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Winter Ecology of Young Antarctic Krill, *Euphausia superba*: Feeding on the Sea Ice Microbial Community with Implications for Growth Models

A Dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Marine Science

by

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ABSTRACT

Winter Ecology of Young Antarctic Krill, *Euphausia superba*: Feeding on the Sea Ice Microbial Community with Implications for Growth Models

By

Stephanie Ann Oakes

The Antarctic krill (*Euphausia superba*) is an important zooplankton grazer and prey item for predators. The Southern Ocean ecosystem is impacted by variation in the seasonal advance and retreat of sea ice. During the austral winter, when light is limited, phytoplankton stocks in the water are reduced to low concentrations that are often insufficient to support krill metabolism. Several aspects of the feeding ecology of young krill in winter were explored.

First, clearance rate, functional response and daily ration were measured for krill feeding on phytoplankton by filtering particles from the water column and scraping surfaces. Maximum clearance rates for small krill when scraping were higher than for large krill, but lower for filtration. Ingestion rates followed a Type II (filtration) or Type III (scraping) functional response. Small krill feeding by scraping met their minimum daily ration when chl *a* was 40% of that required by larger krill. This suggests that small krill are more efficient at feeding on the sea ice surface than larger krill.

Next, clearance and ingestion rates were measured for krill fed endemic sea ice microbes to determine food preference and the relative importance of various food sources. Egestion rates were measured and assimilation efficiencies were calculated. Total and autotrophic carbon ingestion increased with increasing carbon until a critical concentration but heterotrophic carbon ingestion was not correlated with carbon. Winter assimilation efficiencies were 70 to 91% for larval krill. Krill feeding selectivity depended on food concentration and the sea ice microbial community composition.

Finally, a physiological growth model was constructed to explore winter growth of larval and sub-adult krill. Model results indicate that conservative combinations of water-column and sea ice chl *a*, and C:chl *a* ratios sustain krill during winter. Older larvae required the same C:chl *a* ratios but higher chl *a* concentrations than sub-adult krill. Younger larvae required both higher C:chl *a* ratios and chl *a*. Our model predicts krill survival and growth under chl *a* and C:chl *a* conditions that krill are likely to encounter during winter but changing sea ice conditions will impact larval more than sub-adult krill.

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CHAPTER 1:

FEEDING SUCCESS OF ANTARCTIC KRILL (*EUPHAUSIA SUPERBA*) FEEDING BY SCRAPING SURFACES VERSUS WATER COLUMN FILTRATION

ABSTRACT

The Antarctic krill, *Euphausia superba*, has been observed feeding by two modes during winter, by filtering particles from the water column and scraping the sea ice surface. The goal of this study was to determine whether clearance rate, functional response, and daily ration were altered by feeding mode. Small krill (7-19 mm, 20-530 mg) and large krill (15-29 mm, 240-2100 mg) were fed the diatom *Fragilariopsis curta* or endemic phytoplankton at -1.9 to –1.1 °C. Food was grown on 2-dimensional tile surfaces to simulate the under-ice/water column interface or in culture flasks and later diluted in experimental containers to simulate the 3-dimensional 'water column'. Maximum wet mass (WM) specific clearance rates for surface scraping were higher for small krill, 0.26 cm^2 $mgWM^{-1}$ h^{-1}, than for large krill 0.13 cm^2 $mgWM^{-1}$ h^{-1}. When feeding by 'water-column' filtration large krill had higher maximum clearance rates, 12 ml $mgWM^{-1}$ h^{-1}, than small krill, 3.3 ml $mgWM^{-1}$ h^{-1}. Ingestion rates followed a Holling's Type II functional response for 'water-column' filtration but were Type III for surface scraping. Small krill were more efficient feeding by surface scraping and were able to meet their minimum daily ration when surface chl *a* was 2.8 μg $tank^{-1}$ and water column chl *a* was 4.5 μg $tank^{-1}$. Larger krill were unable to meet their minimum daily ration until surface chl *a* was 7.0 μg $tank^{-1}$ but were able to meet their minimum daily ration when 'water-column' chl *a* was 3.5 μg $tank^{-1}$. Ingestion rates for larval krill feeding by surface scraping were 1.5 to 3 times higher than estimates of winter ingestion rates used in krill growth models. This study supports the idea that small krill feed more

efficiently scraping the sea ice surface than previously thought and suggests small krill are better adapted to feeding on the sea ice surface than are larger krill.

INTRODUCTION

Antarctic krill (*Euphausia superba*) hereafter called krill, are arguably the most important zooplankton grazer in the Southern Ocean. Recent work suggests swarms of krill may create turbulence that pumps nutrients into the surface waters (Huntley & Zhou 2004, Kunze et al. 2006, Dewar et al. 2006), transport carbon in the form of fecal pellets from the surface waters to depth (Tarling & Johnson 2006, Swadling 2006), and fuel charismatic Antarctic mega fauna (Hewitt et al. 2002 & references therein), not to mention humans (Kawaguchi & Nicol 2007 & references therein). Krill are well-known as key prey for many Antarctic species (Laws 1985, Miller & Hampton 1989, Hill et al. 1996, Croll & Tershy 1998) and have a long lifespan, 5-7 years (Ettershank 1984, Berman et al. 1989, Miller & Hampton, 1989). During the winter, when light is limited, low phytoplankton stocks in the water column (<0.05 $\mu g\ L^{-1}$) (Morris & Priddle 1984, Nöthig et al. 1992, Huntley et al. 1994) are insufficient to support the metabolic requirements of krill (Daly 1990, Frazer et al. 2002, Meyer et al. 2002). This observation has led to much speculation concerning the winter survival strategies of krill.

