite of the right uropod (Fig. 3B) was measured on both the molted larvae and the molt under a dissecting

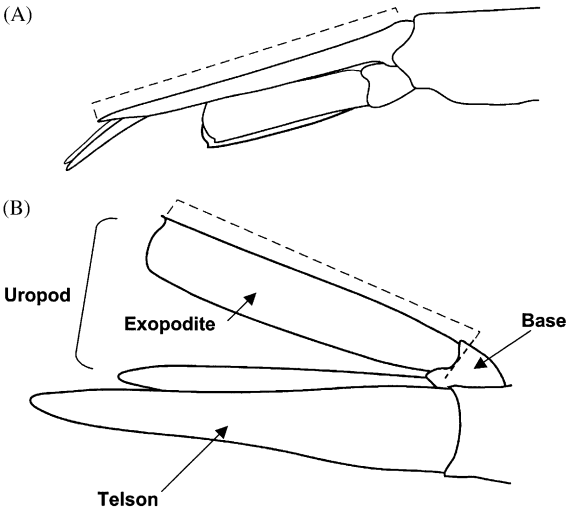


Fig. 3. Illustration of the distal portion of a furcilia 6 abdomen showing the location of growth measurements on the (A) telson in lateral view and on the (B) exopodite of the right uropod in dorsal view. The slightly flexed telson was measured from the middle of the small rise at the anterior end of the telson to the posterior end, excluding the telson spines. The exopodite was placed at about a 35° angle to the telson, then measured from the lowest point of the base to the distal end of the exopodite at the base of the spine.

microscope using a micrometer. If the right uropod was damaged, the left one was measured. Both the uropod and telson were measured for several reasons: (1) to provide a comparison with other studies. Most krill growth investigations are based on uropod measurements (e.g., Poleck and Denys, 1982; Buchholz, 1985; Ikeda and Thomas, 1987; Nicol et al., 1992; Daly, 1998; Pakhomov et al., 2004), but a few are based on telson length (Ross et al., 2000, 2004); (2) uropods are not present on Calyptopis I and II; (3) if either the telson or uropod was damaged, the other could be used to predict growth; and (4) to provide a comparison of both measurements within one data set. The telson was measured in lateral view and the uropods in dorsal view. Care was taken to ensure that the telson and uropod were consistently at the same angle relative to the abdomen as this can affect measurements. All measurements were made by only one person (Daly) to further reduce measurement error. Samples were not preserved because formalin may cause a greater shrinkage in body length relative to uropod length (Miller, 1983).

Growth rates were expressed in several ways to facilitate comparison with other published values. The percent change in uropod or telson length between the post-molt krill and its molt was based on direct measurements and, thus, has the least amount of associated error. The change in body length ($\mathrm{mm\,d^{-1}}$) over the intermolt period was determined from a Model I linear regression of body length (BL) on uropod (UL) or telson length (TL) for the post-molt krill. Because regressions for each experiment were not significantly different ($p > 0.05$), length measurements from all experiments were pooled. The regression based on uropod length was

$$\mathrm{BL} = 7.11\ UL + 1.08,$$

where r^2 was 0.99 ($n = 260$). The regression using telson length was

$$\mathrm{BL} = 4.44\ TL + 0.021,$$

where $r^2 = 0.97$ ($n = 146$). The premolt body length was estimated by substituting in molt values for UL or TL. The finite growth rate ($\mathrm{d^{-1}}$) was calculated as the difference between the premolt and post-molt body lengths divided by the intermolt period (days). Growth rate in terms of dry weight and carbon and nitrogen also were calculated using the relationships shown in Table 1.

Prior to statistical analyses, data were tested for normality, and then appropriate parametric or non-parametric tests were used (Zar, 1984) and noted in the text or figure legends. Many of the data reported here were not normally distributed; therefore the median and range were used to describe the average or central trend of these data. This was particularly important for the growth measurements, where the mean often represented a negative growth rate when the central trend was zero growth or slightly positive. Where the mean is reported there was no difference between measures of central trend. The geometric mean was used for averaging percentage and ratio data (Zar, 1984).

Table 1
The seasonal relationships between body length (L), dry weight (DW), and body carbon (C) and nitrogen (N) of larval (C2–F6) *E. superba*

Season & year	Equation	r^2	n
	L vs. DW		
Fall 2001	$DW = 3.35 \times 10^{-3} L^{2.47}$	0.93	131
Winter 2001	$DW = 2.35 \times 10^{-3} L^{2.48}$	0.46	159
Fall 2002	$DW = 4.51 \times 10^{-2} L^{1.55}$	0.93	16
Winter 2002	$DW = 4.24 \times 10^{-3} L^{2.38}$	0.52	68
	DW vs. Carbon		
Fall 2001	$C = 418\,DW + 0.467$	0.99	52
Winter 2001	$C = 405\,DW - 34.4$	0.98	34
Fall 2002	$C = 406\,DW - 37.2$	0.98	9
Winter 2002	$C = 206\,DW + 54.8$	0.72	15
	DW vs. Nitrogen		
Fall 2001	$N = 85.2\,DW + 4.68$	0.99	52
Winter 2001	$N = 88.9\,DW - 7.01$	0.97	34
Fall 2002	$N = 83.3\,DW - 1.10$	0.99	9
Winter 2002	$N = 55.7\,DW + 15.0$	0.74	15

Length in mm, dry weight in mg, body carbon and nitrogen in μg, n is sample size.

3. Results

3.1. Seasonal and interannual environmental conditions

Sea-ice: During austral fall 2001, most of the study area was ice free except for the most southerly stations. By 13 May, Sta. 4 in George VI Sound had unconsolidated brash ice and many icebergs present, with some new grease ice being formed. Similarly at Sta. 3 in Lazarev Bay (21 May), new sea-ice formation was observed among the glacial rubble and brash ice. Some sea-ice was forming in other parts of the study area by the end of the cruise on 29 May. By the time we returned for the winter cruise on 27 July, most of the study area was covered by first year sea-ice, except for a small polynya (open area surrounded by sea-ice) to the southeast of Adelaide Island, which remained open much of the time.

In contrast, during autumn 2002 some sea-ice still remained from the previous winter, especially in the southern regions of Marguerite Bay, and new ice started forming in the southern end of the bay (Sta. 4) by 1 May. Much of the study area was covered with new and second year ice by the end of the cruise on 13 May. During the winter cruise, satellite images indicated that most of the study area was covered by ice; however, the stations in the inner bay were unobtainable due to ice conditions. Relatively large leads were observed throughout the area, and a small coastal polynya was encountered in the vicinity of Sta. 19 at the southwest end of Adelaide Island. Winter sea-ice extended northeast up along the Antarctic Peninsula and well out over the Drake Passage in both years (Fig. 1).

Seawater temperatures: Temperature variation, either spatially or between autumn and winter, probably did not strongly influence changes in larval physiology. During both fall cruises, sea-surface temperature varied less than 2 °C (−0.59 to −1.82 °C) at all locations where larval krill were collected for growth experiments, with relatively warmer temperatures being at Sta. 1 offshelf in Antarctic Circumpolar Current waters (Figs. 4 and 5). During winter, near-surface temperatures were similar (−1.75 to −1.82 °C) at all locations and between years. In both seasons, temperature increased with depth. The largest temperature gradient that larvae would experience if they occurred throughout the water column would be about 3 °C between surface and deep water.

Food availability: Chlorophyll concentrations in the water column were regionally and seasonally variable. A declining bloom was observed at several locations in both autumn 2001 (Stas 1 and 5) and 2002 (Stas 1, 2, and 4). The bloom species were primarily phaeodarian radiolarians and the diatoms, *Chaetoceros criophilum* and *Synedra antarctica*. The diatoms, *Fragilariopsis kerguelensis*, *Corethron criophilum*, and *Rhizosolenia hebetata*, also were present. In general, however, chlorophyll concentrations were relatively low in the water column during autumn in both years (Table 2). During autumn 2001, the median chlorophyll *a* concentration in the upper 100 m for all stations was $0.10\,\mu g\,l^{-1}$ (range: $0.02–0.52\,\mu g\,chl\,l^{-1}$), but if phaeopigments are included that value doubles (median: 0.23; range: $0.04–1.39\,\mu g$ pigment l^{-1}). On average about 60% of the total pigment was phaeopigments, indicative of phytoplankton senescence and grazing activity.

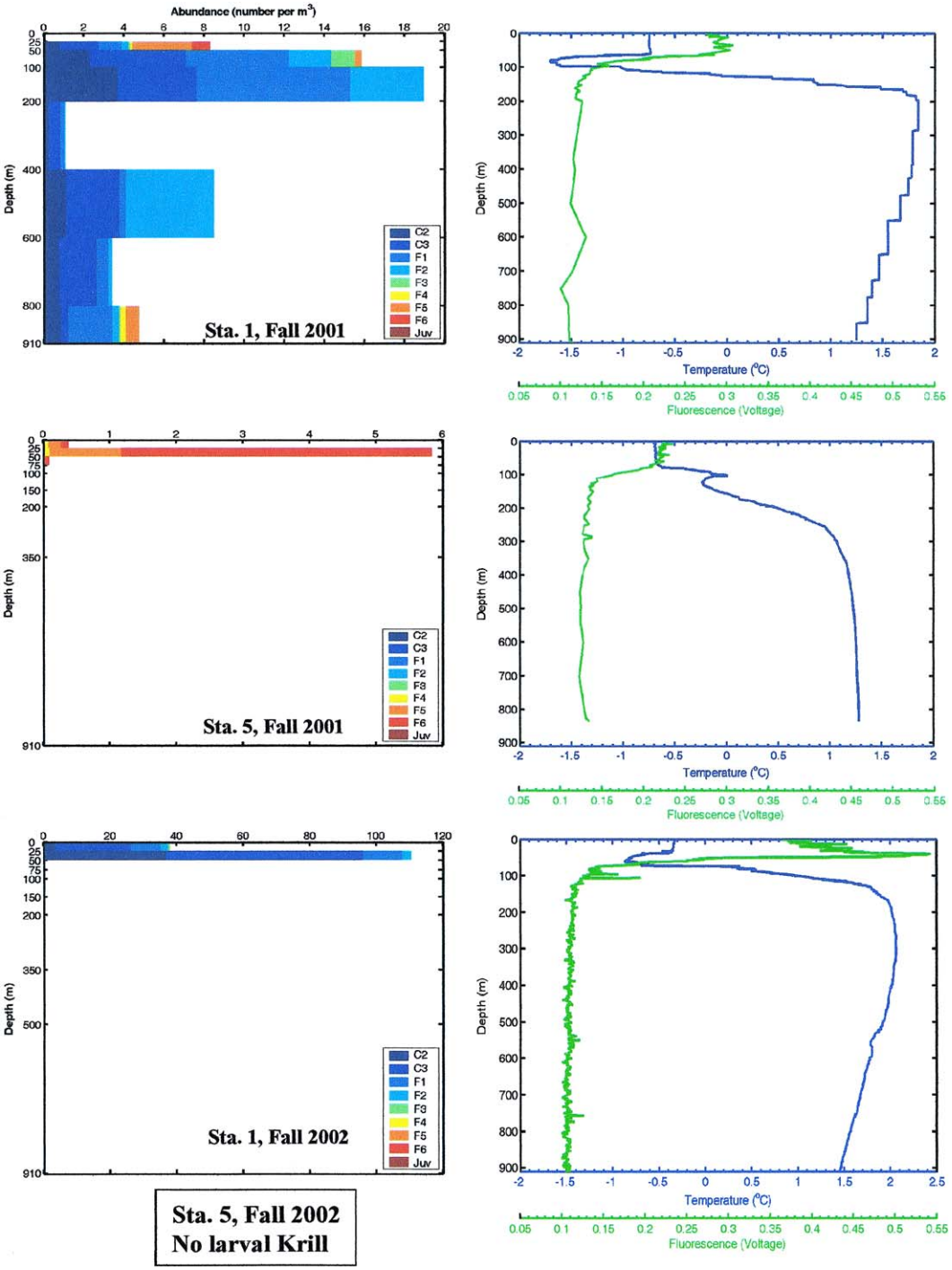


Fig. 4. Vertical distribution of larval stages of *E. superba* (left) in relation to seawater temperature and fluorescence (right) at Sta. 1 (offshelf) and Sta. 5 (inside Marguerite Bay) during autumn.

