Limnol. Oceanogr., 45(1), 2000, 31–43

Growth limitation in young *Euphausia superba* under field conditions

Robin M. Ross and Langdon B. Quetin
Marine Science Institute, University of California at Santa Barbara, Santa Barbara, California 93106

Karen S. Baker and Maria Vernet
Scripps Institution of Oceanography, University of California at San Diego, La Jolla, California 92093-0218

Raymond C. Smith
Institute of Computational Earth Systems Science, University of California at Santa Barbara, Santa Barbara, California 93106

Abstract

Growth rates of late furcilia and juvenile Antarctic krill (*Euphausia superba* Dana) in the spring and summer were related to food quantity and quality. The 4 yr covered by this study (1991–1992, 1993–1994, 1994–1995, and 1995–1996) were part of the seasonal time series of the Palmer Long-Term Ecological Research program. Chlorophyll *a* concentrations represented food quantity, and accessory photosynthetic pigments represented phytoplankton community composition or food quality. Instantaneous growth rates reflected the in situ nutritional history of the previous intermolt period. The response of krill to the food environment was seen on temporal scales of days to weeks. Percent growth per intermolt period (percentage growth IMP^{-1}) varied significantly both within and between years, ranging from ~2 to 10% IMP^{-1}. Percent growth IMP^{-1} increased with increasing chlorophyll *a* (Chl *a*), reaching a maximum of 9.3% IMP^{-1} above a critical concentration of about 3.5 mg m^{-3}. Maximum growth was reached in only 2 yr, 1991–1992 and 1995–1996. In a multiple regression analysis, total Chl *a* and prymnesiophyte–Chl *a* explained over 71% of the temporal variance in growth. In general, highest growth was found toward the end of diatom blooms and lowest during periods of low phytoplankton biomass or blooms dominated by cryptophytes and prymnesiophytes. The results of this study support the hypothesis that maximum growth rates are only possible during diatom blooms and that production in Antarctic krill is limited by both food quantity and quality.

The effects of food quantity and quality on production (growth and egg production) rates in marine and freshwater zooplankton has seldom been studied in situ. In a few previous investigations, egg production in copepods (Checkley 1980; Jónasdóttir 1994; Jónasdóttir et al. 1995) and growth in juvenile oysters (Enright et al. 1986) have been related to food abundance and several aspects of food quality. The expected relationship between production and food concentration is a functional response curve, with production increasing up to a critical food concentration and then remaining at a maximum rate with further increases. The shape of this curve, including the critical concentration and maximum production rate, depends on food quality (Libourel Houde and Roman 1987; Klein Breteler et al. 1995). Food quality has been characterized variously as particle size, particle morphology, taxonomic composition, nutritional value (digestibility and chemical composition), palatability, or toxicity (Kleppel and Burkart 1995).

Acknowledgments

We wish to thank the many staff, graduate students, and undergraduate students that contributed to this work. In particular we would like to acknowledge the efforts of T. Newberger, C. Wyatt-Evens, J. L. Jones, C. T. Shaw, and C. R. Johnson for their assistance with the growth experiments and chlorophyll measurements, and W. Kozlowski and K. Sines for the chromatographic analysis. This material is based upon work supported by the National Science Foundation under Award No. OPP-9011927, The Regents of the University of California, and the University of California at Santa Barbara. This is Palmer LTER contribution No. 173.

In the Southern Ocean, Antarctic krill occupy a key role in the ecosystem, both as grazers and as a prey item for many vertebrates. They have been characterized as omnivorous particle feeders, relying on phytoplankton as their primary food source during the spring and summer (Quetin et al. 1994). Microzooplankton can be a significant proportion of the diet of Antarctic krill in oceanic waters in the summer, with phytoplankton and detrital carbon taking minor roles (Atkinson and Snÿder 1997). But in coastal waters phytoplankton biomass and productivity are high (Smith et al. 1996), and phytoplankton are most likely the primary food source for grazing krill.

Laboratory experiments with Antarctic krill have shown that aspects of the phytoplankton community, e.g., concentration and average size of the phytoplankton cells and taxonomic composition, affect ingestion rate and feeding efficiency of these grazers (Quetin and Ross 1985; Pond et al. 1995; Haberman 1998). The same responses are likely to be true in the field. The chemosensory abilities of Antarctic krill enable them to discriminate among particles (Hamner et al. 1983). Also, when euphausiids encounter patches of phytoplankton their swimming behavior changes and they aggregate in that patch (Price 1989; Strand and Hamner 1990), facilitating their ability to graze on preferred food.

In this study we describe seasonal and interannual variations in the growth rates of late furcilia and juvenile Antarctic krill in the spring and early summer in the waters near Palmer Station, Antarctica. As the sea ice retreats, larval and juvenile krill shift from their under-ice habitat to the open

Table 1. Year, range of dates, number of experiments, and technique used to collect Antarctic krill.

Years	Dates of experiments	Experiment	Collection technique
1991–1992	22 Oct, 29 Nov, 4 Dec	3	Diver
	17 Nov, 18 Nov	2	RV *Polar Duke*
	24 Dec–18 Jan	5	Mark V zodiac
1993–1994	19 Nov–30 Dec	5	Mark V zodiac
1994–1995	18 Nov	1	Diver
	5 Dec–5 Jan	5	Mark V zodiac
1995–1996	18 Nov	1	Diver
	23 Nov–2 Jan	4*	Mark V zodiac
	18 Jan	1	RV *Polar Duke*

*Two experiments were conducted on 2 January 1996 with krill from the same catch.

water column (Quetin et al. 1996), thus shifting from a dependence on sea ice biota to microplankton for nutrition. Variation in the nutritional environment in spring and early summer may impact the annual growth (secondary production) cycle. However, we do not know the timescales over which growth varies in response to variability in food quantity and quality in situ or whether these timescales are similar to those over which the phytoplankton community varies. In this study, we examine the effects of food quantity and quality, represented by phytoplankton biomass and community composition, on estimated in situ growth rates of krill. We pose three questions. Are rates of secondary production during the spring and summer relatively constant within and between years? Does secondary production mirror within year variations in standing stock and composition of the phytoplankton community? Is in situ growth in young Antarctic krill limited by food quantity and/or quality?

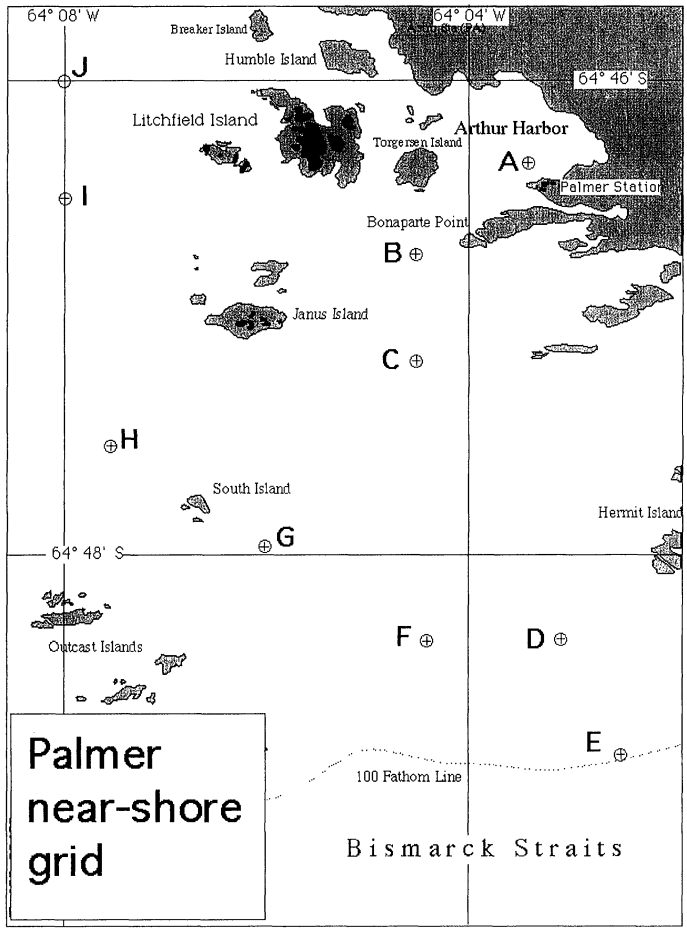

Fig. 1. Standard sampling stations for the Palmer LTER (Long-Term Ecological Research) within 3.7 km of Palmer Station, Anvers Island, Antarctica.

Materials and methods

The seasonal time series of the Palmer Long-Term Ecological Research (LTER) program near Palmer Station, Anvers Island, Antarctica, includes collection of Antarctic krill for growth-rate experiments and sampling of the water column for standing stock and community composition of the phytoplankton. The growth rates reported in this study are for late age class zero (AC0) and early age class one (AC1) krill in the spring and early summer of 4 yr: 1991–1992, 1993–1994, 1994–1995, and 1995–1996 (Table 1). In this study the term early AC1s includes AC0 and AC1 krill that hatched the previous summer. No early AC1s were found in 1992–1993. Antarctic krill used in experiments in the spring and early summer were usually collected within 3.7 km of Palmer Station (Fig. 1). Two additional experiments were conducted with larval and juvenile krill collected about 100 km directly south of Palmer Station in mid-November 1991.