Several winter survival strategies, such as body shrinkage (Ikeda & Dixon 1982), reduced metabolism (Kawaguchi et al. 1986, Quetin & Ross 1991, Torres et al. 1994), stored lipid utilization (Torres et al. 1994, Hagen et al. 1996), and alternate food sources (Kawaguchi et al. 1986, Marschall 1988, Stretch et al. 1988, Daly 1990, Hopkins 1993, Huntley et al. 1994) have been proposed. Evidence suggests that these over-wintering strategies are not used by all stages of krill

universally. Larval, juvenile and adult krill have different biochemical composition and metabolic requirements, and exhibit different winter-feeding behavior (Quetin et al. 1994, Meyer et al. 2002), suggesting that their over-wintering strategies are different. Over-wintering adults appear to meet metabolic requirements through combined strategies (Quetin & Ross 1991) of, reduced metabolism (Atkinson et al. 2002), utilization of lipid reserves (Hagen et al. 1996, Hagen et al. 2001) and carnivorous feeding (Torres et al. 1994).

Larval krill, without the large lipid reserves of adults (Ross & Quetin, 1991, Hagen et al. 2001), are unable to tolerate the long-term starvation (Ikeda & Dixon, 1982) observed in adults (Ross & Quetin 1991, Quetin et al. 1996) and must feed to meet metabolic requirements for survival (Daly 1990, Meyer et al. 2002). Unlike adult krill which feed on copepods during winter (Ju & Harvey 2004), larval krill do not resort to carnivory (Meyer et al. 2002) but continue to rely on algae (Frazer 1996, Frazer et al. 2002), ice –associated organisms, and detritus (Ju & Harvey 2004) as their primary winter food source. Given the low concentration of phytoplankton in the winter water column, it is likely that larval krill rely on sea ice biota during their first winter (Stretch et al. 1988, Daly 1990, Smetacek et al. 1990, Quetin & Ross 1991), a strategy vital to survival (Ross & Quetin 1991). The association of larval krill with the pack ice is well established (Guzman 1983, Daly & Macauly 1988, Marschall 1988, Daly 1990, Smetacek 1990) and survival of larval krill and the young-of-year recruitment into the reproducing population are thought to depend on the presence of sea ice (Siegel & Loeb 1995, Quetin & Ross

2003) and the timing and extent of production in the microbial community in the annual sea ice (Quetin et al. 2003). Although the conceptual link between larval krill and sea ice has existed since the early 1990s, quantitative data on larval krill ingestion rates and food sources in winter conditions are few, and many important questions concerning this survival strategy remain unanswered.

Krill exhibit several distinct feeding behaviors depending on environmental conditions. Adult krill engage in raptorial feeding on copepods (Price 1988, Atkinson et al. 2002). Benthic diatoms, absent in the winter water column, have been found in the guts of krill (Ligowski 2000), implying benthic feeding. Both young-of-year and adult krill feed by compression filtration in the water column and have been observed feeding on ice surfaces during dive operations (as summarized in Quetin et. al. 1996). However, larger sub-adult and adult krill are often found deep in the water column during winter. If ingestion rate were independent of feeding mode and all else being equal (ie. predation risk), it might be beneficial for all krill stages to feed at the ice surface where food sources are at higher levels. Chlorophyll (chl *a*) concentrations (Table 1) in sea ice are significantly higher than that in the water column (< 0.1 $\mu g\ l^{-1}$) and often exceed 1 $\mu g\ l^{-1}$ with concentrations in the tens and hundreds of $\mu g\ l^{-1}$ recorded (Lizotte, 2001). In winter, larger krill are prey items for visual predators such as seals (Lowry et al., 1988, Reid 1995) and penguins (Kirkwood & Robertson 1997, Berrow et al. 1999) and would be more vulnerable at the sea ice surface. Smaller larval krill are often prey for non-visual feeders such as ctenophores (Hamner et al. 1989, Ju et al. 2004, Quetin & Martin

personal communication) and salps (Daly 1990) as well as visual predators such as amphipods (Hamner et al. 1989).

Laboratory observations of krill feeding on ice blocks containing frozen phytoplankton culture (Hamner et al. 1983) and of the foraging behavior of adult krill relative to the presence of melting ice blocks made from cultured phytoplankton and natural sea-ice biota (Stretch et al. 1988) have been made. Adult krill (35-45 mm) feeding on phytoplankton cultured on glass plate surfaces can clear the surface at ~0.7 $cm^2 s^{-1}$ (Marschall 1988) but quantification of food ingestion by feeding mode has not been attempted. No studies have actually quantified ingestion rates of krill feeding on sea-ice surfaces, although models have estimated the input (Hofmann & Lascara 2000). The amount of food actually consumed by krill feeding on sea-ice biota has not been quantified. The only study that quantified the amount of chl *a* ingested from cultured phytoplankton frozen into ice blocks was done with amphipods from the Arctic (Werner 1997).