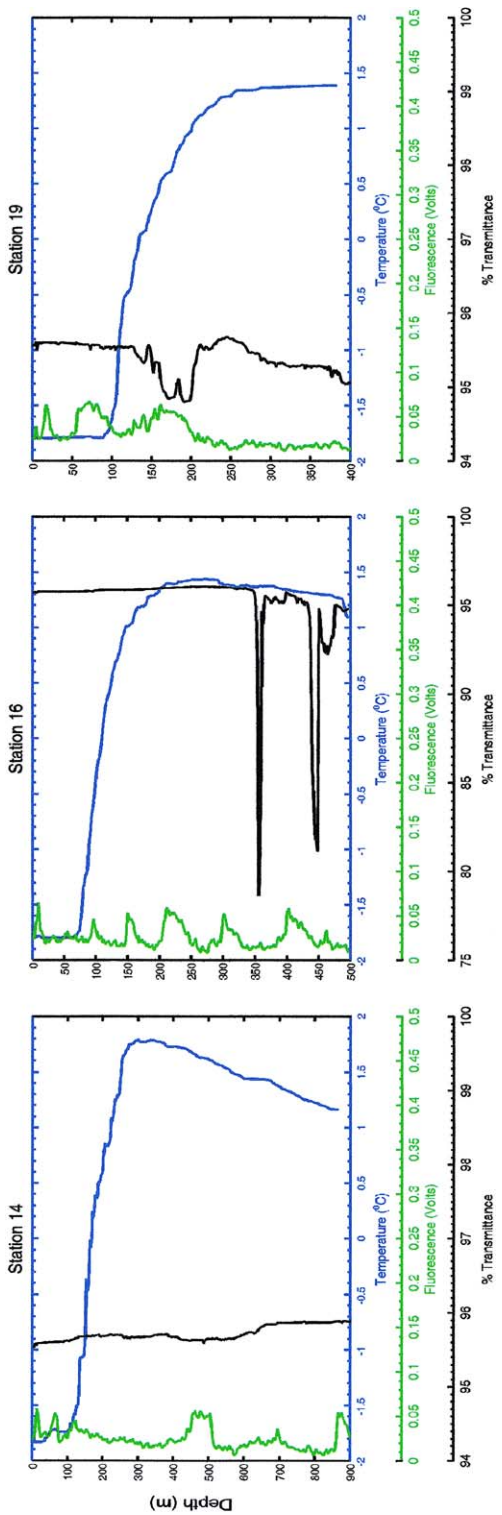


Fig. 5. Vertical profiles of temperature, fluorescence, and particle abundance from CTD casts at three stations across the northern shelf region of the study area in winter 2002. Transmissometer data was used to indicate particle density. Note the change in vertical scale between stations.

Table 2
Median integrated chlorophyll and phaeopigment concentrations ($mg\,m^{-2}$) within the study area during fall

Station	Fall 2001[a]			Fall 2002		
	n	Chl	Phaeo	*n*	Chl	Phaeo
1	6	18.4	29.7	3	35.7	12.2
2	3	4.47	9.76		0.61[b]	0.35[b]
3	3	4.87	11.7			
4	5	6.32	10.6	5	29.1	67.8
5	5	14.9	17.9	4	26.2	156
6				3	16.8	44.5
7				5	12.8	8.30

Pigments integrated 0–100 m, *n* is number of CTD profiles, Chl is chlorophyll *a*, Phaeo is phaeopigments *a*.
[a]Data provided by C. Fritsen.
[b]Surface concentrations ($\mu g\,l^{-1}$).

Integrated chlorophyll concentrations (0–100 m) were highest offshelf at Sta. 1, with the largest diatom concentration in the upper 25 m, and at Sta. 5 in Laubeuf Fjord (Table 2). Integrated pigment values were an order of magnitude lower at the more southerly stations. During autumn 2002, the median chlorophyll concentration in the upper 100 m of the water column was $0.22\,\mu g\,l^{-1}$ (range: 0.04–$1.50\,\mu g\,chl\,l^{-1}$), with phaeopigments averaging about 70% of the total pigment. Average integrated chlorophyll values were higher at all locations than those in 2001, possibly because sampling was about 2 weeks earlier in 2002. At the northern end of the study area, chlorophyll and total pigment maxima occurred below 500 m suggesting that a significant portion of the bloom had sunk out of the water column.

Winter chlorophyll concentrations were an order of magnitude lower throughout the water column than in autumn (Fig. 4 vs. Fig. 5). Median concentrations were $0.017\,\mu g\,chl\,l^{-1}$ (range: 0.001–$0.05\,\mu g\,chl\,l^{-1}$) in 2001 and $0.027\,\mu g\,chl\,l^{-1}$ (range: 0.001–$0.18\,\mu g\,chl\,l^{-1}$) in 2002, with phaeopigments concentrations about 50% and 38% of the total pigment in respective years. The vertical distribution of fluorescence in relation to temperature is shown for three stations across the northern shelf in 2002 to represent conditions in the study area (Fig. 5). Fluorescence was near the limit of sensor detection. In addition to phytoplankton,

detritus, glacial flour (24–260 μm), the pilidium stage of benthic nemerteans (0.5–1 mm diameter; 13–88 individuals $10\,m^{-3}$), larval polychaetes (1–2.5 mm in length), small larvaceans, fish larvae, ostracods, small pteropods, foraminifera, small amphipods, and large and small copepods were present in the 5–25 m depth interval under sea-ice where furcilia also occurred.

Food availability for larval krill on the undersurface of sea-ice also was assessed. During autumn 2001 there was little sea-ice in the study area. In contrast during autumn 2002, ice from the previous winter was still present in some locations and under some second year ice floes there was considerable accumulation of algal biomass as evidenced by golden coloration. Median ice algal chlorophyll concentrations in all types of sea-ice were about an order of magnitude higher ($2.29\,\mu g\,chl\,l^{-1}$, range: 0.601–50 μg $chl\,l^{-1}$) than that found in the water column. During winter 2001, chlorophyll concentrations under sea-ice were relatively low (median: 0.05; range: 0.02–0.48 μg $chl\,l^{-1}$) and similar to that in the water column. During winter 2002, even though sea-ice formed much earlier in the autumn, chlorophyll concentrations on the undersurface of sea-ice, on average, were still relatively low at stations on the shelf outside the bay, with a median concentration of $0.07\,\mu g\,chl\,l^{-1}$ (range: 0.016–3.14 $\mu g\,chl\,l^{-1}$). Because we were unable to sample the inner bay it is not known what ice algal concentrations were under that sea-ice. Total pigment (chlorophyll a + phaeopigments) concentrations in sea-ice biota tended to increase toward the northern end of the study area west of Adelaide Island, with the date of collection and latitude explaining about 40% of the variation in ice chlorophyll concentrations over the study area (Fig. 6).

Particulate organic carbon (POC) and nitrogen concentrations (PON) during autumn 2001 at the depth of the chlorophyll maximum were highest at Sta. 1 (range: 84.8–586 μg $C\,l^{-1}$) and 4.52–46.3 μg $N\,l^{-1}$ and Sta. 5 (range: 56.2–156 μg $C\,l^{-1}$ and 8.94–28.5 μg $N\,l^{-1}$) and lower at the more southern stations (Stas 3 and 4, range: 24.3–93.9 μg $C\,l^{-1}$ and 6.3–11.3 μg $N\,l^{-1}$), following a pattern similar to that of chlorophyll. The median concentrations

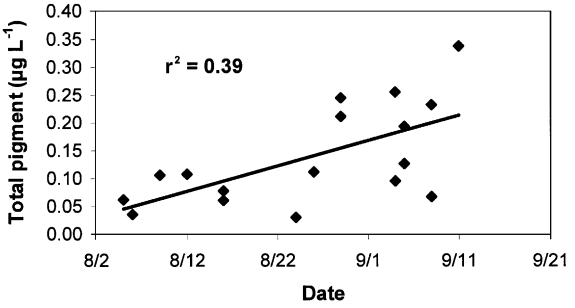


Fig. 6. The relationship between total pigment (chlorophyll + phaeopigment) concentrations on the undersurface of sea-ice and time of year (2002). Sampling was from southwest to northeast along the shelf, so that more northerly stations were sampled in late winter/early spring (i.e. September). Simple linear regression; $p<0.05$.

for all samples were 56.3 μg $C\,l^{-1}$ and 9.59 μg $N\,l^{-1}$, with an average C:N ratio of 6.9. During winter, the median POC and PON concentrations ($n=7$) of water collected from the depths of particle maxima (determined by a transmissometer) were 262 μg $C\,l^{-1}$ and 11.7 μg $N\,l^{-1}$. The concentrations in sea-ice biota, scraped from the undersurface of sea-ice where larval krill were feeding, were substantially higher (median: 544 μg $C\,l^{-1}$ and 33.7 μg $N\,l^{-1}$). The highest concentration of larvae observed by divers was at Sta. 26 where POC/N concentrations in sea-ice biota also were highest (1225 μg $C\,l^{-1}$ and 27.2 μg $N\,l^{-1}$). Winter C:N ratios were high (geomean: 27.8) in both the water-column and sea-ice samples and were significantly higher than ratios during autumn.