Growth experiments were scheduled once a week, with some variation due to weather and krill availability. Standing stock and community composition of phytoplankton in the water column were measured at Sta. B and Sta. E (Fig. 1) approximately twice a week throughout the growth season. The same parameters were measured at the shelf stations in mid-November 1991 (Prézelin et al. 1992; Smith et al. 1992). During the weekly sampling regime, ice conditions were characterized as brash or pack ice, with percent cover and coloration from ice algae noted.

Growth-rate determinations for Antarctic krill

Collection of krill—Three methods were used to collect krill: divers under the ice with aquarium nets, a 1-m ring net (500-μm mesh) deployed from a zodiac with a small A-frame and winch, and a 2-m square fixed frame net (700-μm stretch mesh and 500-μm cod end) deployed from the RV *Polar Duke* (Table 1). The contents of the aquarium net or cod end were gently placed either in large buckets or insulated coolers filled with seawater immediately after collection.

Experimental protocol—Growth-rate experiments usually started within a few hours of collection and lasted four days, as described in Quetin and Ross (1991) and Nicol et al. (1992). The instantaneous growth rate technique first reported by Quetin and Ross (1991) and Ross and Quetin (1991) was based on the premise that maintenance conditions will not affect the length increment at ecdysis for sev-

eral days after capture. Subsequently, Nicol et al. (1992) found that maintenance conditions begin to affect growth as soon as 7 d after capture. Thus, the growth increments measured in this study reflect field growth rates with no laboratory artifacts.

Experiments were either started immediately upon return to station or krill were held for up to 12 h in large flow-through tanks at ambient temperatures or in buckets in an environmental room at ~0.5°C. To start the experiment, 100 krill were randomly selected from the catch. Each individual was placed in a separate 500-ml (krill <16 mm in total length) or 2000-ml glass jar filled with filtered seawater at ambient temperature. Experimental jars were held in a flow-through seawater table at ambient temperature and in the dark. At 12-h intervals all jars were inspected for molts and condition of the individual krill. Water temperature was measured. If an individual molted, the krill and its molt were preserved together in 10% formalin. We noted unhealthy krill (not swimming) and did not include either dead or unhealthy krill in the total number in the experiment. At the end of the experiment, all nonmolters were preserved together in 10% formalin.

Total length (TL) was measured from the tip of the rostrum to the end of the uropods (standard length 1, Mauchline 1981). Total length of krill smaller than ~14 mm was measured under a dissecting microscope equipped with a calibrated graticule. Telson lengths of the preserved molt and the krill were also measured under a dissecting microscope with a calibrated graticule. Total length was usually measured prior to preservation. However, for all experiments in the 1991–1992 season and the first experiment of the 1994–1995 season, total lengths were measured after preservation. These total lengths were corrected for shrinkage with an equation derived from a comparison of the same individuals measured fresh and after preservation in 10% formalin:

$$\text{preserved TL} = 0.925 \cdot \text{fresh TL} + 0.771 \quad (n = 335,\ r^2 = 0.976) \qquad (1)$$

Prior to analysis, the length frequency distribution of krill in each experiment was plotted, and krill that were too large to be early AC1s were removed from further calculations. The upper size thresholds were derived from our knowledge of normal length increments during the year (Quetin et al. 1996): 26 mm in early December, 28 mm in early January, and 30 mm in mid-January. The number of individuals removed from the total of 100 was generally less than four.

The number of healthy early AC1s in an experiment was usually between 80 and 100. The two exceptions were experiments with fewer than 50 healthy early AC1s (5 December 1994 and 30 December 1993). On 2 January 1995, experiments were conducted with 100 krill each from the two size modes of AC1 present (9 to 19 mm and >19 mm). A subset of individuals was randomly selected from the two experiments to represent growth of all sizes of early AC1s present. The number of krill from each experiment was proportional to the size of the mode in the random length frequency distribution from the total catch.

Growth-rate measurements and calculations—Molting frequency was calculated as the percent of healthy animals molting per day. The inverse of the molting frequency (percentage d^{-1}) is the intermolt period (IMP) in days. Linear growth rates for each experiment were estimated both as average percent growth per intermolt period (percentage growth IMP^{-1}) and as average growth rate in mm d^{-1} (GrR).

Percent growth IMP^{-1} normalized growth to krill size. The percentage growth IMP^{-1} is the difference between postmolt and premolt lengths divided by the premolt length. Because total length and telson length are highly correlated, the telson lengths of the krill and molt represent, respectively, the length of the postmolt and premolt krill. Telson lengths of the molt and the krill for an individual molter were measured by the same person. The number of krill for which percentage growth IMP^{-1} could be calculated ranged between 8 and 43 in 25 of the 26 experiments. Mean percentage growth IMP^{-1} and its standard error were calculated for each experiment.

Average growth rate (GrR) of krill in an experiment was estimated from the average percentage growth IMP^{-1}, the average TL of the krill in the experiment, and the average IMP for the 4 yr (IMP_{av}):

$$GrR_i \text{ (mm d}^{-1}) = TL_i \cdot \text{percentage growth } IMP_i^{-1} \cdot IMP_{av}. \qquad (2)$$

The mean GrR and its standard deviation were calculated for each season.

In addition, we summed linear growth increments in mm between sequential growth experiments to integrate the variability in growth found throughout each spring and summer. The linear growth increment between sequential growth experiments was calculated with IMP_{av}. The percentage growth IMP^{-1} and average TL measured at the beginning of the time interval was used for the first half of the time period, and the percentage growth IMP^{-1} and average TL measured at the end of the time interval was used for the second half of the time period. The linear growth increments between experiments were summed and divided by the number of days between the first and last experiments to calculate a seasonal growth rate in mm d^{-1}. This seasonal growth rate was used to calculate the linear growth increment for a standard 8-week period in spring and early summer. In 1991–1992 the first experiment in October was not included in these calculations because the time interval between the experiment in October and the next experiment in mid-November was longer than one intermolt period.

Environmental variables

Water samples were collected with a Niskin bottle at depths corresponding to 100 (surface), 55, 27, 11, 5, and 2% of photosynthetically available radiation (PAR). Depths were established by measuring PAR with a LICOR 193-SA quantum sensor. Chlorophyll *a* (Chl *a*) concentrations were taken to represent the food quantity available to krill in the spring and summer after sea ice retreated from the area. Accessory algal pigments provided a first-order estimation of taxonomic composition of the same phytoplankton community.

Chlorophyll a—Total Chl *a* was determined from filtered samples (Millipore HA filters) with standard fluorometric techniques on a digital Turner fluorometer (Smith et al. 1981). Chl *a* was calculated by subtracting phaeopigment concentration determined by sample acidification.

Vertical profiles of Chl *a*, for both historical (Smith et al. 1996) and Palmer LTER (Dierssen et al. in press) data, generally show a maximum at or near the surface with a gradual decrease with depth. Also, the vertical structure is fairly uniform within the top few optical depths of the water column. As a consequence, there are tight correlations between surface Chl *a* (C_0), Chl *a* integrated to the euphotic depth (C_{eu}), and average Chl *a* concentration within the top 30 m (C_{30}). The latter is estimated by integrating measured Chl *a* concentrations from the surface to a depth of 30 m and dividing by the depth over which the Chl *a* was integrated.

Phytoplankton community composition—Chromatographic analyses of phytoplankton pigments were performed as described in Kozlowski et al. (1995). After sampling, water was stored in a cooler and transported back to station. Duplicate samples were filtered onto Whatman GF/F filters. The filters were immediately frozen with liquid nitrogen and stored at −70°C until analysis. Pigments were extracted with 90% acetone for 24 h and analyzed after clearing the extract by filtration. Analyses were performed by high-performance liquid chromatography on a reverse-phase C-18 column (Waters Resolve C-18 30 cm × 3.9 mm, 5-μm particles). The method of elution followed Wright et al. (1991) with minor modifications. Pigments were monitored by absorption at 440 nm and quantified by calibration of the column with external standards.

Three chemotaxonomic pigments represented the majority of the phytoplankton community in this region: fucoxanthin (fucox) for diatoms, 19′hexanoyl-oxy-fucoxanthin (19′hex) for prymnesiophytes, and alloxanthin (allox) for cryptophytes (Jeffrey et al. 1997). All other pigments were present in minor concentrations and were combined in the 'other' category. A multiple regression analysis was done with carotenoid concentration (conc) data from 1994–1995 and 1995–1996 to derive Chl *a* to taxon-specific carotenoid ratios for the model.

$$\begin{aligned}\text{Total Chl } a \text{ concentration} &= [\text{Chl } a/\text{fucox}]\cdot(\text{fucox conc}) \\ &+ [\text{Chl } a/19'\text{hex}]\cdot(19'\text{hex conc}) \\ &+ [\text{Chl } a/\text{allox}]\cdot(\text{allox conc}) \\ &+ [\text{Chl } a/\text{other}]\cdot(\text{other conc}).\end{aligned}$$

We used 386 samples collected within the euphotic zone during the spring and summer months (October to April). No apparent changes with depth were observed in pigment ratios ($p = 0.05$), so a uniform regression with all data combined was used in further calculations (Table 2).

To obtain taxon-specific Chl *a* for a date (i.e., a krill experiment), we calculated the percentage of Chl *a* attributed to each taxon based on the Chl *a* to carotenoid ratios obtained from the multiple regression. The calculation was done for each sampling depth, and then the taxon-specific Chl *a* was integrated over the euphotic zone (surface to 2% incident radiation). For the years 1991–1992 and 1992–1993, the depth-integrated pigment calculations were based on accessory pigment concentrations of Moline and Prézelin (1996) and Prézelin et al. (1992), the equations in Table 2, and the Chl *a* as measured fluorometrically at the same stations on the same day as the accessory pigments (*see Environmental variables above*).