Pelagic population and ecosystem models must consider zooplankton ingestion of available resources. While it is important to delineate among single resource responses in multiple resource pelagic systems (Gentleman et al. 2003), it is reasonable to delineate between resource locations in systems where seasonal cycles alter the physical environment. Functional response describes predation rate relative to food availability (Solomon 1949). Functional response is described as (Holling 1959a): Type I (linear increase), Type II (hyperbolic curve), and Type III (sigmoidal curve). Use of the appropriate functional response in models is

important because models are sensitive to equation choice (Gentleman et al. 2003). In light of the above, an understanding of the functional response of young-of-year krill to pelagic and ice-derived food is needed (Meyer et al. 2003), and quantification is required (Hofmann & Lascara 2000) to predict both their energy intake from and their grazing impact on the winter sea-ice microbial community. Frazer et al. (2002) suggested an energetic comparison between filter-feeding and ice-scraping feeding modes at winter temperatures (<-1.5°C) may provide insight as to when and why larval krill associate with the sea ice.

This study compares the clearance rates, ingestion rates, functional response and daily ration of two distinct size classes of krill feeding using two modes, scraping on a simulated sea-ice surface and compression filtration in a simulated water column, hereafter called scraping and filtration. The data were derived from feeding experiments conducted at Palmer Station, Antarctica, during 2001 and 2002. Here we report the first estimates of ingestion rates for krill feeding at winter temperatures by scraping and filtration allowing comparison of the energetic differences of these two feeding modes. Estimates of ingestion by scraping are compared to previously assumed ingestion rates from ice scraping used to model growth dynamics of larval krill in winter (Hofmann & Lascara 2000). Ingestion and daily rations indicate that smaller krill may feed more effectively by scraping sea ice than previously thought.

MATERIALS AND METHODS

Feeding experiments with krill were conducted at winter temperatures at Palmer Station, Antarctica during the summer of 2001 and early spring of 2002. Krill were fed *Fragilariopsis curta* (synonym *Nitzchia curta*) and endemic net-collected phytoplankton grown on unglazed ceramic tile surfaces, and suspended in the 'water column' to investigate the dynamics of feeding in these two simulated environments. The details of these experiments follow.

Collection and Maintenance of Krill

Young *Euphausia superba* were collected in November and December 2000 within 2 km of Palmer Station with a 1-m ring net with 333-μm mesh deployed from a zodiac. During October of 2002 young krill were collected from beneath the sea ice by divers with aquarium nets (250 μm - 1000 μm). Once captured, krill were placed in buckets of seawater and transferred back to Palmer Station where they were maintained in 2.5-m diameter tanks kept at ambient food levels and near-ambient temperatures ranging from approximately -1 to 3 °C. Krill collected in 2000 were held in captivity for 2 to 4 mo and developed to the late juvenile and early sub-adult stage (hereafter called large krill) prior to use in experiments. Krill collected in 2002 were held for only 2 to 7 wk prior to use in experiments, and were predominantly late larval and early juvenile stage (hereafter called small krill). One day prior to all experiments, randomly selected krill were removed from the seawater tanks and placed in 20-l of 0.45 μm-filtered seawater in the environmental

room to allow the animals to acclimate to the experimental temperature of approximately -1.5 °C. After acclimation a subset of healthy, actively swimming animals was selected for use in experiments.

Phytoplankton Sources and Maintenance

Fragilariopsis curta, originally isolated from the Antarctic, was obtained from the Bigelow Laboratory for Ocean Sciences (West Boothbay Harbor, Maine) under the synonym *Nitzchia curta* and used in experiments with large krill in 2001. A mixture of diatoms dominated by two *Fragilariopsis spp.* was cultured from a water sample collected with an 80-μm plankton net in the vicinity of Palmer Station during the early austral spring and was used in experiments with small krill in 2002. Prior to experimental setup, cultures were maintained in 2800-ml fernbach flasks at temperatures ranging from 0 to 3 °C, and illuminated by cool, white fluorescent lights on a 10 L:14 D light cycle. All cultures were grown in F/2 media (Guillard & Ryther 1962) with sterile techniques. These stock cultures were used to inoculate cultures used in both scraping and filtering experiments.

Surface Scraping Experiments

Tiles (6.5 cm^2) were placed in rectangular acrylic tanks, 17.8 cm by 25.4 cm at the base hereafter called growth tanks, that contained 1-l F/2 media. The growth tanks were then inoculated with either stock *F. curta* or endemic phytoplankton culture. Phytoplankton was allowed to settle and grow on tile surfaces for 3 d to 2

wk depending on the relative initial chl *a* level desired (low, medium or high). Experimental and control tanks were filled with 2.0-l (2002) or 2.5-l (2001) of 0.2 μm-filtered seawater and placed in the environmental room overnight to bring the seawater to experimental temperature. Sub-samples of the 0.2 μm-filtered seawater were filtered onto 25 mm GF/F or HAWP filters and frozen at -70 °C for chl *a* analysis immediately before the start of the experiment.

Each growth tank contained 60 tiles. Tiles were removed from the growth tanks, gently rinsed in 0.2 μm-filtered seawater and used in one of 3 ways. Ten tiles were selected and frozen in pairs for determination of initial chl *a* (n=5). Tiles were frozen in pairs to ensure sufficient chl *a* for measurement. Another ten tiles were placed in a control tank and two experimental tanks received 20 tiles each. Experimental and control tanks containing the tiles were placed in a water bath in the environmental room at temperatures ranging from -1.9 to –1.1 °C (Table 2) in the dark. Acclimated krill (n=19 to 21) were selected and placed in the experimental tanks. At the end of experiments krill were removed from the experimental tanks. Then the tiles were removed from the control (n=5) and experimental (n=10) tanks and frozen in pairs for chl *a* analysis. The remaining water in both the experimental and control tanks was well mixed and 100-ml sub-samples (n=6) were filtered onto GF/F or HAWP filters and frozen at -70°C for chl *a* analysis.