Particulate organic concentrations are only available from surface samples during autumn 2002. The median for all locations was 135 μg $C\,l^{-1}$ (range: 76.4–316) and 11 μg $N\,l^{-1}$ (range: 2.90–29.6). In contrast, the median concentration under year-old sea-ice, brash ice, and newly formed ice was 457 μg $C\,l^{-1}$ (range: 162–2076) and 71.8 μg $N\,l^{-1}$ (range: 18.7–291), with an average C:N ratio of 9.0. Larvae were only observed feeding under sea-ice at one location (Sta. 4) out of six dives. The winter vertical distribution of particulate material in relation to temperature and fluorescence are shown for three stations across the northern shelf in 2002 (Fig. 4). Particulate concentrations, as assessed by a

transmissometer, were generally very low, with most depths having a greater than 90% light transmittance. Transmissometer maxima, and occasionally fluorescence maxima, were associated with density features. Sampling of particle maxima from a few stations showed a range of relatively low values (35–200 μg Cl^{-1} and 2.83–13.6 μg Nl^{-1}). The median concentrations under sea-ice were 252 μg Cl^{-1} (range: 54–454) and 23.8 μg Nl^{-1} (range: 3.16–42.6). The average C:N ratio for the water column and sea-ice was 13.6 (geomean).

3.2. Larval abundance and distribution

The seasonal stage composition of larvae was similar between 2001 and 2002, but the abundance and depth distribution of stages varied by location in the study area and between years. Larval depth distributions based on discrete-depth 1 m^2 MOCNESS tows at Stas 1 and 5 are shown for autumn 2001 and 2002 to illustrate the contrast between offshelf and on-shelf stations and the difference between years (Fig. 4). During autumn 2001, larvae were very abundant throughout the study area where densities were on the order of 1–19 individuals m^{-3}. At the offshelf station (Sta. 1) where densities were highest (5627 individuals m^{-2}), younger stages (C2–F2) were nine times more abundant than older larvae (F3–F6). C3–F1 and F5 were the dominant modes suggesting that there were at least two reproductive pulses during the previous summer. Larvae were found in net samples between 25 and 910 m (the 0–25 m tow malfunctioned); however, the highest densities of younger stages were concentrated between 50 and 200 m in relatively warmer water but lower chlorophyll concentrations. The older stages were most abundant between 25 and 100 m. Many small larvae in the 800–910 m net appeared to have died prior to net collection, based on observations of an intact exoskeleton with internal body deterioration, and may have been sinking into deep water. These individuals were not included in the figure.

Onshore and inside Marguerite Bay, older larvae were more common and often concentrated in a narrow layer near surface. For example at Sta. 5 in Laubeuf Fjord, only F4–F6 larvae were found in net samples, with F6 having five-fold higher densities. Larvae were collected between 0 and 75 m, but were most abundant (ca. 6 m^{-3}) in the 25–50 m net in association with colder water and higher chlorophyll concentrations (Fig. 4). *E. superba* larvae were the dominant component of this sample both numerically (62%) and by weight (78%). Acoustic echograms give a more detailed picture of larval distribution in this depth interval, suggesting that most furcilia occurred in a highly aggregated, narrow layer at about 30 m depth, vertically separated from other deeper scattering organisms (Fig. 7). Because this spatial pattern was observed at many locations in the bay, food concentrations at these shallow depths were likely to be the most critical for larval growth rates during autumn 2001.

During winter 2001, F6 was the dominant stage. Furcilia were observed feeding on the undersurface of sea-ice at all seven dive sites, with the highest densities at Stas 5 and 26 at the northern end of the study area. The 2001 winter depth distributions of euphausiids are reported in Ashjian et al. (2004).

In general, larval densities were substantially lower throughout the study area during 2002. Although high densities were observed offshelf in

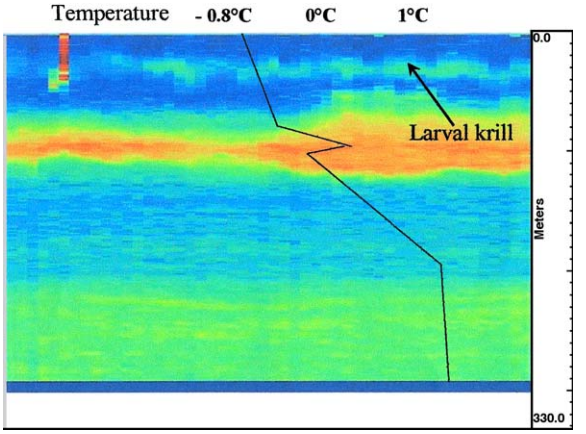


Fig. 7. Acoustic volume backscattering shows the narrow depth distribution of larval *E. superba* in relation to seawater temperature at Sta. 5 in Laubeuf Fjord during austral autumn 2001. Backscattering data were collected using a 120 kHz Hydroacoustic Technology Inc. Model 244 split-beam echosounder (Daly, unpublished). Depth scale, surface to 330 m. Net tows confirmed that the layer was primarily composed of krill larvae.

the Antarctic Circumpolar Current (Sta. 1), larvae were scarce at most locations on the shelf (Fig. 4). During autumn, C3 was the dominant stage offshelf and densities of the C2–F4 larvae were somewhat higher than in 2001 (0.01–110 m^{-3}; 3731 individuals m^{-2}). In contrast to the dispersed vertical distribution in 2001, larvae were concentrated near surface where the late fall diatom bloom was located. Many dead larvae were observed again, but this time in the 0–25 m net samples, along with larvae in good condition. The depth of maximum larval abundance was 25–50 m, in colder surface water and higher fluorescence. No *E. superba* larvae were found at Sta. 5 inside Marguerite Bay. The dominant overwintering stage was again F6; however, the 2002 individuals were not strongly associated with the undersurface of sea-ice. Krill larvae were observed near the undersurface of sea-ice in relatively low densities at only six out of nine dives. When few larvae were observed under sea-ice or in MOCNESS tows, we deployed Reeve and Rings nets in the upper 25 m where larvae were likely under-sampled by the MOCNESS. These net samples showed that *E. superba* larvae occurred consistently between 5 and 25 m in depth, albeit at low densities (2–23 furcilia $10\,m^{-3}$), coincident with benthic larvae, diatoms, and radiolarians. Larval densities were generally higher at the northern end of the study area (Stas 4, 13, 17, 26), west of Adelaide Island, than in the southern region.

3.3. Feeding behavior

Many furcilia had green or dark-colored guts and hepatopancreas during autumn, implying that they were feeding on plant material, while other larvae had off-white colored guts, presumably from feeding on microzooplankton or detritus. During winter, furcilia gut color ranged from no color (i.e. empty) to light green and off-white. Since chlorophyll *a* is not a conservative tracer of gut processes in *E. superba* (Daly, 1998), gut pigment values reported here are only intended to be a relative index of herbivory to assess potential feeding on phytoplankton and/or sea-ice algae. During autumn 2001, furcilia collected in the upper 50 m of the water column throughout the study area on average contained 7.62 ng pigment individuals^{-1} (range: 1.92–54.3 ng pigment individuals^{-1}, $n = 58$). Furcilia collected feeding under recently formed pancake ice at Sta. 3 had lower gut fluorescence (3.47 ng pigment individuals^{-1}, range: 1.56–6.46, $n = 25$). Winter values were even lower and were similar for furcilia collected from the water column and from under sea-ice [1.57 ng pigment individuals^{-1} (range: 0.52–7.44, $n = 23$) versus 1.63 ng pigment individuals^{-1} (range: 0.57–3.16, $n = 21$)]. During autumn 2002, average gut pigment was 28.4 ng individuals^{-1} for only two groups measured since larvae were scarce. During winter 2002, most furcilia were collected in the upper 25 m of the water column. Furcilia gut pigment was relatively low in most locations (2.27 ng pigment individuals^{-1}, range: 0.86–5.67, $n = 5$), but much higher at Stas 11 and 13 (51.3 ng pigment individuals^{-1}, range: 19.8–70.7, $n = 4$) in early September, when ice algal concentrations were increasing (Fig. 6). The few groups of larvae collected feeding on the undersurface of ice averaged 2.48 ng pigment individuals^{-1} (range: 0.62–4.61, $n = 3$).

Observations from experiments and microscopic examination of gut and fecal pellet contents suggest that furcilia are efficient scavengers, capable of ingesting most available small particles in the water column or under sea-ice, including phytoplankton, sea-ice biota, molt exuviae, detritus, and microzooplankton. Because much of the detritus was aggregated and sticky, many small particles such as glacial flour also were ingested.

3.4. Length, dry weight, and carbon and nitrogen content of larval stages

The average size of larval stages varied between seasons (Table 3). Mean lengths of F4–F6 were significantly larger ($p < 0.05$) during autumn (April–May) than during winter (August) in both years, but were similar between years for respective seasons. Dry weights also showed a significant decrease ($p < 0.05$) between autumn and winter in both years as a function of both larval stage (Table 4) and length (Fig. 8A and B). Larval dry weights, however, were significantly higher

Table 3
Comparison of mean (± SD or range) length (mm) of *E. superba* calyptopis (C), furcilia (F), and Y0 juvenile (<14 mm) stages between seasons and years

Location, season & year	Stage								
	C2	C3	F1	F2	F3	F4	F5	F6	Juvenile
This study									
Fall 2001	3.00±0.39 (23)	3.72±0.49 (66)	4.42±0.71 (55)	5.53±1.01 (36)	7.43±1.21 (21)	8.85±1.22 (43)	9.99±1.15 (77)	11.68±1.58 (107)	0
Winter 2001						7.56±0.89 (5)	8.57±1.54 (58)	10.4±1.4 (268)	11.9±1.4 (66)
Fall 2002	2.41±0.37 (38)	3.21±0.35 (48)	5.19±0.94 (40)	6.38±0.69 (36)	7.32±0.62 (45)	8.85±0.94 (22)	9.84±0.56 (16)	11.0±0.0 (4)	0
Winter 2002						7.21±0.64 (28)	8.23±0.73 (37)	9.82±1.43 (27)	11.5 (1)
Other published data									
Lab[a]	2.90±0.14	4.26±0.00	5.38±0.29	6.65±0.35	8.24±0.06	8.82±0.18	9.60±0.23	10.66±0.23	
Gerlache St.,[b] Jan.–Mar. 1987		4.4	6.1	7.1	8.2	9.7			
Bransfield St.,[b] Jan.–Mar. 1987		4.0	5.5	6.9	7.8	9.0			
Drake Passage,[b] Jan.–Mar. 1987		3.81	4.9	6.2	7.4	8.3			
Marguerite Bay,[c] Feb–Mar, 2000		4.7±0.1	6.1±0.2	7.2±0.1					
Bransfield St.,[d] March 1984	3.35±0.02	4.21±0.35	5.33±0.26	6.35±0.62	7.11±0.41	7.75±0.18	9.30		
Scotia Sea,[d] March 1984	2.99±0.35	4.35±0.40	5.42±0.48	6.80±0.29	7.78±0.27	7.64			
N Elephant Is.,[d] March 1984	3.08±0.23	4.32±0.36	5.50±0.64	6.39±0.56	7.37±0.48	8.05±0.34	9.09±0.06		
Scotia Sea,[e] April 1928	2.88 (2.5–3.07)	4.15 (3.77–4.67)	5.15 (4.17–6.00)	6.32 (5.33–6.87)	7.46 (6.33–8.50)	8.37 (6.67–9.46)	9.45 (8.25–10.83)	10.49 (9.25–11.96)	
Circumpolar,[e] August 1928								10.11 (8.00–11.00)	
Scotia Sea,[f] August 1988						7.00	8.40±0.54	10.17±0.97	

Sample size in parentheses.
[a]Ikeda (1984).
[b]Huntley and Brinton (1991).
[c]Meyer et al. (2003).
[d]Brinton et al. (1986).
[e]Fraser (1936).
[f]Daly (1990).