Table 2. Multiple regression analysis of relationship between total Chl *a* and taxon-specific pigments for 1994–1995 and 1995–1996, with Chl *a*:taxon-specific carotenoid ratios, their standard errors, and the statistical significance of the equation for each year. The multiple regressions are based on all samples taken in one season within the same region that krill were collected for experiments (Fig. 1).

	Chl *a*:taxon-specific ratio	Statistics
1994–1995		
Chl *a*/fucox	1.76±0.03	r^2=0.98
Chl *a*/allox	2.94±0.13	F=2194
Chl *a*/19′hex	1.41±0.65	n=152
Chl *a*/others	2.97±0.45	df=147
1995–1996		
Chl *a*/fucox	1.57±0.03	r^2=0.95
Chl *a*/allox	2.24±0.32	F=1055
Chl *a*/19′hex	2.30±0.88	n=234
Chl *a*/others	0.19±0.45	df=229

Krill—food quantity and quality interaction

Possible correlations between growth in early AC1 krill in the field and the food environment were examined with estimates of Chl *a* on several time and space scales. Chl *a* concentrations from different locations (Sta. B and Sta. E, average of B and E), and from several depths (C_0, maximum, and C_{30}) were used singly and in combination to represent the quantity of food available. The Chl *a* maximum is typically at or close to the surface (Smith et al. 1996). Krill growth (average percentage growth IMP^{-1} for an experiment) was plotted against these concentrations, either measured on the date closest to the date of krill collection (usually ±2 d) or averaged over the 2 weeks prior to collection. The Chl *a* parameter that showed the best correlation with krill growth (C_{30}) was used in further quantitative analysis. In the evaluation of the relationship between krill growth and phytoplankton biomass in the field, we omitted growth data from experiments on krill that were either collected from the under-ice surface (diver collected) or that were closely associated with colored pack ice (19 November 1993). For those experiments, total food was a combination of phytoplankton in the water column and sea ice biota, and the contribution of sea ice biota was unknown.

Results

The first experiment of the season was usually conducted with krill from the under-ice habitat. Later in the season krill

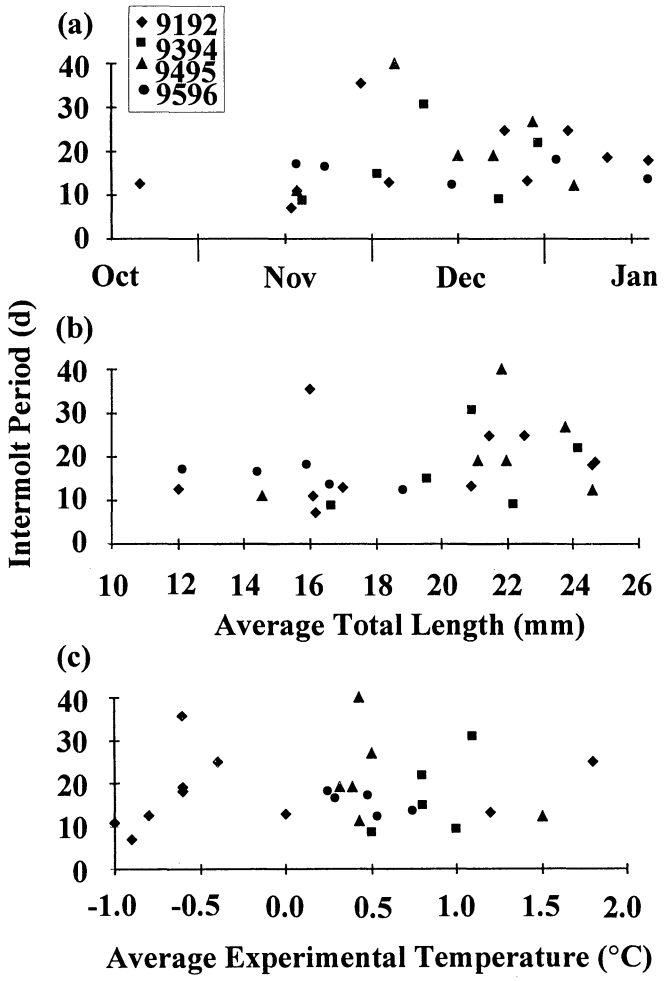

Fig. 2. Intermolt periods for early AC1 krill as a function of (a) time in the spring and early summer, (b) average total length of the krill in the experiment, (c) average experimental temperature.

were from the water column with either intermittent and low concentrations (1–5%) of brash ice or no ice. In 1993–1994, krill for the first experiment were from the water column, but collected near pack ice with ice algae, suggesting that these krill had recently been associated with the under-ice habitat. Experimental temperatures were between −1.0 and 1.8°C, and generally 0.5°C warmer than ambient surface seawater temperature. In the Palmer area, seawater temperatures during the spring and early summer range from −1.8 to 1.0°C, increasing as the season progresses (Moline and Prézelin 1996).

Seasonal and interannual variability in growth

Intermolt period—Intermolt period ranged from 7 to 40 d over the 4 yr (Fig. 2), with no discernible pattern with season (Fig. 2a), average size of the krill in an experiment (Fig. 2b), or average experimental temperature (Fig. 2c). IMP was also not correlated with percentage growth IMP^{-1} (Spearman's rank correlation coefficient, $\rho = 0.203$, $p = 0.3208$). Average IMP for any one year was between 15 and 21 d, with high coefficients of variation (Table 3). There were no significant differences among years in IMP (Kruskal-Wallis one-way analysis of variance: $H = 1.053$, $p = 0.7885$). The average IMP for early AC1s for all years was 18.27 d (95% CI = ±3.33 d, $n = 26$).

Table 3. Average intermolt periods for the 4 yr, with standard error and coefficient of variation.

Years	Average intermolt period (d)	Standard error	Coefficient of variation (%)
1991–1992	17.89	2.71	47
1993–1994	17.02	4.18	55
1994–1995	21.33	4.40	50
1995–1996	15.44	1.11	16

Percent growth IMP^{-1}—Percent growth IMP^{-1} varied significantly during the spring and early summer in all years (Kruskal-Wallis one-way analysis of variance: 1991–1992, $H = 101.373$, $p = 0.0001$; 1993–1994, $H = 17.977$, $p = 0.0012$; 1994–1995, $H = 12.838$, $p = 0.0121$; 1995–1996, $H = 23.351$, $p = 0.0001$) (Fig. 3). In 1991–1992, mean percentage growth IMP^{-1} was high both in early spring in krill from ice-covered waters, and again in early summer (Fig. 3a). Lowest growth was found in krill from open water in mid-November (Fig. 3a). In both 1993–1994 and 1994–1995 (Figs. 3b, 3c), mean percentage growth IMP^{-1} had a narrower range and never reached the highs of either 1991–1992 or 1995–1996. In 1995–1996, highest percentage growth IMP^{-1} were found earlier in the season than in 1991–1992 (Fig. 3d). The range in mean percentage growth IMP^{-1} in krill from under pack ice (5–10%, $n = 5$) (Fig. 3) was similar to the range in krill from open water.

Percent growth IMP^{-1} was chosen as the standard index of growth in this study for two reasons. First, intermolt period was not significantly different either within or among seasons. Second, for the 4 yr combined, average percentage growth IMP^{-1} was not correlated with the average total length of krill in the experiment (Spearman's rank correlation coefficient, $\rho = 0.002$, $p = 0.9925$, $n = 25$). Thus percentage growth IMP^{-1} is normalized to body length and can be used to compare growth of early AC1s within and among seasons.

Average experimental and seasonal growth rates—Experimental growth rates varied by nearly an order of magnitude and increased with increasing average total length (Fig. 4). The cumulative impact of the large within-season variation in growth rates is illustrated by the interannual variability in seasonal growth rates. Seasonal growth rates varied by about 15%, ranging from a high of 0.084 mm d^{-1} in 1991–1992 to a low of 0.073 mm d^{-1} in 1993–1994, and were similar to the average experimental growth rate for each season (Table 4). The estimated increase in total length over the 8-week period from mid-November to mid-January was about 4.4 mm but differed by more than 0.6 mm among years (Table 4).