Eight experiments were done with the large size krill. Four experiments lasted 3 h, two lasted 4 h and two lasted 6 h. Halfway through each experiment

water samples were taken from the mid-depth and filtered for chl *a* analysis (n= 4 to 6) to estimate whether chl *a* was released from the tiles by krill scraping but not consumed. Nine experiments were done with the small size krill and lasted approximately 3 h. No water samples were taken at the mid-point of the experiments.

'Water Column' Feeding Experiments

Fragilariopsis curta or endemic phytoplankton stock for filtration experiments was cultured in 20-l clearboy containers. Before each experiment, sub-samples from these cultures were filtered and extracted in 90% acetone for at least 12 h to determine the approximate concentration of phytoplankton biomass. Experimental and control containers were filled with 0.2 μm-filtered seawater and placed in the environmental room overnight to equilibrate to the experimental temperature. The following day aliquots of the phytoplankton culture were added to the containers to obtain the desired chl *a* concentration for each experiment. Filtered seawater was added to bring the experimental and phytoplankton control containers up to 20-l (large size krill) or 10-l (small size krill). After mixing well, the experimental and control containers were allowed to stand for 3 hours, mixed again, and 100-ml sub-samples (n=5 or 6) were filtered through GF/F or HAWP filters for determination of initial chl *a* concentration. This delay in the sub-sampling after mixing reduced the variability in the initial chl *a* values. Krill were then added to the experimental containers and allowed to feed at -1.9 to -1.1 °C

(Table 2) for approximately 2.5 h to 3 h except for one large krill experiment that lasted 4.4 h. At the end of the experiment krill were removed from the experimental containers. The water was mixed and 100-ml sub-samples (n= 5 or 6) were removed and filtered for determination of chl *a*. Filters were stored frozen at -70°C in glass scintillation vials until analysis. Seven replicate filtration experiments were done with each size class of krill.

Morphometric Analysis

The developmental stages of krill were determined by examining the number of post-lateral spines on the telson under a dissecting microscope (Makarov 1980). Total length (TL) was measured from the tip of the rostrum to the end of the uropods (standard measure 1, Maucline 1980). Telson length (TelL) was measured from mid-bump at the insertion point on the abdomen to the tip. In some experiments wet mass (WM) was measured directly. Krill were removed from experimental tanks, blotted with a kimwipe and weighed on a Mettler AE-240 balance. In 7 experiments with the large size krill, individuals were removed from the experimental tanks and placed in 0.2 μm-filtered seawater until they were measured for TL and WM within 2 hours. In 4 experiments with the large size krill, TL and WM were calculated from relationships between TelL, TL and WM (r^2 = 0.85 and 0.88 respectively) established with a sub-sample taken from the maintenance tank. These TL to TelL and TelL to WM relationships allowed us to estimate TL and WM in experiments where only TelL was measured. For the small

size krill, TL and WM were determined from TelL , and relationships to TL and WM ($r^2 = 0.95$ and 0.92 respectively) were determined with freshly caught individuals.

Chlorophyll and Carbon Analysis

Chl *a* in GF/F or HAWP filters was stored frozen at –70 °C in 20-ml glass scintillation vials prior to extraction in 10 ml 90% acetone for 24 h at –20 °C. The extract was decanted into a test tube, centrifuged in the dark for 5 min at approximately 1500 RPM, and then the fluorescence read on a Turner Designs 10-AU-005 digital fluorometer. Tile samples were treated the same as the filtered samples except they did not require filtration and were placed directly into 60-ml falcon tubes at -70 °C prior to extraction 25 ml of 90 % acetone. Blanks were prepared for both the filters and tiles. Chl *a* was calculated in $\mu g\ l^{-1}$ for comparison to other studies but the comparison of ingestion rates for each feeding mode was made using the total chl *a* per experimental tank ($\mu g\ tank^{-1}$).

To estimate the carbon content of phytoplankton cultures fed to the large krill, a series of 4 sub-samples ranging from 1 to 4 ml were removed from a high concentration stock culture and filtered onto 13-mm pre-combusted (500 °C, 1 h) A/E filters. For experiments with the small krill, determinations of the carbon in the phytoplankton cultures were made for each of the 7 experiments with 4 sub-samples ranging from 5 to 250 ml filtered onto 25 mm pre-combusted GF/F filters. The samples were subsequently dried for approximately 4 hours before being placed in

pre-combusted (450 °C, 24 h) aluminum sleeves and plates. Samples were stored in a drying oven at 60 °C prior to elemental analysis for organic carbon and nitrogen with a Control Equipment Corporation CEC 440HA automated organic elemental analyzer (Dumas combustion method) at the University of California Marine Science Institute Analytical Laboratory. Carbon to chl *a* ratios were used to convert chl *a* units to carbon.

Ingestion Rate Calculations

Phytoplankton growth rates and krill grazing rates were calculated (see Chapter 2) according to the equations of Frost (1972) modified such that if the percent reduction in the phytoplankton remained approximately 30% or less, then the initial phytoplankton concentration was used to calculate ingestion rates (Marin et al. 1986). In 41 of 57 experimental containers the chl *a* reduction was greater than 30%. For these experiments, the chl *a* concentration at the mid-point of the experiment was used to yield a conservative estimate of ingestion rate. An exponential curve was fit to the initial and final chl *a* and the mid-point concentration was determined. The initial concentration of chl *a* used for each filtration experiment was the average of replicates and for comparison to scraping experiments, the initial chl *a* concentration was converted to total chl *a* ($\mu g\ tank^{-1}$) by multiplying by the experimental volume. For scraping experiments total amount of chl *a* per experimental tank (the sum of chl *a* on replicate pairs of tiles) was measured.