Table 4
Comparison of mean (± SD) or range of dry weights (mg) of *E. superba* calyptopis (C), furcilia (F), and Y0 juvenile (<14 mm) stages between seasons and years

Location, season & year	Stage								
	C2	C3	F1	F2	F3	F4	F5	F6	Juvenile
This study									
Fall 2001		0.150±0.030 (18)	0.277±0.247 (9)	0.247±0.057 (8)	0.684±0.239 (10)	0.811±0.303 (36)	1.15±0.35 (34)	2.04±0.75 (32)	
Winter 2001						0.378±0.091 (3)	0.321±0.131 (15)	0.892±0.435 (103)	1.79±0.32 (3)
Fall 2002	0.180±0.067 67 (2)	0.358±0.11 (2)		0.488 (1)	0.770±0.304 (2)	1.17±0.082 (3)	1.92±1.92 (3)	2.27±0.22 (2)	
Winter 2002						0.514±0.274 (8)	0.809±0.416 (10)	1.08±0.51 (26)	2.1 (1)
Other published data									
Gerlache St.,[a] Jan.–Mar. 1987		0.437	0.500	0.706	0.882	1.12	1.25		
Bransfield St.,[a] Jan.–Mar. 1987		0.059	0.323	0.397	0.500	0.823			
Drake Passage,[a] Jan.–Mar. 1987		0.058	0.059	0.323	0.353	0.529			
Marguerite Bay,[b] Feb.–Mar. 2000		0.219±0.039	0.340±0.061	0.509±0.084					
Lazarev Sea,[c] Apr. 1999					0.335–0.400				

Sample size in parentheses is the number of groups of individuals measured for C2–F3, or number of individuals for F4–F6.
[a]Huntley and Brinton (1991).
[b]Meyer et al. (2003).
[c]Meyer et al. (2002).

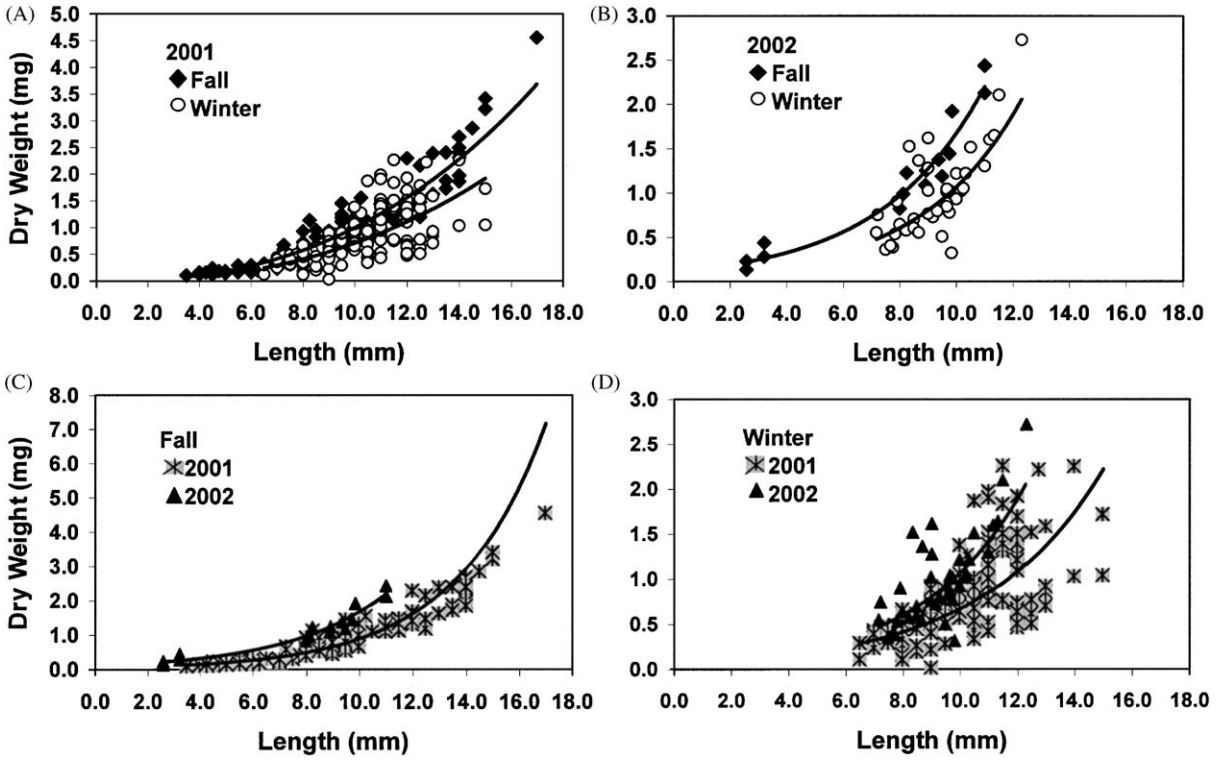


Fig. 8. Comparisons of the relationships between dry weight and length of larval *E. superba* between fall and winter in 2001 (A) and 2002 (B), and between both autumns (C) and winters (D) in each year. Regression relationships are shown in Table 1.

($p<0.05$) in 2002 compared to weights of larvae in 2001 (Fig. 8C and D). The similarity of F4 and F5 weights in winter 2001 (Table 4) was probably due to the small sample sizes as larvae were scarce and the broad range of winter weights. Fig. 8 data also suggest that the seasonal weight decrease was greater for larger larvae. Based on seasonal dry weight to length regressions (Table 1), the decline in dry weight for a 10 mm individual over 91 days, using 15 May and 15 August as arbitrary seasonal midpoints, was on the order of 0.003 mg DW d^{-1}, or about 0.3% of body DW d^{-1}, in 2001 and almost twice that in 2002.

Body carbon and nitrogen, as a percent of dry weight, was similar among larval stages C3–F6 (no data for C2) within each season, so stage data were pooled. The geometric mean percent C significantly decreased ($p<0.05$) between autumn and winter in both years, while N significantly decreased between seasons in 2001 but not in 2002 (Table 5). The percent decline in C and N between seasons was similar to that of dry weight. The mean percent C and N for all stages was not significantly different between fall 2001 and 2002, but percent C was significantly lower during winter 2002 than in 2001 ($p<0.05$), while nitrogen was not. The effects of starvation on dry weight and body C and N of winter F4–F6 were experimentally determined (Fig. 9). A substantial number of larvae (>30) survived and continued to molt for a 27-day period during which they were held without food. Numerous individuals were frozen at regular intervals throughout the experiment. Mortality did occur, but was not quantified. On average a starved 10-mm larva decreased 0.009 mg DW d^{-1}, 6.49 μg C d^{-1}, and 0.927 μg N d^{-1}. This is equivalent to about 1% of body DW, 1% of body C, and 1% of body N d^{-1}. Larger larvae experienced a greater weight loss than smaller larvae, similar to that observed in the 2001 field samples.

Table 5
Mean seasonal body carbon and nitrogen content and the C:N ratios for larval *E. superba*

	Fall 2001	Winter 2001	Fall 2002	Winter 2002
n	52	35	24	38
% Carbon	41.2 (32.6–63.6)	34.7 (26.4–45.7)	37.5 (35.5–42.2)	28.2 (21.2–40.9)
% Nitrogen	9.21 (7.59–12.1)	7.66 (5.00–9.00)	8.27 (7.73–8.73)	7.52 (5.36–9.86)
C:N	4.47 (3.44–5.60)	4.53 (4.10–6.56)	4.49 (4.35–5.17)	3.74 (3.55–4.63)

C and N given as percent of dry weight, *n* is sample size, range in parentheses.

3.5. Larval development

Larval krill showed evidence of delayed development, especially during winter. During autumn, almost all of the youngest stages (C2–Fl, and F3) developed to the next larval stage when molting (Table 6). Very few showed indirect development to an intermediate or variant form based on telson spine morphology. However, older furcilia (F2, F4–F5) occasionally remained at the same stage when they molted even during autumn. This indirect or delayed development was most prevalent in F6 individuals during autumn, and the dominant behavior during winter. Even though larvae continued to molt in winter, 87% and 88% of the F6s in 2001 and 2002, respectively, did not develop to the juvenile stage during the study period.

Incomplete molting may have been an important source of mortality for C2–F5 stages, where the molt remained partially attached to the larvae and often resulted in death after several days. Incomplete molting occurred in 12% of the larvae (F1–F5) in growth experiments during autumn 2001 and in 50% of the larvae (C2–F3) during autumn 2002 at the offshelf station. No F6 showed evidence of incomplete molting.

3.6. Molting and growth rates

Larval krill continue to molt during autumn and winter. The intermolt period (IMP) varied, but in general the number of days between molting was shorter during autumn and increased during winter (Table 7). The median IMP for both years was 19 days in autumn and 40 days in winter. Multiple linear regression analysis ($p<0.001$) indicated that about 43% of the variation in the IMP between seasons was explained by sea-surface temperature and surface chlorophyll concentrations.