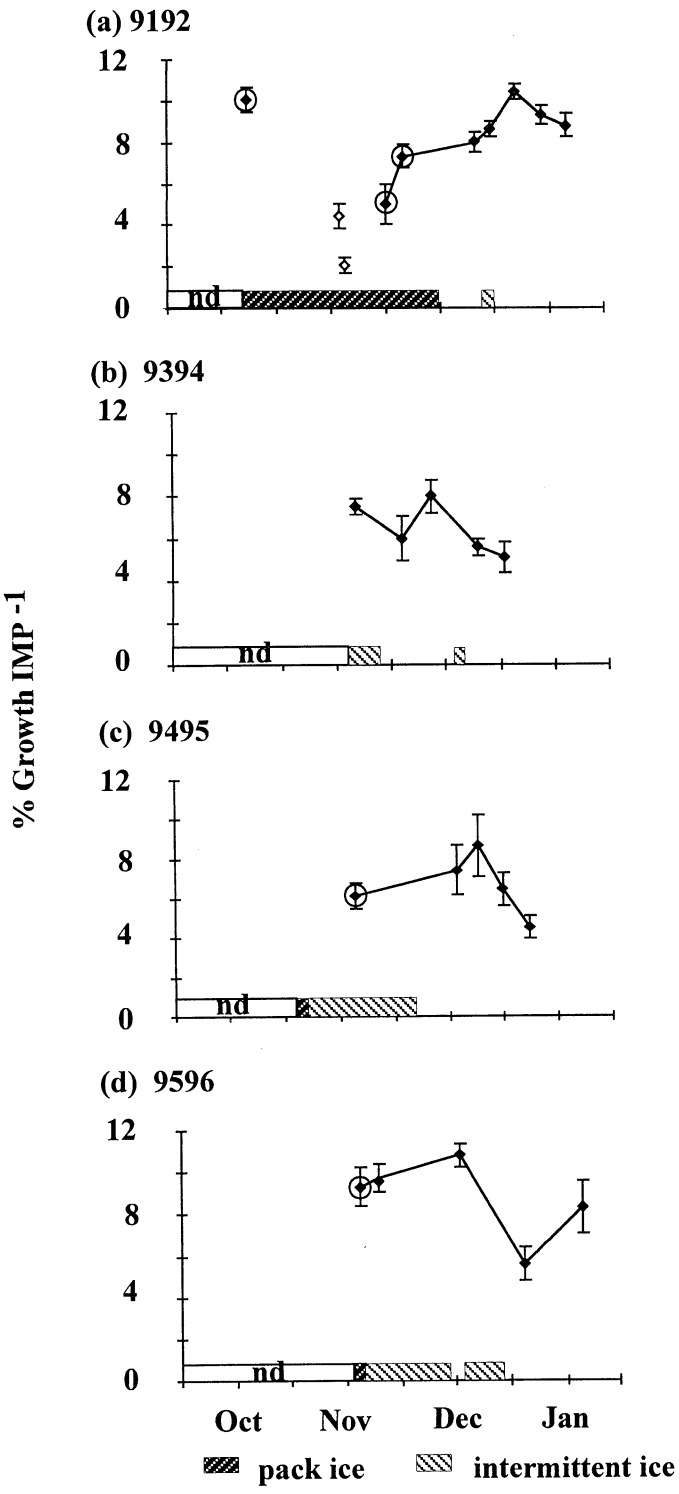

Fig. 3. Mean percentage growth IMP^{-1} versus time in (a) 1991–1992, (b) 1993–1994, (c) 1994–1995, (d) 1995–1996. Diamonds are coded for collection method and sampling area: circled = diver collected, closed = collected within 3.7 km of Palmer Station, open = collected about 100 km from Palmer Station. Error bars are standard error. nd = no data.

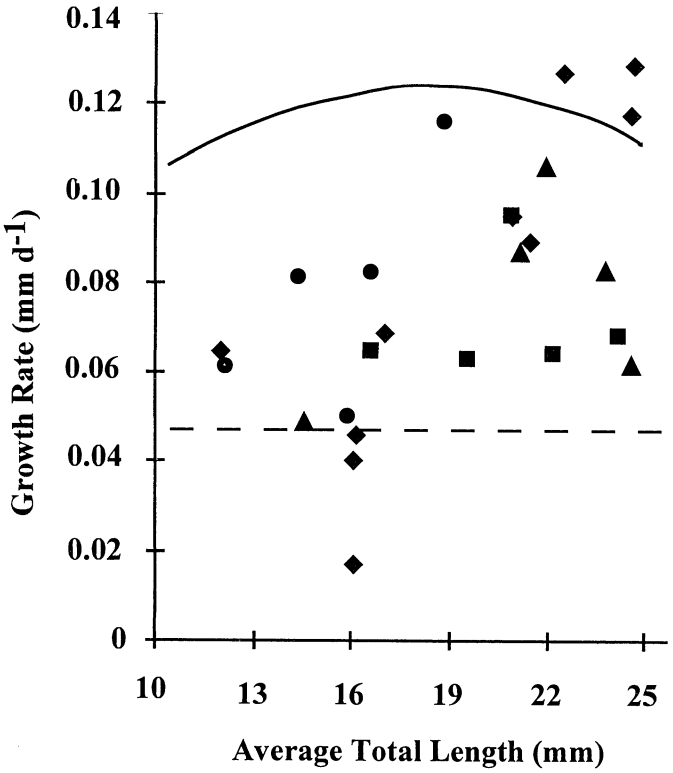

Fig. 4. Growth rates (mm d^{-1}) plotted as a function of average total length of the experimental krill. Symbols for years as in Fig. 2. The solid line is from a growth-rate model that assumes no winter growth (Ikeda 1985); the dashed line is the maximum growth rate observed in the laboratory by Ikeda and Thomas (1987).

Influence of food quantity and quality

Phytoplankton biomass accumulation in the Palmer region begins in early to mid-December, with a series of 2–3 peaks during the season. During the spring and early summer, higher peak biomass concentrations were found in the 1991–1992, 1994–1995, and 1995–1996 seasons (8, 16, and 17 mg m^{-3}) than in 1993–1994 (3 mg m^{-3}) (Smith et al. 1998). Timing of blooms also varied, with blooms in late December and early January in 1991–1992, early through late December in 1993–1994, and a small bloom in mid-December followed by a large bloom in mid to late January in both 1994–1995 and 1995–1996. These patterns in phytoplankton

Table 4. Growth rates (mm d^{-1}) of early AC1 *Euphausia superba*: year, seasonal growth rate, growth increment during 8 wk from mid-November to mid-January; average experimental growth rate, standard deviation, and number of experiments.

	Seasonal		Experimental		
Years	Rate (mm d^{-1})	Growth (mm)	Average (mm d^{-1})	Standard deviation	*n*
1991–1992	0.084	4.70	0.082	0.041	9
1993–1994	0.073	4.09	0.072	0.011	5
1994–1995	0.078	4.37	0.077	0.022	5
1995–1996	0.079	4.42	0.075	0.023	5

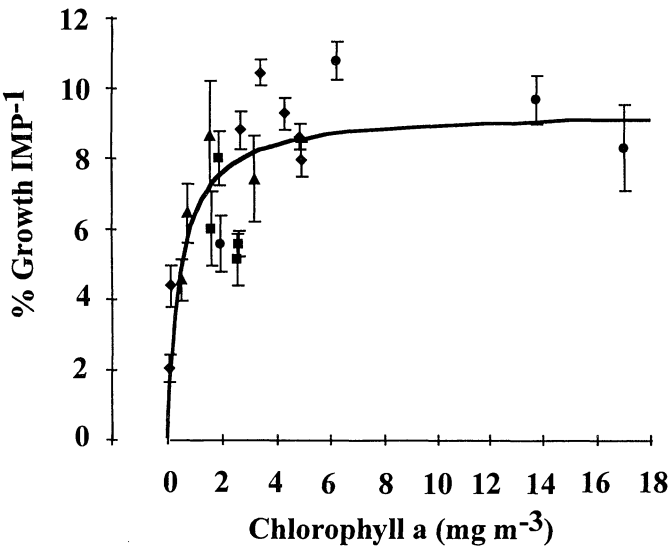

Fig. 5. Percentage growth IMP^{-1} as a function of average Chl *a* concentration in the top 30 m of the water column at Sta. B and Sta. E. Symbols for years as in Fig. 2. Error bars are standard error. The curve is a Michaelis-Menten uptake function: percentage growth $IMP^{-1} = 9.326 \times [\text{Chl } a/(0.498 + \text{Chl } a)]$.

bloom dynamics were similar to the seasonal patterns found in percentage growth IMP^{-1} (Fig. 3). Highest growth was associated with periods of peak phytoplankton biomass.

Plots of growth against the various indices of food availability were all curvilinear functional response curves (Fig. 5). The average Chl *a* concentration in the upper 30 m, C_{30}, was chosen as the best index of food quantity. The relationship between growth rate and food concentration can be described with the expression for Michaelis-Menten kinetics, $v = (V_m \times S)/(K_s + S)$, where v is percentage growth IMP^{-1}, S is Chl *a*, and V_m and K_s are constants representing, respectively, maximum growth and the Chl *a* concentration at which growth is half the maximum. K_s reflects the ability to grow at low food concentrations. The constants and their lower and upper 95% confidence intervals (CI) were derived with a nonlinear regression program (Wilkinson 1989): maximum growth, 9.326% IMP^{-1}, 7.709–10.943% IMP^{-1}; and K_s, 0.498, 0.006–0.989. The relationship between Chl *a* and percentage growth IMP^{-1} is

$$\%\ \text{growth IMP}^{-1} = 9.326 \cdot [\text{Chl } a/(0.498 + \text{Chl } a)] \quad (n = 19,\ r^2 = 0.621). \qquad (3)$$

Percent growth IMP^{-1} increased with increasing Chl *a*, reaching a maximum of 9.3% above an apparent critical concentration of about 3.5 mg m^{-3} (Fig. 5). Maximum growth was reached in only 2 of the 4 yr, 1991–1992 and 1995–1996.

One measure of food quality, phytoplankton community composition, also varied within and among seasons during the spring and early summer. In 1991–1992, diatoms dominated the phytoplankton community as the bloom developed throughout December, peaking at 90% of the phytoplankton biomass during the height of the bloom; cryptophytes replaced diatoms by mid-January (Moline and Prézelin 1996). In 1993–1994, cryptophytes dominated the phytoplankton community during the December bloom and were slowly replaced by diatoms in early January (Moline and Prézelin 1996). Prymnesiophytes comprised up to 25% of the phytoplankton community during the spring and early summer of 1993–1994, considerably higher than in the previous year. The pattern in 1994–1995 was similar to that in 1993–1994; cryptophytes dominated a low-level bloom in mid-December, with diatoms and prymnesiophytes progressively replacing the cryptophytes in late December and early January (Fig. 6a). In 1995–1996, diatoms dominated except during a brief time from mid-December to early January when a mixture of cryptophytes and prymnesiophytes comprised a significant proportion of the phytoplankton community (Fig. 6b).