The phytoplankton growth coefficient (k) was calculated from controls with no krill and experimental phytoplankton loss coefficient (b) was calculated from the experimental tanks. The grazing coefficient (g, h^{-1}) was calculated using k and b. The clearance rate for filtration experiments (ml gWM^{-1} h^{-1}) was calculated by multiplying g by the ratio of the experimental volume (ml) and the wet mass (g) of the krill. For scraping experiments the clearance rate (cm^2 gWM^{-1} h^{-1}) was obtained by multiplying g by the ratio of surface area of the experimental algal tiles (cm^2) and wet mass. The ingestion rate (μg gWM^{-1} h^{-1}) of chl *a* was calculated by multiplying the clearance rate by the chl *a* concentration (filtration, μg l^{-1}) or density (scraping, μg cm^{-2}).

Functional Response Determination

Functional response curves were fit to the ingestion rate data and the 99% confidence intervals of the best fit line were computed with JMP (SAS Institute, 1999). The best non-linear fit was determined by least-squares. We selected 99% over 95% confidence intervals for the best fit lines because they are wider and constitute a more conservative estimate.

Daily Ration Calculation

Daily ration is the carbon ingested per day expressed as a percent of krill body carbon. Average krill body carbon was calculated from the average wet mass

of the krill in the experiment and the relationship between wet mass and carbon content derived by Quetin and Ross (unpublished data) as reported by Elias (1990)

(1) $C = -113.185 + 92.884 * WM$

where C is carbon (μg) and WM is wet mass (mg) ($r^2 = 0.98$).

RESULTS

Developmental Stage and Total Length

Krill were larger, predominantly late juvenile to sub-adult (large krill) in summer of 2001 experiments, and smaller, predominantly furcilia VI to juvenile (small krill), in spring of 2002 experiments. The relationships between TelL and TL were linear while WM increased exponentially with TelL (Table 3). The TL of large krill ranged from 15 to 29 mm and of small krill ranged from 7 to 19 mm. There was very little overlap in size between the two groups of krill (Figure 1).

Krill Feeding

Krill were fed a range of chl *a* concentrations at temperatures at or near winter values (Table 2). For comparison between the two feeding modes we opted to use the total μg of chl *a* per tank (Table 2). The C:chl *a* ratio for cultures used in experiments with larger krill was 41.5. For smaller krill the value was 39.9, except for two filtration experiments done using older cultures with a C:chl *a* ratio of 116.

Krill in the filtration experiments were observed to feed by compressing the feeding basket in a rhythmic fashion. Those in scraping experiments were observed to swim along the tile surface opening and closing their feeding baskets to scrape phytoplankton from the surface. Occasionally individuals left the surface to feed by filtration before returning to the surface to resume scraping. In some cases the amount of phytoplankton on the surfaces was visibly reduced in 15 min. When small krill were given initial chl *a* >3.5 μg $tank^{-1}$ in scraping experiments, they

displayed evidence of food bolus formation and rejection that was not present with initial chl *a* <3.5 μg tank^{-1}. When feeding by filtration, bolus formation occurred at both high (113 μg tank^{-1}) and low (4.5 μg tank^{-1}) initial chl *a* values. Bolus formation data was not recorded for large krill filtration experiments, but when feeding by scraping bolus formation was noted in experiments with initial chl *a* >16.8 μg tank^{-1}.

We converted our mass-specific clearance rates from chl *a* to carbon units for comparison to previous studies. Mass-specific clearance rates for large krill feeding by filtration were above those for small krill though the initial carbon concentration reached a higher maximum for large krill experiments (Table 4). Small krill exhibited higher clearance rates for scraping over a similar range of initial carbon concentration (Table 4).

Mass-specific ingestion rates for large and small krill feeding by filtration approached similar maximum values over similar amounts of initial total chl *a* available per tank (Figure 2a, 2b). The ingestion rates were plotted against total chl *a* per tank because, although the distribution of the phytoplankton was more condensed in the scraping experiments, the total amount overlapped in both the scraping and filtration experiments in the low range. Large krill feeding by scraping did not reach a maximum ingestion rate but reached a maximum ingestion rate when feeding by filtration (Figure 2a). Large krill ingestion rates at lower initial chl *a* where not significantly different ($\alpha = 0.01$) when feeding by filtration and scraping (Figure 3a). In contrast, small krill reached a maximum ingestion rate for feeding

by scraping that was comparable to the maximum ingestion rate for feeding by filtration (Figure 2b). The small krill fed at significantly higher rates ($\alpha = 0.01$) by scraping at low initial chl *a* values than by filtration (Figure 3b).

Functional Response

When the feeding mode was filtration, both large and small krill exhibited a Type II functional response (Figure 2a, 2b), with ingestion increasing non-linearly with increasing chl *a*. However, when feeding by scraping the functional response appeared to be Type III, indicating that the increase in ingestion with increasing chl *a* for scraping occurred at higher chl *a* than filtration. The effect was greater for larger krill (Figure 2a) than for small krill (Figure 2b).