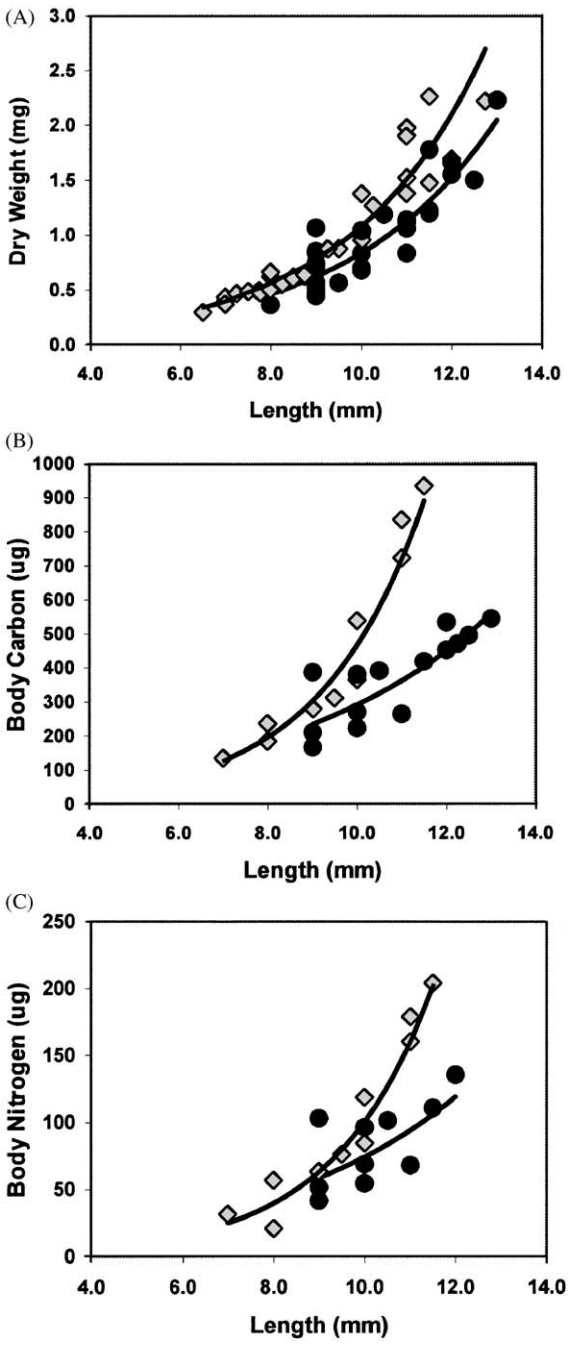
Both uropod and telson measurements were evaluated in order to determine their usefulness in estimating larval growth or shrinkage and to determine whether the results of the two methods were comparable. Uropods were less frequently damaged (ca. 2%) than the telson (ca. 18%) during molting, thus making uropods a more reliable measure. Telson and uropod lengths were compared for 56 larvae (F4–F6 and Y0 juveniles) during winter, when accurate measurements are critical to determine whether growth or shrinkage occurs. Both the right and left uropod exopodites also were measured on 21 of these larvae to assess the variability of that measure. The results show that the percent change in telson length was not correlated with the percent change in length of either uropod (left: Spearman $r_s = 0.13$, $p = 0.57$; right: $r_s = -0.21$, $p = 0.40$), whereas the percent change in right and left uropods was highly correlated ($r_s = 0.90$, $p<0.001$). The average difference in the percent change in length between the right and left uropod was 1.5% (range: 0–2.3%). The telson measurements also indicated negative growth 7% more frequently than did the uropod. These differences may be explained by the fact that the telson of the post-molt krill has a larger volume than the telson of the molt, while the uropods are relatively flat in both. Consequently, it is more difficult to accurately measure a small

change in length on a telson. Although the differences between telson and uropod measurements were relatively modest, small differences may result in very different interpretations of larval growth, particularly in winter. Lastly, uropod length was consistently a better predictor of total body length, based on R^2 values from Model I linear regressions (see Methods section). For these reasons and because the uropod was used more frequently in published growth studies, I used uropod length to estimate growth.

Table 6
Percentage of larval *E. superba* following direct and indirect developmental pathways

Larval stage	Fall 2001		Winter 2001		Fall 2002		Winter 2002	
	%D	%I	%D	%I	%D	%I	%D	%I
C2					100			
C3					100			
F1	100				100			
F2	67	33			100[a]			
F3	100							
F4	92	8						
F5	91	9	100[a]				67	33
F6	4	96	13	87			12	88

D is direct development to the next stage (i.e., F4→F5) and I is indirect development to the same stage or an intermediate form (i.e., F4→F4) when molting. C is calyptopis, F is furcila.
[a]One individual.



Larval growth rates were variable during autumn and were significantly lower ($p<0.001$) in winter, decreasing to near zero in both years (Fig. 10). Because larvae were scarce in 2002, there were only three growth experiments. The rates measured in the last experiment in September were significantly higher ($p<0.001$) than other winter rates. There was no significant difference ($p>0.05$) in growth rates, based either on percent change in uropod length or on calculated growth (mm d^{-1}), among stages or length of larvae within seasons.

Fig. 9. Decrease in dry weight (A), body carbon (B), and body nitrogen (C) of starved larval *E. superba*. Initial condition of furcilia 4–furcilia 6 larvae on 28 July (diamonds) contrasted with larval condition on 24 August 2001 (circles). Regression relationships for Day 1 and Day 27 are: (A) $DW_{t1} = 0.039e^{0.332L_{t1}}$ ($r^2 = 0.95$, $n = 29$) and $DW_{t27} = 0.042e^{0.298L_{t27}}$ ($r^2 = 0.76$, $n = 31$), (b) $C_{t1} = 6.24e^{0.431C_{t1}}$ ($r^2 = 0.95$, $n = 10$), $C_{t27} = 33.4e^{0.217C_{t27}}$ ($r^2 = 0.63$, $n = 10$), and (c) $N_{t1} = 0.965e^{0.465N_{t1}}$, ($r^2 = 0.86$, $n = 10$), $N_{t27} = 7.01e^{0.236N_{t27}}$ ($r^2 = 0.42$, $n = 10$).

Table 7
Growth and intermolt period (IMP) for larval and first-year (Y0) juvenile *E. superba*

Sta.	SST (°C)	Chl ($\mu g\,l^{-1}$)	Larval stages	*n*	IMP (d)	% Change in uropod length	Growth rate ($mm\,d^{-1}$)
Fall 2001							
1	−0.59	0.37	F1–F6	13	19	8.5	0.030
1	−0.59	0.37	F1–F2	3	—	—	—
2	−0.82	0.22	F5–F6	16	17	8.31	0.020
2	−0.82	0.22	F2–F5	6	18	8.01	0.020
3	−1.75	0.08	F5–F6	20	20	7.02	0.036
4	−0.87	0.08	F4–F6	11	40	1.62	0.013
5	−0.64	0.09	F5–F6	16	18	5.94	0.030
Fall 2002							
	−0.20	0.35	C2–F3	16	21	6.9[a]	0.013
Fall median for both years				82	19	6.52	0.027
Winter 2001							
5	−1.75	0.05	F6	15	23	0.00	0.000
17							
26	−1.79	0.04	F5–F6	10	51	0.00	0.000
51	−1.81	0.04	F5–Juv	11	31	1.63	0.005
Winter 2002							
	−1.83	0.05	F6–Juv	12	40	4.25	0.013
	−1.82	0.03	F4–Juv	9	61	0.00	0.000
Winter median for both years					40	0.00	0.00

Growth is given as the median percent change in the length of uropods on all pairs (a krill and its molt) of molted individuals over the IMP and as the median daily growth rate. Sea-surface temperature (SST) and chlorophyll (Chl) concentrations at each location are shown. Larval stage *F* is furcilia, Juv is juvenile, *n* is number of molted individuals.
[a]Uropods damaged, used telson length.

There also was no significant difference in rates between years for each season (e.g., autumn 2001 vs. autumn 2002), therefore the rates from the 2 years were combined. The median IMP and growth rates for autumn and winter are shown in Table 7. The percent uropod change in length is shown because it is a direct measurement of growth, whereas the growth in terms of $mm\,d^{-1}$ was calculated and therefore subject to additional uncertainty. Using the relationships in Table 1 and the average daily growth rate ($0.027\,mm\,d^{-1}$), the estimated daily weight increase for a 10 mm furcilia in autumn 2001 is about $6.75\,\mu g\,DW\,d^{-1}$, $2.82\,\mu g\,C\,d^{-1}$, and $0.575\,\mu g\,N\,d^{-1}$.

Because the variance in field rates is likely more important than an average rate in understanding population dynamics, the histograms of growth rates for autumn and winter are shown in Fig. 11. Only a small percentage of the larval population had negative growth (1.3%) during autumn, while 37% showed a 0–5% increase in uropod length and the majority (55%) had a 6–15% increase in

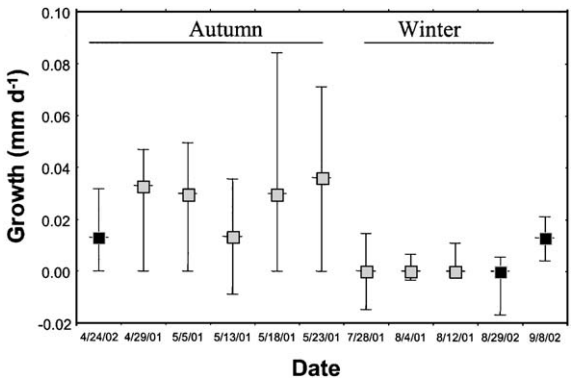


Fig. 10. Seasonal change in median growth rates for larval *E. superba* during autumn and winter in 2001 (gray boxes) and 2002 (black boxes). The vertical bars indicate the range.

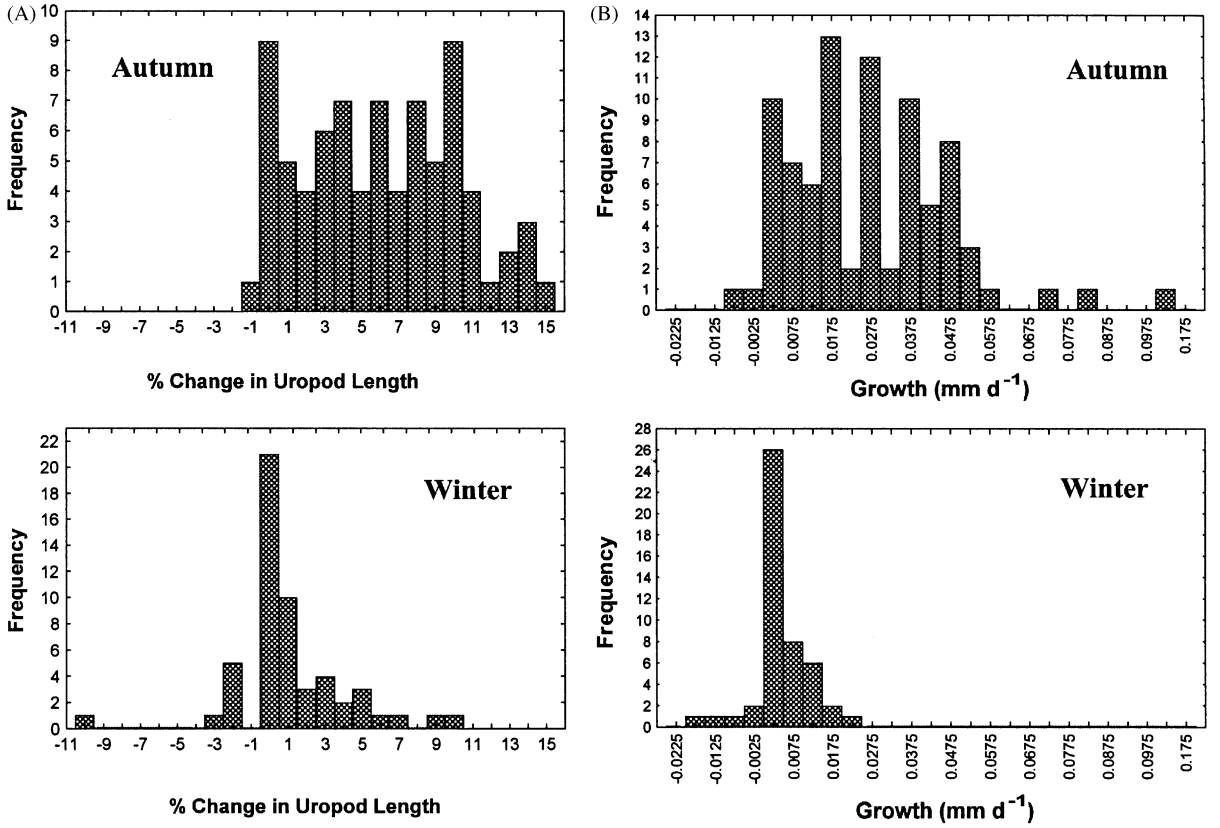


Fig. 11. Histograms of growth rates of larval *E. superba* to show the seasonal variation and range of values for (A) percent change in uropod length and (B) calculated growth rates ($mm\,d^{-1}$) during autumn and winter.

uropod length upon molting. During winter about 13% of the larvae had negative growth, 57% showed 0–1% growth, and 30% had a 2–10% increase in uropod length.