In general, highest percentage growth was found toward the end of a phytoplankton bloom dominated by diatoms, and lowest percentage growth was found during periods of low phytoplankton biomass or blooms dominated by cryptophytes and prymnesiophytes (Figs. 3 and 6). In an analysis of interactions between growth and the proportions of the individual taxonomic groups (Fig. 7), the correlation between growth and prymnesiophytes was negative, whereas that with diatoms was positive. Cryptophytes did not appear to be correlated with percentage growth IMP^{-1}. A Spearman's rank correlation coefficient (ρ) was calculated to test for correlations between percentage growth IMP^{-1} and the relative contribution of the three taxa: percentage prymnesiophytes, $\rho = -0.701$, $p < 0.05$ (Fig. 7a); percentage diatoms, $\rho = 0.313$, $p < 0.10$ (Fig. 7c); percentage cryptophytes, $\rho = -0.070$, not significant (Fig. 7e).

Patterns of growth with the Chl *a* equivalents of each taxonomic group were somewhat different (Figs. 7d, 7e, 7f). Growth increased with increasing prymnesiophyte–Chl *a* concentrations to a maximum, then decreased as concentrations increased from 7 to 20 mg m^{-2} (Fig. 7b). For diatom–Chl *a* the response was curvilinear (Fig. 7d), similar to that seen with total Chl *a* (Fig. 5). A Michaelis-Menten equation describing the relationship between growth and diatom–Chl *a* was derived as described for total Chl *a*. The equation explained 44% of the variance in growth. Maximum growth was 8.756% growth IMP^{-1} (95% CI, 7.286–10.226); K_s was 2.315 (95% CI, −0.110–4.741).

Multiple linear regression analysis—Some variables considered may act simultaneously but independently to affect growth. Therefore we used a multiple linear regression analysis (Wilkinson 1989) to elucidate the relative importance of food quantity and food quality to growth in early AC1 krill. The variables tested in the multiple linear regression model were chlgrow [= Chl *a*/(0.498 + Chl *a*)]; percent diatoms, cryptophytes, and prymnesiophytes; taxon-specific Chl *a* for the prymnesiophytes and cryptophytes; and diagrow [= diatom–Chl *a*/(2.315 + diatom–Chl *a*)]. The expressions Chl *a*/(0.498 + Chl *a*) and diatom–Chl *a*/(2.315 + diatom–Chl *a*) transform the curvilinear relationships between percentage growth and the pigment into linear relationships. The criteria used to remove variables from the model were low tolerance values (<0.2) that suggested col-

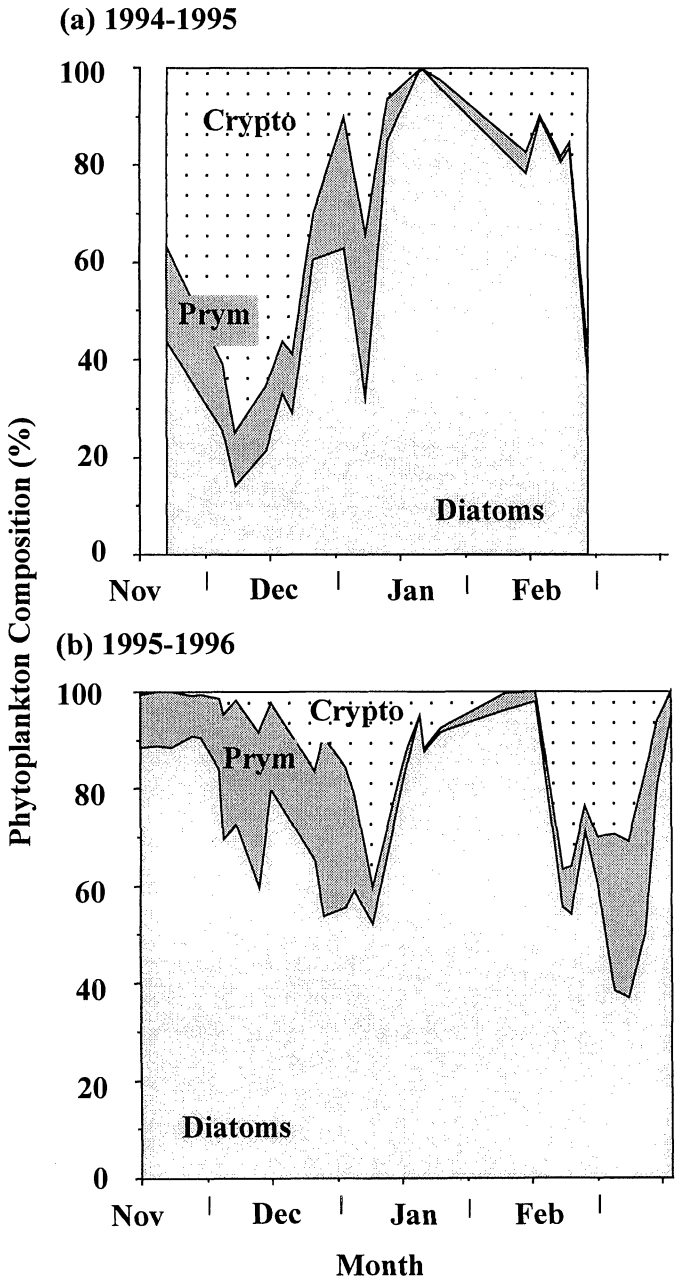

Fig. 6. Percentage phytoplankton community composition, average at Sta. B and Sta. E during (a) 1994–1995 and (b) 1995–1996. The contribution of the taxon-specific pigment is expressed as the proportion of the taxon-specific Chl *a* of the sum of the Chl *a* biomass in the three major groups: diatoms, prymnesiophytes (prym), and cryptophytes (crypto).

linearity among variables and T values <1.5, indicating variables that did not contribute significantly to the variance. Pairs of variables showing collinearity were tested individually to determine which variable was the most useful predictor, i.e., chlgrow and diagrow (Table 5). Single variables with low T values were removed in sequence.

In the multiple regression analysis, chlgrow and prymnesiophyte–Chl *a* (prymnconc) explained over 71% of the variance in growth in Antarctic krill (Table 5) (r^2 = 0.712):

$$\%\ \text{growth IMP}^{-1} = 1.328 + 9.209 \cdot \text{chlgrow} - 0.151 \cdot \text{prymnconc} \quad (n = 19). \tag{4}$$

The standard coefficient for chlgrow was twice that of prymnconc, indicating that total Chl *a* was a more important factor than the prymnesiophyte–Chl *a* (Table 5). Despite the significant effect when variables were considered independently, neither diagrow nor percentage diatoms in the phytoplankton community accounted for a significant portion of the variance when all variables representing food quantity and quality were considered. We suggest the reason lies in the significant correlation between chlgrow and diagrow (r^2 = 0.607 this study; Vernet and Kozlowski in prep.). Chlgrow was the better predictor of the two variables (Table 5), representing variability in both total Chl *a* and diatom–Chl *a*.

Discussion

Measurement of growth rates of pelagic crustaceans under field conditions faces practical obstacles. One common approach is cohort analysis, i.e., calculating growth rates from changes in length of a population or in the lengths of age groups over time. With cohort analysis the assumptions are that the same population is being sampled and that mortality is not size dependent. Verifying these assumptions in the pelagic ocean is difficult. For Antarctic krill, uncertainties in growth-rate estimates from cohort analysis are a result of sampling issues, size-dependent mortality (Pakhamov 1995), and overlap in the size range of different age classes due to shrinkage (Ikeda and Dixon 1982). Also the response of growth rate to environmental variables may be on smaller timescales than possible with cohort analysis, e.g., McClatchie (1988) used monthly length frequency samples in an analysis of seasonal growth rates of *Euphausia superba.*

Alternatively, we can conduct experiments with recently captured animals over short time periods; the observed rates will then reflect growth under field conditions. The molt cycle of euphausiids is the basis of the success of the instantaneous growth rate technique with *E. superba* (Quetin and Ross 1991; Nicol et al. 1992). Euphausiids molt throughout their lifespan and can increase or decrease in length or stay the same size at each molt (Ikeda and Dixon 1982; Buchholz 1991; Quetin and Ross 1991; Ross and Quetin 1991; Nicol et al. 1992). Growth rates (mm d^{-1}) are the combination of the growth increment (mm) at molting and the molting frequency (d^{-1}). The length increment at ecdysis is set several days before the exoskeleton is actually shed (Buchholz et al. 1989) and, thus, reflects the nutritional environment and the physiological status of the individual during the previous intermolt period. The molting frequency measured for a group of krill is a function of both the environment over the previous intermolt period and whether the group is molting randomly or synchronously. When measured over a brief time period, the molting frequency of a group of euphausiids will only yield accurate estimates of the intermolt period if molting is random.