Daily Ration

We converted the ingestion rates of krill feeding by scraping into daily ration in order to compare their daily ration to estimates of daily carbon required for similar sized krill at comparable temperatures (Table 4). Both large and small krill exhibited increasing daily ration with increasing food availability (Figure 4). At low amounts of chl *a* (0 to 40 $\mu g\ tank^{-1}$) large krill reached a similar daily ration for both feeding modes (Figure 4 a). In contrast, small krill reached a higher daily ration in scraping experiments (Figure 4b).

DISCUSSION

Krill Developmental Stage and Total Length

Krill from the two sets of feeding experiments were in different stages of development. The large and small groupings for these krill generally correspond to phases in the krill lifecycle that inhabit different winter habitats. Since the early 1980's researchers have reported larval and juvenile krill feeding on the under-ice surface during winter months when water column *chl a* is minimal (Guzman 1983, Quetin et al. 1988, Marschall 1988, Stretch et al. 1988, Daly 1990, Daly 2004, Quetin et al. 1994, Frazer, 1996, Frazer et al., 1997a 2002, Ross et al. 2004). Yet, larger krill appear to move inshore during fall and winter, (Siegel 1988, Lascara et al. 1999) perhaps to graze on sea-bed detritus in shallow waters (Kawaguchi et al. 1986) as supported by observations of krill near the sea floor (Gutt & Siegel, 1994). Adult krill are rarely observed feeding under ice during winter (summarized by Quetin et al. 1996).

The physiological ability to withstand long-term starvation may enable adult krill to avoid the higher predation risk associated with close proximity to the sea ice surface (Quetin et al. 1996). Qualitative modeling of krill survival strategies in open water predicts that if predation risk is size-dependent, small krill may feed at the surface at times when larger krill migrate vertically (Alonzo & Mangel 2001) leading to reduced daily ingestion for larger krill. Similar trade-offs between predation risk and feeding may apply to large krill at the sea-ice surface in winter (Quetin & Ross 1991, Quetin et al. 1994, Quetin et al. 1996).

This spatial segregation represents a strategy that reduces intraspecific competition for food between larvae and adults (Siegel 1988, Smetacek et al. 1990). Given the distinct size difference between the two experimental groups of krill and behavior differences observed between krill in their first winter compared to the rest of the population, we suggest that these groups represent size classes of krill that may use different feeding modes as over-wintering strategies.

Krill Feeding

Several studies have reported ingestion rates for krill feeding under temperature conditions more representative of late summer and fall than winter (Table 4). The lack of data for krill fed at winter temperatures makes direct comparisons to other studies problematic. Our krill were fed at average temperatures ranging between -1.9 and -1.1 °C with cumulative average temperatures of -1.5 °C for the two sets of filtration experiments and -1.8 °C and -1.7 °C for the two sets of scraping experiments. The clearance and ingestion rates reported for similar sized krill are for temperatures ranging from -1.5 to 0 °C. Higher clearance rates may result from higher experimental temperatures, given that ectotherm feeding rates generally increase with temperature (Atkinson 1994). Another factor making comparisons complex is that clearance rates are higher at lower food concentrations (Frost 1972).

We compared our clearance rates for filtration experiments to results from other studies with krill and conditions that were as similar to those in our

experiments as was possible (Table 4). Some discrepancies in size range of krill grouped in a particular stage exist in the literature. In order to alleviate confusion in the size groupings of our krill we report the stages or size for comparison with each study. Our maximum clearance rates for small krill (furcilia 5 to juvenile) feeding by filtration were similar to those measured by for furcilia V, but only 33% of furcilia VI larvae fed the diatom *Thalassiossira sp.* at -1.5 °C in laboratory incubations (Ross & Quetin unpublished data). The maximum clearance rate estimated by gut fluorescence for furcilia (8mm) feeding in situ at winter temperatures but measured at -0.5 °C (Daly 1990) were 6 times higher than the maximum reached by our small krill (furcilia 5 to juvenile) feeding by filtration. The clearance rates for small krill (furcilia 5 to juvenile) in this study were similar to those for furcilia III incubated at 0 °C (Table 4) over a lower range of carbon concentrations (Meyer et al. (2002). For furcilia II fed at 0 °C over a similar range of carbon concentration, maximum clearance rates were lower than ours (Meyer et al. 2003). Maximum clearance rates, adjusted to -1 °C, for "juvenile" krill (28-38 mm) incubated in natural and enriched sea water (Atkinson et al. 2002) were only 4% of that obtained for our large krill (juvenile to sub-adult, 15 – 29mm) feeding by filtration. Our clearance rates for small krill fell within the range reported in other studies however, our clearance rates for large krill were much higher than those reported in the only study with conditions and krill of a size overlapping our large krill.

All of these studies had a range of carbon concentrations that were reasonably similar to ours (Table 4). Ingestion rates (Figure 2) for krill feeding at winter temperatures indicate that they are able to feed at rates comparable to late summer and fall rates if food concentrations are higher than those typically found in the winter water column. When considering low food concentration relevant to the winter water column and sea ice conditions, the larger krill had similar ingestion rates for feeding by scraping and filtration (Figure 2a). In contrast, ingestion rates for the small krill were higher for feeding by scraping (Figure 2b), indicating they may be better suited to feeding on sea ice surfaces at low food availability than their larger counterparts.