3.7. Recruitment

A substantial number of larvae appeared to survive overwinter and recruit to the juvenile class during spring 2001. The evidence for recruitment is that during autumn and winter 2001 there were few intermediate sized krill (20–40 mm) in the study area and all of these were immature adults and therefore probably not recruits in their second year; none were juveniles (Fig. 12). During autumn and winter 2002, however, there were a significant number of small to intermediate sized krill and many of these were juveniles, as well as immature adults. Although we do not know with certainty that these juveniles came from Marguerite Bay, their presence indicates that larvae survived overwinter somewhere in the general vicinity.

4. Discussion

Juvenile recruitment of *E. superba* in spring on the western Antarctic Peninsula shelf depends on several factors: (1) successful adult reproduction and larval survival during the prior summer, (2) entrainment onto the shelf of young larvae spawned offshore, (3) larvae retained on-shelf, and (4) survival of older larvae overwinter. In both autumn 2001 and 2002, larval abundances at the

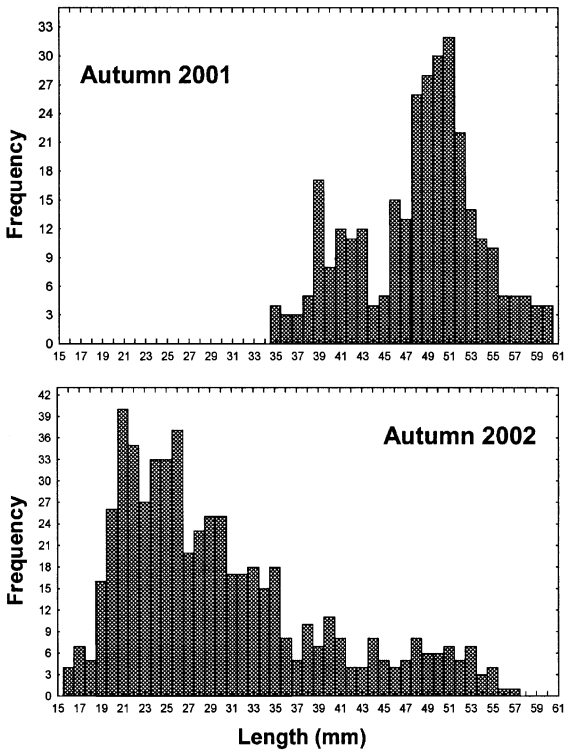


Fig. 12. Length-frequency of *E. superba* collected in net tows in autumn 2001 and autumn 2002 to show the recruitment of juvenile krill (15–30 mm in length) in 2002 resulting from overwintering 2001 larvae.

offshelf station in the Antarctic Circumpolar Current (ACC) are within the range of those reported for 1980–1981 (Brinton et al., 1986; Kittel and Jażdżewski, 1982), a year noted for high krill recruitment (Siegel and Loeb, 1995). Our larval densities suggest that there was successful adult reproduction during both summers prior to the GLOBEC cruises, but the timing and extent of summer reproduction may have varied between the two years. *E. superba* undergo a long, complex larval development (Fraser, 1936). Based on a laboratory study (Ikeda, 1984), calyptopis I (CI) larvae appear about 30 days and furcilia 6 (F6) larvae appear about 120 days after hatching. In April and May 2001, late stage furcilia were common throughout the study area, indicating that reproduction probably started in December and that larvae were retained on the shelf. A second mode of smaller larvae occurred offshelf, suggesting that spawning continued into March. Pakhomov et al. (2004) observed higher larval densities, but a similar distribution of stages (i.e. later stages dominant over the shelf) a few weeks earlier in April. The lack of larvae on-shelf and the dominance of small larvae (C3) offshelf in April 2002 indicate that spawning may have started later in 2002, that earlier spawned larvae had poor survival, or that larvae were advected downstream in the ACC.

During our cruises, the ACC was observed to pump circumpolar deep water onto the shelf where the Marguerite Trough intersects the shelf break (Klinck et al., 2004). This episodic exchange was detected previously in this region (Hofmann and Klinck, 1998) and may be one mechanism whereby krill are entrained onto Antarctic shelves in general (Prézelin et al., 2000; Endo et al., 2002). The highest concentrations of larvae during winter 2002 were found on the shelf west of Adelaide Island. Another winter study noted a similar distribution pattern, with the highest concentrations of larvae along the outer shelf west of Adelaide Island and along the shelf break to the northeast (Siegel, 1989). There also was a large gyre on-shelf in the study area and sluggish circulation in the middle of the bay, which may act to retain larvae (Klinck et al., 2004; Beardsely et al., 2004). The combination of physical and biological processes that led to enhanced larval abundance in the study area during autumn 2001 may not have been as strongly developed or occurred at different times in 2002. Even though larvae were abundant during autumn 2001, net densities (Ashjian et al., 2004) and acoustic backscattering (Lawson et al., 2004) indicate that the abundance of all zooplankton in the study area significantly decreased between autumn and winter possibly due to advection and/or mortality.

4.1. Autumn and winter food limitation

Many factors influence krill overwintering survival. The ability of an individual furcilia to withstand a suboptimal winter environment, in part, will be a function of its body size, weight, and composition (e.g., lipid storage) at the end of the

productive season. Larger, more developed larvae with considerable lipid storage should be in better condition or more robust than smaller individuals with little lipid. Growth and development rates, as well as an assessment of an individual's condition at any point in time, reflect an integration of the environment experienced by that individual over a period of weeks prior to collection. Huntley and Brinton (1991) provided evidence from a summer field investigation that regional variability in larval body size, weight, growth, and development was positively correlated with higher food concentrations. Since chlorophyll concentrations are typically higher on-shelf than offshelf west of the Antarctic Peninsula during summer (Huntley and Brinton, 1991; Smith et al., 1996), on-shelf larvae may be in better condition to overwinter in this region.

Body length and weight: A comparison of body length (Table 3) and body weight (Table 4) among larvae collected during late summer, autumn, and winter in different locations, or raised in a laboratory supports this hypothesis and indicates that GLOBEC larvae collected over the shelf were in better than average condition prior to winter. Larvae with the largest size and highest dry weights were collected from Gerlache Strait (north end of the Antarctic Peninsula) during March, where integrated (0–50 m) chlorophyll *a* values averaged about 150 mg m^{-2} between January and March (Huntley and Brinton, 1991), and from inner Marguerite Bay (5–25 μg chl *a* l^{-1}) in February and March (Meyer et al., 2003). Furcilia collected from Bransfield Strait and the Drake Passage, however, had lower dry weights, concomitant with a substantially lower food supply (integrated chlorophyll $\leqslant$50 mg m^{-2}). F3s collected during April in the Lazarev Sea had dry weights similar to those from the Drake Passage, although April chlorophyll concentrations in the surface mixed layer were substantially lower (0.06–0.09 μg chl *a* l^{-1}) and more typical of winter concentrations (Meyer et al., 2002b). The dry weights of these larvae suggest that food availability may have been higher during the preceding summer. Pakhomov et al. (2004) found integrated chlorophyll values during early April 2001 ranging from 15 to 165 mg m^{-2}, with the highest values occurring over the shelf. They also estimated relatively high carbon ingestion rates (16.5–44.5% body C d^{-1}) for larval krill. Thus, summer chlorophyll values in Marguerite Bay may be similar to those in Gerlache Strait, providing a favorable environment for larval growth. Late April and May chlorophyll values in Marguerite Bay were an order of magnitude higher than those in the Lazarev Sea during April, which is at a higher latitude than Marguerite Bay.

During GLOBEC, young (C2–Fl) larvae were collected primarily offshelf and were either similar to or smaller than individuals collected by other investigators in the Scotia Sea and from the northern Antarctic Peninsula region during March and April. The dry weight of these young larvae provides further confirmation of poor feeding conditions offshelf. Based on both length and weight, the larger GLOBEC furcilia (F4–F6), which were collected primarily on-shelf, appeared to be in similar or better condition than larvae reported from other regions or from the lab study, except for the Gerlache larvae or Marguerite Bay larvae collected during late summer 2000. The higher gut pigment values in autumn compared to that in winter suggest that the declining bloom and prevalent microzooplankton on the shelf may have further enhanced late summer and fall larval growth and development prior to overwintering.

There are few winter data to compare larval size or weight, particularly in relation to food availability. The length of winter F6 larvae (the dominant stage), collected from the water column and under sea-ice, either were similar to or slightly smaller than larvae reported from other winter studies at more northern Southern Ocean latitudes (Table 3). Both the average water-column (0.1 μg l^{-1}) and sea-ice (7.0 μg l^{-1}) chlorophyll concentrations in the Scotia–Weddell study (Daly, 1990) were higher than in Marguerite Bay. The very low chlorophyll concentrations in Marguerite Bay were similar to other Antarctic Peninsula winter values (Kottmeier and Sullivan, 1987). Chlorophyll on the undersurface of sea-ice was much more variable, but on average also very low and the same order of magnitude as values in the water column. The low gut pigment in winter suggests that little nutrition was derived from autotrophs either in the water column or under

sea-ice, consistent with measured chlorophyll concentrations. Average Marguerite Bay gut pigments during August were lower than values (4.0–21.0 ng individual^{-1}) for F6 larvae collected under sea-ice in the Scotia–Weddell seas, even after correcting Marguerite Bay larval values for a 32% degradation loss assumed in the Scotia–Weddell study (Daly, 1990). The higher gut pigments in September on the northern shelf of Marguerite Bay, coincident with increasing chlorophyll concentrations under sea-ice (Fig. 6), suggest that ice algal biomass was starting to accumulate and be utilized as a food source.