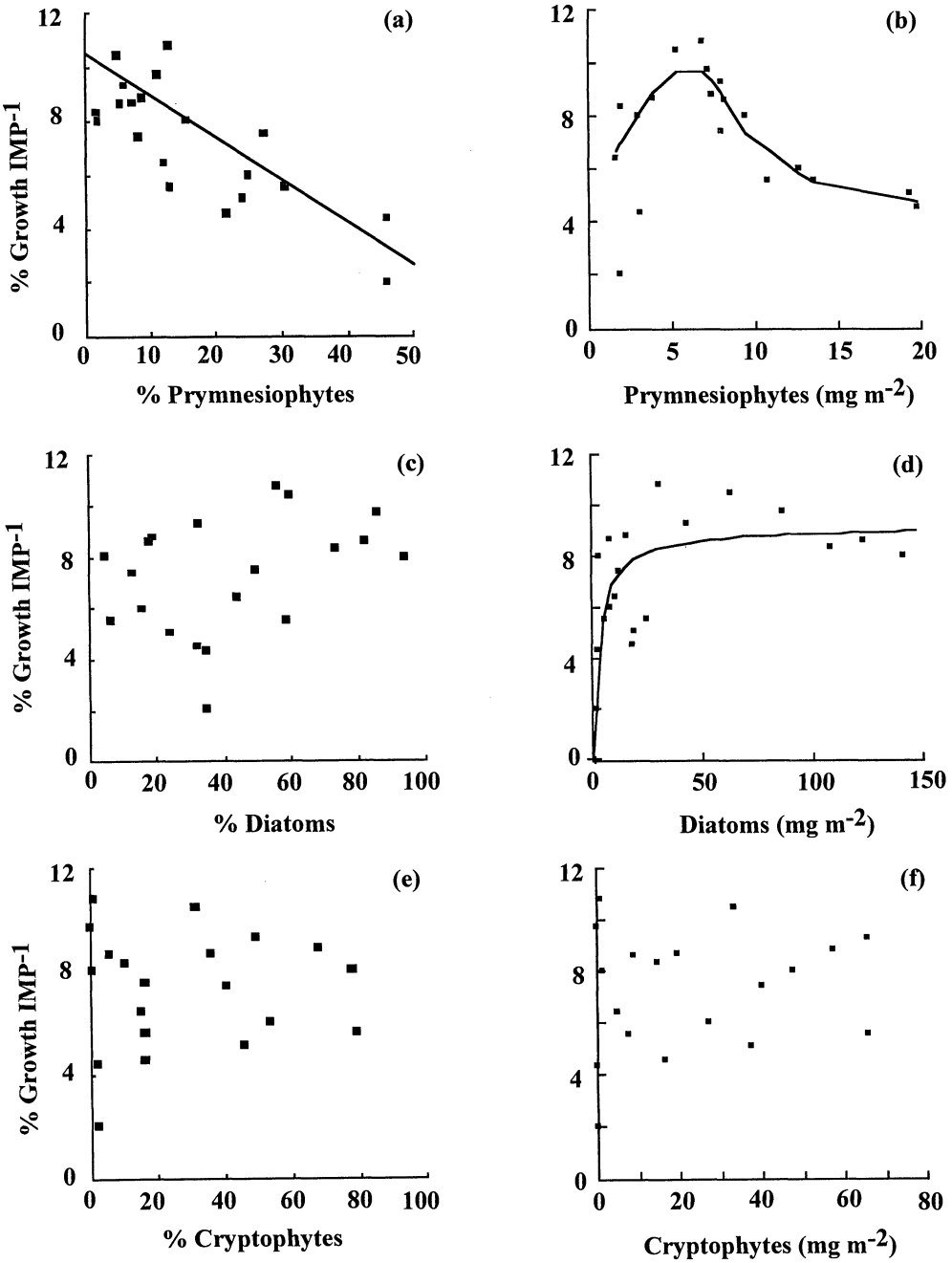

Fig. 7. Percentage growth IMP^{-1} as a function of phytoplankton community composition: percentage composition (a, c, e); concentration of taxon-specific Chl *a* (b, d, f). The taxa shown are prymnesiophytes (a and b), diatoms (c and d), and cryptophytes (e and f). The curve in b is derived with the LOWESS function in Systat (Wilkinson 1989). The curve in d is a Michaelis-Menten uptake function: percentage growth $IMP^{-1} = 8.756 \times$ [diatom–Chl $a/(2.315 +$ diatom–Chl $a)$] ($n = 19$, $r^2 = 0.440$).

Seasonal and interannual variability in molting and growth

Molting cycle—For most planktonic crustaceans, the principal modifiers of the molt cycle are temperature and food availability. In controlled laboratory settings, temperature, food availability, and animal size have all been shown to affect molting frequency in *E. superba* (reviewed in Quetin et al. 1994). The average intermolt period (IMP) for late larval stage and juvenile (early AC1) krill in this study (18.3 d) was within the range found in most laboratory and field studies of molting frequency in late larvae, juveniles, and subadults (Buchholz 1985; Quetin and Ross 1991; Quetin et al. 1994; Daly 1998; Quetin and Ross unpubl. data for winter). The sole exception was the single estimate of IMP for furcilia in winter (Daly 1990), which was significantly less than the average found in this study.

In the present study, the intermolt period showed no re-

Table 5. Multiple regression analysis of growth of Antarctic krill and variables representing food quantity and quality. r^2, proportion of variance explained; Coeff, coefficient in multiple linear regression equation; SE, standard error of that coefficient; Std coeff, coefficient weighted for the relative magnitude of the variables; Tol, indication of collinearity; *P*, significance of the statistic *T* (two-tailed). Variables: chlgrow, [Chl *a*/(0.498 + Chl *a*)]; diagrow, [diatom Chl *a*/(2.315 + diatom Chl *a*)]; prymconc, prymnesiophyte Chl *a*.

Variable	Coeff	SE	Std coeff	Tol	*T*	*P*
$r^2 = 0.712$						
constant	1.328	1.161			1.145	0.269
chlgrow	9.209	1.410	0.833	0.985	6.534	0.000
prymconc	−0.151	0.055	−0.348	0.985	−2.730	0.015
$r^2 = 0.528$						
constant	0.476	1.836			0.259	0.799
prymconc	−0.168	0.071	−0.388	0.962	−2.351	0.032
diagrow	9.802	2.199	0.736	0.962	4.457	0.000
$r^2 = 0.704$						
constant	0.670	1.455			0.460	0.652
chlgrow	7.741	2.388	0.700	0.352	3.242	0.005
diagrow	2.235	2.912	0.168	0.344	0.768	0.455
prymconc	−0.158	0.057	−0.364	0.959	−2.783	0.014

lationship with total length of krill, experimental temperature, percentage growth IMP^{-1}, or date. We did not expect either size or experimental temperature to affect the intermolt period. First, we focused on a single age class and therefore a narrow size range of krill. Second, a correlation between the intermolt period and experimental temperature would only be predicted if the experimental temperature represented or integrated the temperature of the krill habitat (30–50 m) during the entire intermolt period, not just the 4-d experiment.

However, the range in molting frequency found in field populations of krill is greater than predicted by environmental effects alone, suggesting that synchrony in the molt cycle may also impact estimates of the intermolt period. Synchronous molting, which has been seen in some aggregations of krill in the field (Buchholz 1985; Buchholz et al. 1989), may thus obscure relationships with environmental variables and lead to differences in results from field and laboratory studies. For example, estimates of the IMP in this study were as low as 7 d and as high as 40 d (Fig. 2) outside the IMP documented for individual krill of this age class in the laboratory. These results emphasize the need to measure molting frequency in field populations either with a series of experiments over time or with krill from multiple aggregations.

Growth rates—The uncertainty associated with any one estimate of the IMP led us to use percentage growth IMP^{-1} for comparison of experimental growth rates. The ranges in growth in young krill in under-ice and water column habitats were similar, supporting the concept that sea ice biota provides an adequate alternate food source for young krill when phytoplankton concentrations in the water column are low. The experimental percentage growth IMP^{-1} in this study spans the range found in previous studies of young krill: late furcilia under heavy pack ice, 5.43% (Ross and Quetin 1991); juveniles in summer, 2.4–9.1% (Nicol et al. 1992); 23–30-mm subadults in spring, 6.4% (Daly 1998).

In general, growth rates (mm d^{-1}) of *E. superba* in the field (this study) are higher than growth rates of Antarctic krill maintained in the laboratory on diets presumed adequate in both quantity and quality (reviewed in Quetin et al. 1994). Maximum growth rates in this study (Fig. 4) agreed with predictions (0.10–0.13 mm d^{-1}) for a 180-d growth period generated with two methods, a growth model (Ikeda 1985) and an age class analysis (Pakhamov 1995). Maximum growth rates were also similar to summer rates for AC0+ *E. superba* estimated by McClatchie (1988). Minimum growth rates were in the range of winter growth rates from McClatchie's cohort analysis (1988) and from a laboratory study of furcilia maintained under winter food conditions (Elias 1990). In summary, instantaneous growth rates in the field reach the predicted maximum, whereas published laboratory rates are well below the predicted maximum.

Food quantity and quality

Most field evidence suggests that production (growth and reproduction) in pelagic crustaceans in temperate oceans is determined primarily by diet and not by temperature (Kleppel 1993; Klein Breteler et al. 1995). The Southern Ocean ecosystem (Clarke 1988) and krill populations (Quetin et al. 1994) have also been characterized as food, not temperature, limited. Variation in growth rates of Antarctic krill on seasonal timescales has previously been documented (McClatchie 1988). With the instantaneous growth rate technique we have been able to document variability and correlation of growth rates with the nutritional environment on much finer temporal scales than previously possible.