Functional Response

Analysis of the data from large and small krill feeding by filtration and scraping indicated that filtration follows a Type II functional response while feeding by scraping follows a Type III functional response (Figure 2). Choice of a non-linear modified Gompertz equation (1825) fit to the large krill scraping data produced an improved r^2 (0.95 vs. 0.88) but not for small krill data (0.78 vs. 76). Residuals from linear regression of the data are not evenly distributed which indicates a linear fit may not be the best fit regardless of r^2 values. For example, residuals for a linear fit to data for both size groups suggest a linear fit systematically underestimates ingestion at low and high initial chl *a* but overestimates ingestion when initial chl *a* is in the midrange. Type III functional

responses may not be fit to water-column ingestion data for lack of a satiation point (Price et al. 1988). *Euphausia pacifica* exhibited Type II and Type III functional responses for feeding on diatoms and copepods, respectively (Ohman 1984). For *E. Pacifica* the comparison was between two prey types and in our experiments with *E. Superba* the comparison was between 'habitat' types containing the same prey.

Zooplankton display different single resource functional responses. This is often attributed to reasons such as the predator's ability to perceive and capture particular prey (Green 1986, De Mott & Watson 1991), variability in handling and assimilation time, or differences in nutritional content (Fenchel 1980, Jonsson 1986). Type II functional responses are most often reported (Jeschke et al. 2002). However, failure to detect Type III responses could result from declining precision of experimental techniques at low food levels (Sarnelle 2003), and thus Type III responses may be more common than thought.

Many explanations have been given for a Type III functional response, including development of a search image (Tinbergen 1960) and prey switching (Begon et al. 1990). Development of a search image and prey switching are relevant to predators that feed in a raptorial style and must learn to visually distinguish prey types. Larval and juvenile krill in fall did not feed in this manner and engaged in unselective feeding across a wide range of prey size and motility (Meyer et al. 2002) but adults were found to feed primarily on copepods (Atkinson et al. 2002). Since the krill in our study were offered the same prey type for both feeding modes and were fed in the dark, it might be reasonable to assume that the

learning behavior is related to feeding mode rather than to a new food type. However, in the time just prior to the feeding experiments, the large krill were observed to graze phytoplankton that grew on the surface of holding tanks and the small krill were observed feeding on the under side of the sea ice during collection by divers. These observations eliminate consideration of surface scraping as a 'new' behavior to the krill used in these experiments. Reduction in feeding effort at low prey density is another explanation for Type III functional response (Ohman 1984, Sarnelle 2003) and agrees with optimal foraging theory (Lam & Frost 1976, Lehman 1976). If this were the case in our feeding experiments, we would expect to see the reduction in both filtration and scraping incubation if the efficiency of food capture with concentration varied similarly for both feeding modes.

Results from this study (Figure 2a, 2b) suggest that krill feeding by scraping showed a more gradual increase in ingestion rate with increasing chl *a* which was not evident when krill fed by filtration. Although both size groups of krill appeared to reach similar maximum ingestion rates with both feeding modes, larger krill feed less effectively than smaller krill when scraping surfaces at lower chl *a* levels. The contrast of the results may relate to the size difference in the krill groups used. Water samples taken mid-experiment during the large krill scraping experiments show that the amount of chl *a* kicked up into the 'water column' during surface scraping increases logarithmically with the amount of chl *a* offered initially (data not shown). The process of feeding by scraping may be a combination of loosening the algae by scraping followed by compression of the feeding basket to filter the

cells. Filtration experiments suggest that large krill began to reach maximum ingestion rates when chl *a* concentration in the water was ~ 6 μg l^{-1}. Yet, *chl a* concentration in the water at the mid-point of scraping experiments never reached more than 1 μg l^{-1} (data not shown) when initial chl *a* was as high as 32 μg. Large krill may need higher concentrations of phytoplankton kicked up into the 'water column' to feed effectively in the 'water column' when they leave the surface and thus are less efficient feeders at lower initial surface chl *a*. Marschall (1988) postulated krill could feed on ice algal in two modes, scraping the surface and filtering algae released by ablating ice or brine discharge. This may be analogous to feeding in the field where, in groups of krill scraping the ice surface, individuals periodically leave the surface and filter by compression (Langdon Quetin & Dan Martin personal communication). The assumption is that that they would not engage in this behavior if no food were in the water near the ice surface.

Another factor affecting ingestion rates may be a difference in the adherence algae to the tile surface. Two possible differences are the nature of the culture, one a diatom monoculture and the other cultured from a water sample collected in the vicinity of Palmer Station, and the length of time the culture on the tiles was grown. The coexistence of different species in biofilms may affect attachment strengths and the biofilm matrix may stabilize smaller cells in the mucilage (Becker 1998). Biofilms formed from natural seawater are colonized by bacteria that dominate the community for the first 3 d of development, after which phototrophic alga become dominant (Mueller et al. 2006). The minimum growth time for tiles in this study

was 3 d which should enable establishment of an algal dominated community. Bacteria and diatoms settle on a variety of surfaces immersed in natural seawater after 3 h but improve their attachment strength considerably after 2 to 5 d depending on the substrate (Becker 1998). Tiles with lower chl *a* were grown for a shorter length of time and may not have had time to develop a stable algal biolayer. In this case ingestion rates would possibly be increased when krill feed by scraping tiles grown for d (ie. lower chl *a*) and decreased when krill feed on tiles grown for w (ie. higher chl *a*). This was not detectable in the data.