Few studies have investigated alternative food sources that may be exploited by larval krill during winter. Although ice algae may not have been prevalent on the undersurface of sea-ice in either year, heterotrophs are another important component of sea-ice assemblages (Palmisano and Garrison, 1993). Indeed, ciliates and other heterotrophs were relatively abundant in diver-collected sea-ice samples, near surface, and at the pycnocline during 2001, but not 2002 (S. Gallager, personal communication). Winter particulate organic concentrations in both years were higher on the undersurface of sea-ice than in the water column, even directly below sea-ice, possibly due to detritus. C:N concentrations and microscopic examination of samples from under ice and from the water column indicated a significant detrital component. Microzooplankton and detritus, in the water column and in sea-ice biota, may have been the most abundant food sources in 2001. In August 2002, when microzooplankton were scarce, other potential food sources included sparse diatoms, small benthic larvae, other small zooplankton, and detritus aggregated in the upper 25 m along with larval krill. Although alternative food sources may have been exploited during winter, the decrease in larval length-specific dry weights between autumn and winter during GLOBEC suggest that most furcilia were food limited (Fig. 8). Length-specific dry weights also were more variable in winter than fall, indicative of the variation in the ability of individuals to cope with a low-food environment.

One other study (Frazer et al., 2002b) reported size of larvae during early spring (September 1991 and 1993) from net and dive collections in the vicinity of the GLOBEC study area, but not in terms of larval stage, so the data were not included in Table 4. Chlorophyll also was not measured. These authors observed that the mean size of larvae collected by divers was larger (1991: 10.1 mm; 1993: 9.12 mm) than those collected by nets between 0 and 300 m (1991: 9.46 mm; 1993: 8.30 mm). The GLOBEC larvae were similar to or slightly larger in size by comparison.

Body composition: Body carbon (C) and nitrogen (N) may be better predictors of larval robustness than weight or length. Pakhomov et al. (2004) observed comparable larval C:N ratios and percent body carbon in early April 2001; therefore, these body parameters did not appear to substantially change between April and May. The average C and N content of fall larvae also is similar to that measured for CIII, FI, and FII larvae from Marguerite Bay during late summer, with lipid concentrations between 13.8% and 19.7% DW (Meyer et al., 2003). Protein and lipids usually account for most of the body C and N in zooplankton, with carbohydrates being generally negligible (<5% of dry weight; Kolakowski and Szyper-Machowska, 1989). Since the C:N ratio for protein is about 3, the average C:N ratio of larvae from this study (4.47; Table 5) indicates that lipid storage was moderate during autumn and winter. Ju and Harvey (2004) also found low lipid storage in larval krill. Similarly, Stübing et al. (2003) measured a total lipid content in F3–F4 larvae of about 12% DW and F4–F6 had a mean lipid content of about 20% DW in this region during early April 2001. Relatively low lipid levels were reported for calyptopis (15% DW) and furcilia (18% DW) collected during autumn from the Weddell Sea (Hagen et al., 2001). Meyer et al. (2002b) also found a lipid level of 15% DW and a C body content of 36% DW in autumn F3s from the Lazarev Sea. Thus lipid storage appears to be variable and moderate in larval krill prior to overwintering. The decrease in C and N in Marguerite Bay larvae between autumn and winter, particularly in 2002, supports the observation of food limitation in winter; however, this measure is uncertain. If larvae were not retained in the study area, then the same population may not

have been sampled in both seasons. Additional data on dry weight, proximate composition, and lipids are needed to adequately assess regional and interannual differences.

Larval development: The delayed development of F6 larvae (Table 6) provides additional verification of suboptimal food and was a dominant behavior during both winters. Larval *E. superba*, like many invertebrate larvae, are characterized by phenotypic plasticity and demonstrate functional flexibility in the timing of molting and metamorphosis and the modes of development in response to changing environmental conditions. For example, indirect larval development or delayed development is believed to be evidence of food limitation (Brinton et al., 1986). Furthermore, the high mortality of younger stages in autumn due to incomplete molting and the appearance of dead larvae (deteriorated body within the exoskeleton) in net samples may have been due to food limitation or a higher age-specific mortality. Pakhomov et al. (2004) noted this phenomenon as well. Our combined observations suggest that the high mortality started at least by April and continued during May, and occurred in both years. Fraser (1936) describes in detail the variable or intermediate forms of furcilia. In Marguerite Bay, the younger stages (C2–F1, F3) that did not die when molting, all developed directly to the next stage. The fact that variant forms occurred in F2, F4, and F5 larvae, plus the delayed development of F6, may reflect an increasing flexibility by larvae to withstand poor food conditions with age.

The results of Melnikov and Spiridonov (1996) offer further support for the delayed development strategy. They reported that krill sampled under sea-ice in the western Weddell Sea (72–63 °S) during austral summer and autumn (early February–June) were mainly F6. They concluded that these larvae must have originated in the southeastern Weddell Sea during the previous summer (thus, 1+ age group) and that they had very low growth rates due to low food concentrations. Chlorophyll concentrations in the water column were less than $0.1\,\mu g\,l^{-1}$ and sea-ice biota was not well developed under sea-ice. In contrast, Daly (1990) observed continued larval development from F4 to juveniles between June and August within the pack ice at about 60 °S in the Scotia–Weddell confluence. This more northerly location was characterized by similar low chlorophyll concentrations in the water column, but with a visible and measurable accumulation of sea-ice biota on the undersurface of first-year sea-ice as noted above.

Larval growth: Lastly, growth and molting rates offers strong evidence that Marguerite Bay larvae were food-limited overwinter, with a significant part of the variability of the intermolt period (IMP) explained by seasonal decreases in temperature and surface chlorophyll. Buchholz (1991) reviewed laboratory studies of juvenile and adult krill, as well as his own findings, and concluded that the molting rate in older life history stages decreased with temperature, whereas growth rates were more sensitive to the quality and quantity of food and were not well correlated with temperature. The intermolt period also varies for body size as small larvae have a shorter IMP than adults during summer. A seasonal comparison of larval and Y0 juvenile growth rates and IMP from field and laboratory investigations (Table 8) show that my average IMP in autumn was similar to other reported rates for summer. The larvae having the longest fall IMP (i.e., Sta. 4; 40 d) may have already adjusted to a winter mode (Table 7). Larval molting rates decreased about two fold between autumn and winter; consequently, less energy was invested in molting.

Marguerite Bay larval growth increments during autumn (percentage change in uropod length; Fig. 11) are within the range of other published values (−15% to 21%, Buchholz, 1991; also see Table 8). The measured growth rates ($mm\,d^{-1}$) of larvae and Y0 juveniles in autumn and early spring were generally lower than published summer rates, and winter rates were near zero. Ross et al. (2004) measured even lower ($-1.49\%\ IMP^{-1}$) growth increments during winter within the study area. In contrast to the consistently low winter growth rates, my September rate (Fig. 10) was similar to fall rates and suggests that larvae were responding to improved food conditions in early spring. Larval gut pigments also increased in September. These larvae were collected at the northern end of the study area (Stas 11, 13, 17), where the ciliate,

Table 8
Seasonal comparison of growth rates and intermolt period for furcilia stages 3–6 and Year 0 juvenile *E. superba*

Month season	Growth (mm d^{-1})	% Growth	IMP (d)	Measurement	References
Summer	0.06	9[c]	13–15	Lab experiment	Ikeda (1984)
Feb.–Mar.	0.082	18.3[c]	18	Field experiment	Huntley and Brinton (1991)
April–May	nd	10.2–18.5[a]	6–17	Field experiment	Pakhomov et al. (2004)
April–May	0.027	6.52[a]	19 (17–40)	Field experiment	This study
Fall/winter	0.047	nd	nd	Field samples	Hosie and Stolp (1989)
Winter	0.017[d]	5.43[b]	nd	Field experiment	Ross and Quetin (1991)
Winter	nd	−3.42[b]	nd	Field experiment	Ross and Quetin (1991)
Winter	0.020[d]	nd	48 (28–80)	Field experiment	Quetin et al. (1994)
Winter	−0.001 to −0.006	−1.6[b]	31 (22–115)	Field experiment	Ross et al. (2004)
August	0.070	14[c]	20	Field experiment	Daly (1990)
August	0.00	0.00[a]	40 (23–61)	Field experiment	This study
September	0.013	4.25[a]	40	Field experiment	This study
November	0.049	6.4[a]	33	Field experiment	Daly (1998)
Dec.–Jan.	0.07	2–10[b]	18 (7–40)	Field experiment	Ross et al. (2000)

IMP is the intermolt period (range in parentheses), nd is no data. Percentage growth is represented by the percent change over the intermolt period between a krill and its molt for:
[a]uropod length,
[b]telson length,
[c]total length.
[d]Elias (1990) cited in Quetin et al. (1994).

Mesodinium sp., was present in higher concentrations in the sea-ice biota than previously observed (S. Gallager, personal communication) and chlorophyll in sea-ice biota was relatively high (ca. 0.23 μg l^{-1}, Fig. 6).

It is not known whether the younger stages of larvae found in autumn can survive until winter. Fraser (1936), Daly (1990), and Frazer et al. (2002b), as well as this study, observed that F4–F6 larvae were the most common stages in early winter, with F6 being the dominant stage by late winter. Assuming that my average IMP is representative for April through June, the C3 larvae observed in late April could develop to the F3 stage by mid-June. Given food limitation, evidence of indirect or delayed development, increasing IMP and decreasing growth rates, and higher mortality of younger stages, it seems more probable that the overwintering larvae are primarily the F2–F6 stages found in autumn.

4.2. Body growth or shrinkage strategy

Even though larvae may decrease in biomass during winter, this study does not support the premise that most larvae shrink in length. Only 13% of the winter larvae showed negative growth, whereas the majority (87%) of larvae showed no growth or positive growth (Fig. 11). Not decreasing exoskeleton length, perhaps by increasing relative water content, would allow krill larvae the maximum flexibility to increase in body mass when food is available. Variability in growth is expected as individuals exploit small-scale differences in the quality and quantity of food in the water column or under sea-ice over the intermolt period. Although the average size of furcilia stages decreased between autumn and winter, this may not be due to shrinkage in length. Larvae occur as F4–F6 stages in early winter, with F6 being the dominant stage by late winter. If growth rates decreased in early winter, when F4 and F5 larvae were developing to the next stage, then the average size of F6 individuals by late winter would show an apparent decrease. The lower growth rates observed by Ross et al. (2004) are equivalent to only a 0.03–0.18 mm decrease over their average intermolt period (30.6 d). Our different results may be due to the fact that my growth rates were based on furcilia collected from both the undersurface of

sea-ice and from the water column or differences in experimental (uropod vs. telson, preservation issues, etc.) and/or statistical methodology.