Food quantity—Growth of early AC1 Antarctic krill in the spring and summer followed the expected functional response curve, e.g., growth rate increased curvilinearly to a maximum level that remained constant with further increases in phytoplankton concentration. This functional relationship was derived using a single sampling day to represent the food available during the previous intermolt period. Despite this temporal disparity, a large amount of the variance in growth was explained by food quantity. Krill appear to respond to change in their environment on relatively short timescales, i.e., a week or less. Change occurs in the phytoplankton population on similar timescales (Fig. 6; Moline and Prézelin 1996). These results imply that the response of krill to their food environment is on the same timescale as accumulation of phytoplankton biomass.

The critical concentration for maximum growth in this study was about 3.5 μg l^{-1} Chl *a*, a concentration at the lower end of the range for bloom conditions (defined as >1 μg l^{-1} Chl *a*). Because this estimate of critical concentration represents food levels on a single day during the entire intermolt period, it should not be confused with values from krill feeding in controlled conditions in the laboratory. Our estimate of the critical concentration for maximum growth must be interpreted in the context of a variable environment

(patches, layers) and the manner in which the samples were collected. The results support the hypothesis that growth in early AC1 *E. superba* was limited at food concentrations below those of minor blooms, but the exact concentration and duration are unknown.

Two earlier studies, one laboratory and one field, also estimated critical concentration. From results of a laboratory study of *E. superba* fed *Phaeodactylum tricornutum,* Ikeda and Thomas (1987) suggested that food almost always limits growth, except at extremely high concentrations (17 μg l^{-1} Chl *a*). McClatchie (1988), in his cohort analysis, suggested the reverse, that growth was maximal during most of the spring and summer. During the rest of the year growth was positive, although limited by food availability. McClatchie's (1988) critical concentration (1–2 μg l^{-1} Chl *a* for group 0 krill) is an underestimate because it was based on unrealistically high winter growth rates (Quetin et al. 1994). The finer temporal scale sampling in this study demonstrated that growth is limited except during phytoplankton blooms when phytoplankton biomass has accumulated.

Food quality—Optimal foraging theory suggests that the shape of the functional response curve for ingestion, including the critical concentration, will vary with food quality (Lehman 1976). Thus food quantity may not be the only factor underlying the variation seen in growth rates of Antarctic krill. The relatively high critical concentration of Ikeda and Thomas (1987) may be a result of the lower food quality of cultures of *P. tricornutum* compared to phytoplankton communities in the field.

Although food quality is frequently described with stoichiometric ratios (carbon to nitrogen), the taxonomic approach generally provides greater detail on the interaction between the food environment and growth. In this study, the choice of chemotaxonomic pigments was based on several factors. First, one measure of food quality is size of the cell. We know that the filtration efficiency of Antarctic krill is higher on larger cells (Quetin and Ross 1985) and that the size range of each major taxa is different. Single-cell prymnesiophytes are 3–6 μm, cryptophytes 6–10 μm, and diatoms generally >20 μm if chain length is considered. Colonial prymnesiophytes are much larger, up to several mm in diameter. Second, another measure of food quality is the presence and abundance of lipids and specific fatty acids. These required compounds must be acquired from algal lipids because many species of herbivorous zooplankton cannot synthesize them (Enright et al. 1986; Ahlgren et al. 1990). Thus, food value will vary with both proximate chemical composition (lipid, protein, and carbohydrate) and the presence of specific nutritional requirements. Taxonomic groups may be good markers for both the dominant storage compound (Ahlgren et al. 1990; Kleppel 1993; Rai 1995) and specific nutritional requirements (Jónasdóttir et al. 1995). For example, diatoms both store lipids (Rai 1995) and contain large amounts of two essential long-chain polyunsaturated fatty acids (PUFAs) (Weers and Gulati 1997). The prymnesiophyte *Phaeocystis pouchetti* is low in both total lipid and essential fatty acids (Nichols et al. 1991) and, thus, likely a poor food source.

However, the composition and concentration of specific compounds vary with growth conditions and the physiological state of the phytoplankton cells (Jónasdóttir 1994; Ederington et al. 1995; Kleppel and Burkart 1995). In experiments on egg production rates of copepods, specific fatty and amino acids were found to be more useful than taxonomic composition alone to characterize the food environment on timescales of hours to weeks (Jónasdóttir 1994; Kleppel and Burkart 1995). However, Virtue et al. (1993) suggest that Antarctic krill are able to synthesize PUFAs from shorter chain fatty acids. With this biosynthetic capability, food quality for Antarctic krill may be more dependent on the presence and concentration of lipids in the food than on the presence of specific essential fatty acids.

The results of this seasonal time series demonstrated that the importance of food quality to growth in Antarctic krill is not restricted to controlled laboratory conditions. The relationships between growth rates and individual taxonomic groups support the hypothesis that diatoms are superior to prymnesiophytes as a food. Although neither percent composition of diatoms nor diatom–Chl *a* were included in the multiple regression describing the relationship between the food environment and growth in krill, we attribute this lack to the fact that a relatively low percentage of diatoms is adequate for high growth rates, as suggested by the functional response to diatom–Chl *a* (Fig. 7d). Thus, the absolute concentration of diatoms is more important to growth than the relative proportion of diatoms in the phytoplankton community. The strong correlation between total Chl *a* and diatom–Chl *a* means that when total food increases, so does the concentration of diatoms. And in contrast to the positive effects of diatoms, growth is negatively affected by the presence of prymnesiophytes except at very low concentrations.

The composition of the diet is determined by the feeding response of the grazer to the food environment, often through complex interactions. The ability of zooplankton to discriminate between food items, and thus selectively ingest food particles of greater nutritional value, has been established with laboratory experiments (DeMott 1989). This ability to select certain particles also occurs in the field (Kleppel 1993). For *E. superba* in the laboratory, clearance rates on different phytoplankton taxa differ (Quetin and Ross 1985; Pond et al. 1995; Haberman 1998). Antarctic krill have recently been shown to select diatoms over either cryptophytes or prymnesiophytes (*Phaeocystis antarctica*) in experiments with both natural phytoplankton assemblages and known mixtures of cultures of different phytoplankton species (Haberman 1998). The result held whether *P. antarctica* was single-celled or similar-sized colonies. This selectivity, presumably on the basis of cell size and/or the chemosensory abilities of the krill, would enhance the effect of variation in phytoplankton community composition on growth under field conditions.

In conclusion, growth rates of early AC1 Antarctic krill in the field vary on multiple timescales, both subseasonal and interannual. The results support the hypothesis that production in Antarctic krill in the Southern Ocean is limited by both food quantity and quality during most of the spring and summer. In the past, the effects of variation in food quality on the success of Antarctic krill in the field may not have been sufficiently valued. Only at the height of phyto-

plankton blooms dominated by diatoms did we find maximum growth. The link between diatom productivity and krill production merits further investigation. Differences in phytoplankton community composition caused by changes in environmental conditions, including climate change, will thus be reflected at higher trophic levels in the grazer community and their level of productivity.

References

AHLGREN, G., L. LUNDSTEDT, M. BRETT, AND C. FORSBERG. 1990. Lipid composition and food quality of some freshwater phytoplankton for cladoceran zooplankters. J. Plankton Res. **12:** 809–818.

ATKINSON, A., AND R. SNŸDER. 1997. Krill-copepod interactions at South Georgia, Antarctica, I. Omnivory by *Euphausia superba.* Mar. Ecol. Prog. Ser. **160:** 63–76.

BUCHHOLZ, F. 1985. Moult and growth in Euphausiids, p. 339–345. *In* W. R. Siegfried, P. R. Condy, and R. M. Laws [eds.], Antarctic nutrient cycles and food webs. Springer.

———. 1991. Moult cycle and growth of Antarctic krill *Euphausia superba* in the laboratory. Mar. Ecol. Prog. Ser. **69**: 217–229.

———, D. J. MORRIS, AND J. L. WATKINS. 1989. Analyses of field moult data: Prediction of intermoult period and assessment of seasonal growth in Antarctic krill, *Euphausia superba* Dana. Antarct. Sci. **1:** 301–306.

CHECKLEY, D. M., JR. 1980. Food limitation of egg production by a marine, planktonic copepod in the sea off southern California. Limnol. Oceanogr. **25:** 991–998.

CLARKE, A. 1988. Seasonality in the Antarctic marine environment. Comp. Biochem. Physiol. **90B:** 461–473.

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

———. 1998. Physioecology of juvenile Antarctic krill (*Euphausia superba*) during spring in ice-covered seas, p. 183–198. *In* M. P. Lizotte and K. R. Arrigo [eds.], Antarctic sea ice biological processes, interactions, and variability. Antarctic Research Series, v. 73. American Geophysical Union.

DEMOTT, W. R. 1989. Optimal foraging theory as a predictor of chemically mediated food selection by suspension-feeding copepods. Limnol. Oceanogr. **34:** 140–154.

DIERSSEN, H., M. VERNET, AND R. C. SMITH.. Optimizing models for remotely estimating primary production in Antarctic coastal waters. Antarct. Sci. In press.

EDERINGTON, M. C., G. B. MCMANUS, AND H. R. HARVEY. 1995. Trophic transfer of fatty acids, sterols, and a triterpenoid alcohol between bacteria, a ciliate, and the copepod *Acartia tonsa.* Limnol. Oceanogr. **40:** 860–867.