The comparison of uropod and telson measurements suggests that estimates of growth based on the telson may give erroneous results; thus, a standardization of methodology is needed to achieve a better understanding of winter growth processes, as pointed out by Nicol (2000). Growth is usually considered to be the change in weight or biomass per unit time. Since weight is proportional to the cube of the length, length is often used as a proxy of growth, especially as it is relatively easy to measure change in length of an individual and not possible to measure a change in weight over time. Given the large variability in dry weight versus length during winter (Fig. 8), however, length alone is not a good indicator of biomass change during this season.

Although my results indicate that most larvae did not shrink in length, some portion of the larval population did appear to be starving and may have combusted body lipid and protein to support metabolism. The greater variability and decrease of length-specific dry weights (Fig. 8) and C and N content in winter compared to that in autumn supports this observation. Clearly the results of the starvation experiment demonstrate that some percentage of the population can survive without eating for at least one month. Larvae did reduce their metabolic rate between autumn and winter (J. Torres, personal communication), so that they required less food. A mass-balance calculation using average winter ingestion, respiration, and egestion rates indicate that C ingestion about equaled C losses in many larvae (K. Daly and J. Torres, unpublished). Nevertheless, more than 30% of individuals in winter growth experiments showed evidence of positive growth and, therefore, must have ingested sufficient food to support both metabolism as well as growth.

4.3. Role of sea-ice

Does an early and long-lasting ice cover provide a dependable food supply and enhanced survival of larval krill? The answer to this question does not appear to be straightforward. Winter sea-ice coverage over the study area and surrounding environs was extensive and similar between years (Fig. 1) and, therefore, not expected to be a factor affecting differences in larval behavior. The timing of sea-ice formation, however, did vary between the two years. Despite the fact that in 2002 first-year sea-ice formed several weeks to 2 months earlier, depending on the location, than in 2001 and that second-year sea-ice had visible accumulations of ice algae, sea-ice did not appear to significantly enhance the food supply for larval krill in either year. Much of the increased biomass in second year sea-ice in 2002 occurred in internal assemblages up inside the sea-ice, which were not accessible to krill. The average concentration of ice algae at the ice–water interface was very low in both winters (0.05 vs. 0.07 $\mu g\,chl\,l^{-1}$). In general it is difficult to make an accurate assessment of the availability of sea-ice biota to krill, however, because, (1) the under-ice surface is highly variable and physically complex, (2) krill can access surface areas under rafted floes or inside brine channels which are not easily sampled, (3) sample collections must be made at the ice–water interface on the spatial scale of feeding krill, and (4) sea-ice biota includes a heterotrophic component that is not assessed by chlorophyll, the most common indicator measured in most studies. Furthermore, assessments based on chlorophyll concentrations in the bottom section of ice cores, which is what is typically reported (see review in Palmisano and Garrison, 1993), often imply relatively high ice algal concentrations, but do not accurately depict the available food supply at the ice–water interface. The sea-ice chlorophyll concentrations reported here were from samples collected by divers from surfaces where krill were feeding. Hence, in spite of the relatively small sample size, they represent the variety of food concentrations exploited by larvae.

Numerous processes influence the location and biomass of ice assemblages (Ackley and Sullivan, 1994). For example, the type, size, and concentration of particulate matter that can be scavenged by forming ice crystals or pumped into unconsolidated ice by wave passage will vary spatially and interannually, as well as ice substructure (e.g., frazil vs. congelation ice), location of ice growth

(e.g., bottom vs. surface-flooding), ice ablation, and deformation processes. Due to low irradiance levels at high latitudes in autumn, such as in Marguerite Bay, ice algae may not be able to accumulate sufficient biomass on the undersurface of sea-ice to support larvae during winter, even when sea-ice forms relatively early. Freezing and melting processes at the ice–water interface during winter also may prevent biomass from accumulating. Instead, the ability of some larvae to survive at least a month without food, as evidenced by the results of the starvation experiment, coupled with opportunistic feeding on microzooplankton and detritus, may sustain much of the population until irradiance levels become sufficient to allow ice algal growth during September. In regions or years when the availability of winter ice biota is greater, there may be increased larval survival. The timing of the ice algal biomass increase during spring, which will be a function of latitude as well as physical characteristics of ice, such as snow cover, may be critical to larval survival if they are severely food limited in winter. Increased solar irradiance in spring also causes ice melt, which will give larvae access to internal ice communities through draining brine channels and sloughing ice at ice edges.

Alternatively, sea-ice at all latitudes may have an indirect effect on larval survival that is not yet appreciated. Ice floes release particulate matter during deformation, such as ridge formation, which could provide additional food if it remains suspended near surface. However, a limited number of chlorophyll and POC/N samples, collected just below or next to ice floes to examine this hypothesis, did not have higher concentrations than those deeper in the water column (data not shown).

Sea-ice, when present, also may provide a more dependable source of food for overwintering larvae in more northern latitudes of the Southern Ocean. Unlike Marguerite Bay larvae, winter furcilia in the Scotia–Weddell seas at 60°S, where irradiance levels are higher and for longer periods of the day, did not show evidence of food limitation in their molting, growth and development (Daly, 1990). For example, F6 larvae continued to develop during August (molting to the juvenile stage), they had a shorter IMP, and higher growth rates than Marguerite Bay larvae (Table 8). The growth rates were derived from changes in the length frequency of larvae collected in June and August in the vicinity of a satellite-tracked ice floe. Even though these rates were not experimentally determined and subject to greater uncertainty, the results are consistent with the experimentally determined molting and development rates, as well as the size of larvae and Y0 juveniles later in spring. Larvae in offshelf waters of the ACC west of the Antarctic Peninsula may not experience as favorable a food environment during summer and autumn as larvae on-shelf. Individuals advected northeastward in the ACC, however, may obtain enhanced food from sea-ice biota in years when the Scotia Sea is covered by sea-ice, compared with larvae overwintering on the shelf at high latitudes such as Marguerite Bay.

A more rigorous evaluation of the role of sea-ice in the winter survival of larval krill needs to include information on the water-column depth distribution of the larval population in relation to alternative food sources, including sea-ice biota. In one study, winter furcilia were collected throughout the water column down to 1000 m, with the highest densities in the upper 100 m (range: 0.01–63 individuals m^{-3}), while larval densities under sea-ice were on the order of 1000 m^{-2} (Daly and Macaulay, 1991). Frazer et al. (2002b) also reported higher densities of winter larvae in net tows than divers counted under sea-ice. Preliminary results from diver and ROV (Gallager et al., 2002) observations and MOCNESS net samples (Ashjian et al., 2004) during winter 2001 indicate that larvae occurred both on the undersurface of sea-ice and throughout the upper 150 m of the water column. In contrast, during 2002 larvae were much less abundant under sea-ice until mid-September when light levels and biomass of sea-ice biota increased. Instead, larvae appeared to be concentrated in the water column between 5 and 25 m. Even if sea-ice biota is not well developed, sea-ice may provide a refuge from predators (Daly and Macaulay, 1988, 1991). Food acquisition, however, appeared to be a stronger driver than predator avoidance, since some portion of the larval population during 2001, and most of the

larvae during 2002, did not retain a strong fidelity to sea-ice and occurred elsewhere in the water column. A better understanding is needed on the interannual variation of larval distribution in the water column and under sea-ice, the food sources in different habitats, and whether larvae migrate between depths.

5. Summary

An evaluation of the seasonal composition and body characteristics of *E. superba* larvae west of the Antarctic Peninsula indicates that individuals that hatch earlier in the summer and are retained in waters over the shelf are more likely to sustain maximal growth rates and achieve a greater length and weight prior to overwintering. The fact that F4–F6 are the primary stages observed in samples between June and August from different investigations suggests that larvae that have not developed to at least the F4 stage by June probably will not survive. The relatively high mortality of young larvae due to incomplete molting in autumn may have been a harbinger of their eventual decline. Larval krill stage composition, length, and weight, and larval growth and development rates from this study support the finding that larvae were actively feeding and growing during autumn, but were food limited during both winters in the vicinity of Marguerite Bay. Little nutrition was derived from autotrophs during winter; microzooplankton and detritus were the likely food sources, especially in 2001. A comparison of growth methodology also suggests that body length is not a good indicator of "growth" or the body combustion strategy in overwintering larvae. Future winter studies should include dry weight and proximate body composition in addition to length to investigate questions related to body shrinkage.

During this winter study at a relatively high latitude (65–70°S), larval krill employed a variety of overwintering behaviors including, (1) flexible feeding behavior and prey switching (i.e. feeding on algae, microzooplankton, and detritus either on the undersurface of sea-ice or in the water column (2) flexible morphology (i.e. delayed development), (3) flexible physiology (i.e. increased intermolt period and reduced growth) (4) reduced metabolism (J. Torres, personal communication), (5) moderate lipid storage, and (6) ability to withstand starvation for weeks by combusting body C and N. Although much of the larval population showed evidence of a loss in dry weight and body C and N between autumn and winter, about 30% of the larvae also had $>2\%$ increase in body length in winter. The large juvenile recruitment in 2001 was likely due to the large number of late stage larvae that were retained on the shelf, the condition of larvae prior to winter, as well as alternative food sources available to krill during winter. The physiological processes underlying population dynamics and the effect of variable overwintering growth rates on recruitment may best be investigated through energetic-based, size-structure models.

Overwintering larval *E. superba* clearly accrue some benefit from their association with sea-ice on an evolutionary level as their presence on the undersurface of ice is a persistent behavior. Nevertheless, furcilia have the flexibility to exploit a number of alternative food sources, such as microzooplankton and detritus, and therefore sea-ice is not the only parameter that must be assessed in order to obtain a mechanistic understanding of factors controlling larval survival. Additional winter studies at different latitudes are needed to fully evaluate the direct and indirect affects of sea-ice on overwintering larval krill.

Acknowledgements

I thank the officers and crew of the R.V. *L.M. Gould* and the R.V.I.B. *N.B. Palmer* and Raytheon Polar Services personnel, particularly Alice Doyle, for project planning and support at sea. I am grateful to Mari Butler, Scott Polk, Kerri Scolardi, Hyoung-Chul Shin, Tracey Sutton, Emily Yam, and Jason Zimmerman for their able assistance at sea and to Jason Zimmerman and Kerri Scolardi for net sample and laboratory analyses. John Klinck and Eileen Hofmann kindly provided CTD data, Chris Fritsen provided water column chlorophyll profiles for autumn 2001, Gabriel Vargo identified the phytoplankton, and S. Bosch the

pilidium larvae. I also thank Meng Zhou, Yiwu Zhu, Ryan Dorland, Dan Mertes, and Joe Smith for collecting the 1m MOCNESS samples. Diver observations and collections were made by Jose Torres, Christian McDonald, Kerri Scolardi, Joel Bellucci, Melanie Parker, and Stian Alesandrini. Finally, I thank two anonymous reviewers for their comments. Funding for this research was supported by NSF grants OPP-9910610 and OPP-0196489. This publication represents GLOBEC contribution #457.

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