ELIAS, M. C. 1990. Effects of photoperiod, phytoplankton level and temperature on the growth, development and survival of larval *Euphausia superba* (Dana). Master's thesis. Univ. of California, Santa Barbara.

ENRIGHT, C. T., G. F. NEWKIRK, J. S. CRAIGIE, AND J. D. CASTELL. 1986. Evaluation of phytoplankton as diets for juvenile *Ostrea edulis* L. J. Exp. Mar. Biol. Ecol. **96:** 1–13.

HABERMAN, K. L. 1998. Feeding ecology of the Antarctic krill, *Euphausia superba:* The role of phytoplankton community composition in the krill's diet. Ph.D. thesis. Univ. of California, Santa Barbara.

HAMNER, W. M., P. P. HAMNER, S. W. STRAND, AND R. W. GILMER. 1983. Behavior of Antarctic krill, *Euphausia superba:* Chemoreception, feeding, schooling, and molting. Science **220:** 433–435.

IKEDA, T. 1985. Life history of Antarctic krill *Euphausia superba:* A new look from an experimental approach. Bull. Mar. Sci. **37:** 599–608.

———, AND P. DIXON. 1982. Body shrinkage as a possible overwintering mechanism of the Antarctic krill, *Euphausia superba.* J. Exp. Mar. Biol. Ecol. **62:** 143–151.

———, AND P. G. THOMAS. 1987. Moulting interval and growth of juvenile Antarctic krill (*Euphausia superba*) fed different concentrations of the diatom *Phaeodactylum tricornutum* in the laboratory. Polar Biol. **7:** 339–343.

JEFFREY, S. W., R. F. C. MANTOURA, AND S. W. WRIGHT. 1997. Phytoplankton pigments in oceanography: Guidelines to modern methods. UNESCO.

JÓNASDÓTTIR, S. H. 1994. Effects of food quality on the reproductive success of *Acartia tonsa* and *Acartia hudsonica:* laboratory observations. Mar. Biol. **121:** 67–81.

———, D. FIELDS, AND S. PANTOJA. 1995. Copepod egg production in Long Island Sound, USA, as a function of the chemical composition of the seston. Mar. Ecol. Prog. Ser. **119:** 87–98.

KLEIN BRETELER, W. C. M., S. R. GONZALEZ, AND N. SCHOGT. 1995. Development of *Pseudocalanus elongatus* (Copepoda, Calanoida) cultured at different temperature and food conditions. Mar. Ecol. Prog. Ser. **119:** 99–110.

KLEPPEL, G. S. 1993. On the diets of calanoid copepods. Mar. Ecol. Prog. Ser. **99:** 183–195.

———, AND C. A. BURKART. 1995. Egg production and the nutritional environment of *Acartia tonsa:* The role of food quality in copepod nutrition. ICES J. Mar. Sci. **52:** 246–255.

KOZLOWSKI, W., M. VERNET, AND S. K. LAMERDIN. 1995. Palmer LTER: Predominance of cryptomonads and diatoms in Antarctic coastal waters. Antarct. J. U. S. **30:** 267–268.

LEHMAN, J. T. 1976. The filter-feeder as an optimal forager, and the predicted shapes of feeding curves. Limnol. Oceanogr. **21:** 501–516.

LIBOUREL HOUDE, S. E., AND M. R. ROMAN. 1987. Effects of food quality on the functional ingestion response of the copepod *Acartia tonsa.* Mar. Ecol. Prog. Ser. **40:** 69–77.

MAUCHLINE, J. 1981. Measurement of body length of *Euphausia superba* Dana. BIOMASS Handbook No. **4.** SCAR/SCOR/IABO/ACMRR.

MCCLATCHIE, S. 1988. Food-limited growth of *Euphausia superba* in Admiralty Bay, South Shetland Islands, Antarctica. Cont. Shelf Res. **8:** 329–345.

MOLINE, M. A., AND B. B. PRÉZELIN. 1996. Long-term monitoring and analyses of physical factors regulating variability in coastal Antarctic phytoplankton biomass, *in situ* productivity and taxonomic composition over subseasonal, seasonal and interannual time scales. Mar. Ecol. Prog. Ser. **145:** 143–160.

NICHOLS, P. D., J. H. SKERRATT, A. DAVIDSON, H. BURTON, AND T. A. MCMEEKIN. 1991. Lipids of cultured *Phaeocystis pouchetii:* Signatures for food-web, biogeochemical and environmental studies in Antarctica and the Southern Ocean. Phytochemistry **30:** 3209–3214.

NICOL, S., M. STOLP, T. COCHRAN, P. GEIJSEL, AND J. MARSHALL. 1992. Growth and shrinkage of Antarctic krill (*Euphausia superba* Dana) from the Indian sector of the Southern Ocean during summer. Mar. Ecol. Prog. Ser. **89:** 175–181.

PAKHOMOV, E. A. 1995. Demographic studies of Antarctic krill *Euphausia superba* in the Cooperation and Cosmonaut Seas (Indian sector of the Southern Ocean). Mar. Ecol. Prog. Ser. **119:** 45–61.

POND, D. W., J. PRIDDLE, J. R. SARGENT, AND J. L. WATKINS. 1995. Laboratory studies of assimilation and egestion of algal lipid by Antarctic krill—methods and initial results. J. Exp. Mar. Biol. Ecol. **187:** 253–268.

PRÉZELIN, B. B., N. P. BOUCHER, M. MOLINE, E. STEPHENS, K. SEYDEL, AND K. SCHEPPE. 1992. Palmer LTER program: Spa-

tial variability in phytoplankton distribution and surface photosynthetic potential within the peninsula grid, November 1991. Antarct. J. U. S. **27:** 242–244.

PRICE, H. J. 1989. Swimming behavior of krill in response to algal patches: A mesocosm study. Limnol. Oceanogr. **34:** 649–659.

QUETIN, L. B., AND R. M. ROSS. 1985. Feeding by *Euphausia superba:* Does size matter?, p. 372–377. *In* W. R. Siegfried, P. R. Condy, and R. W. Laws [eds.], Antarctic nutrient cycles and food webs. Springer.

———, AND ———. 1991. Behavioral and physiological characteristics of the Antarctic krill, *Euphausia superba.* Am. Zool. **31:** 49–63.

———, ———, AND A. CLARKE. 1994. Krill energetics: Seasonal and environmental aspects of the physiology of *Euphausia superba,* p. 165–184. *In* S. El-Sayed [ed.], Southern Ocean ecology: The BIOMASS perspective. Cambridge Univ. Press.

———, ———, T. K. FRAZER, AND K. L. HABERMAN. 1996. Factors affecting distribution and abundance of zooplankton, with an emphasis on Antarctic krill, *Euphausia superba,* p. 357–371. *In* R. M. Ross, E. E. Hofmann, and L. B. Quetin [eds.], Foundations for ecological research west of the Antarctic Peninsula. Antarctic Research Series, v. 70. American Geophysical Union.

RAI, H. 1995. The influence of photon flux density (PFD) on short term ^{14}C incorporation into proteins, carbohydrates and lipids in freshwater algae. Hydrobiologia **308:** 51–59.

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

SMITH, R. C., K. S. BAKER, AND P. DUSTAN. 1981. Fluorometer techniques for measurement of oceanic chlorophyll in the support of remote sensing. Scripps Institution of Oceanography, Univ. of California. Ref. 81–17, 14p.

———, ———, K. K. HWANG, D. MENZIES, AND K. J. WATERS. 1992. Palmer LTER program: Hydrography and optics within the peninsula grid, November 1991 cruise. Antarct. J. U. S. **27:** 250–253.

———, ———, AND M. VERNET. 1998. Seasonal and interannual variability of phytoplankton biomass west of the Antarctic Peninsula. J. Mar. Syst. **17:** 229–243.

———, H. M. DIERSSEN, AND M. VERNET. 1996. Phytoplankton biomass and productivity in the Western Antarctic Peninsula region, p. 333–356. *In* R. M. Ross, E. E. Hofmann, and L. B. Quetin [eds.], Foundations for ecological research west of the Antarctic Peninsula. Antarctic Research Series, v. 70. American Geophysical Union.

STRAND, S. W., AND W. M. HAMNER. 1990. Schooling behavior of Antarctic krill (*Euphausia superba*) in laboratory aquaria: Reactions to chemical and visual stimuli. Mar. Biol. **106:** 355–359.

VIRTUE, P., P. D. NICHOLS, S. NICOL, A. MCMINN, AND E. L. SIKES. 1993. The lipid composition of *Euphausia superba* Dana in relation to the nutritional value of *Phaeocystis pouchetii* (Hariot) Lagerheim. Antarct. Sci. **5:** 169–177.

WEERS, P. M. M., AND R. D. GULATI. 1997. Growth and reproduction of *Daphnia galeata* in response to changes in fatty acids, phosphorus, and nitrogen in *Chlamydomonas reinhardtii.* Limnol. Oceanogr. **42:** 1584–1589.

WILKINSON, L. 1989. SYSTAT: The system for statistics. SYSTAT.

WRIGHT, S. W., S. W. JEFFREY, R. F. C. MANTOURA, C. A. LLEWELLYN, T. BJORLAND, D. REPETA, AND N. WELSCHMEYER. 1991. Improved HPLC method for the analysis of chlorophylls and carotenoids from marine phytoplankton. Mar. Ecol. Prog. Ser. **77:** 183–196.

Received: 29 December 1998
Accepted: 28 July 1999
Amended: 1 October 1999