Phytoplankton grown on a tile surface and mixed in the 'water-column' represent heterogeneous and homogeneous spatial distribution of the food source, respectively. The effect of spatial distribution of prey on ingestion rates has rarely been studied. Fecal pellet production of copepods fed equal amounts diatoms was slightly higher in homogenous treatments than when the food source was confined to a thin-layer (Bochdansky & Bollens 2004). In contrast, fecal production rates were the same in homogeneous and thin-layer treatments (Tiselius 1992). The spatial scales of the two sets of experiments were different and thus it seems the effect of spatial distribution on ingestion rates remains equivocal. Our experiments showed reverse trends for the two size classes of krill when similar amounts of food were offered in either a spatially heterogeneous or homogeneous manner. Smaller krill had higher ingestion rates when the food source began confined to the tile surface than when the food source was mixed throughout the 'water column'.

Larger krill had higher ingestion rates when the food was homogeneously mixed throughout the 'water column'.

Daily Ration

Our daily rations agreed well with those obtained in feeding incubations with furcilia II at similar maximum carbon concentration and measured at 0 °C (Meyer et al. 2003). Three studies had maximum carbon concentrations roughly half of that offered to our small krill. For purposes of comparison we used the daily ration for the food concentration in our study closest to those studies, 9 % body C d^{-1} at 228 μgC l^{-1} for scraping and 13 % body C d^{-1} at 258 μgC l^{-1} for filtration. The daily ration for small krill in this study feeding by scraping and filtration were 20% and 29% of the maximum ration measured by gut evacuation and adjusted to -1 °C for furcilia III to V krill (Pakhomov et al. 2004), 32% and 46% that for furcilia III incubated at 0 °C (Meyer et al. 2002) but were nearly 5 and 6 times higher than that estimated by gut fluorescence at -0.5 °C for krill collected under ice (Daly 1990). This was surprising given the lower temperature in our experiments and may indicate our estimates are not conservative and in situ rates may depend on the condition of the ice surface.

Daily ration for our large krill feeding by scraping (4.5 % body C d^{-1} at 278 μgC l^{-1}) and filtration (23 % body C d^{-1} at 223 μgC l^{-1}) were 6 and 29 times higher than those reported for juvenile krill fed a maximum carbon concentration of ~300 μgC l^{-1} and corrected to -1 °C (Atkinson et al. 2002). Their juvenile krill (28 to 38

mm) were bigger than our large krill (15-29 mm) and may have adopted a compromise strategy of lowered ingestion and metabolism at the onset of winter. Freshly caught winter krill (24-28 mm) had carbon egestion rates equivalent to daily rations exceeding 15% (Huntley et al. 1994), which falls in the range of daily ration found for large krill in this study. One data point was high (84%) and corresponded to an experiment in which the C:chl *a* of the food source was significantly higher (116 vs. 40) than other experiments.

Previous experiments, with furcilia IV-VI and some juveniles, indicate a 10-mg krill feeding at winter temperatures (-1.5 °C) requires a standard daily ration of 1.34% body C d^{-1} when feeding on primarily lipid and 1.80% body C d^{-1} when feeding primarily on protein (Frazer et al. 2002) to meet metabolic needs. Respiration loss, adjusted to -1°C, for freshly caught juvenile krill (28 to 33 mm) was near 1% body C d^{-1} (Atkinson et al. 2002). These values represent the minimum daily carbon ingestion krill require to maintain basic metabolic functions. We compared our daily ration results to these minimum daily carbon requirements for each size class of krill and for each feeding mode. Our results indicate that large krill feeding by scraping may not feed efficiently enough to meet their standard winter carbon ration until chl *a* reaches 7 μg (2.3 μg l^{-1} eq.) but may be able to do so at 3.5 μg (0.18 μg l^{-1} eq.) feeding by filtration (Figure 5a). Small krill may be able to meet the standard winter carbon ration when chl *a* is 2.8 μg (1.0 μg l^{-1} eq.) when feeding by scraping but do not begin to meet their metabolic needs until 4.5 μg (0.5 μg l^{-1} eq.) when feeding by filtration (Figure 5b).

Estimates of Ingestion Rates for Modeling

One of the key parameters in assessing larval krill winter survival is an accurate estimate of ingestion rates both for ingestion by filtration and grazing on sea ice biota. Measurements of larval ingestion rates by filtration have been made in previous studies (Table 4) but no measurements of ice or surface grazing have been made prior to this study. With measured estimates lacking, larval ingestion rates for ice grazing used in bioenergetic models may have underestimated total winter ingestion. For their model, Hofmann and Lascara (2000) estimated ingestion by ice grazing at time t as

$$(2) \qquad I^{ig} = y\, F^{ig}\, SI_{(t)}$$

where y is a constant representing alteration between area-intensive feeding and long-distance foraging movements (0.9 for krill <12 mm and 0.75 for krill >12 mm), F^{ig} is the ice grazing filtration rate ($m^3\ d^{-1}$) which is assumed to be 5% of the compression filtration rate, and SI(t) is the time-dependent sea ice algae concentration (mg C m^{-3}). The compression filtration rate ($m^3\ d^{-1}$) was determined by the equation

$$(3) \qquad F^{cf} = 0.0085\ DW^{0.825}$$

where DW is the dry weight in mg for krill less than 26 mg DW (Hofmann & Lascara 2000). According to the authors the definition of F^{ig} results in ingestion rates for ice grazing when sea ice algae is maximum that are similar to ingestion rates for compression filtration when phytoplankton concentrations are average (Hofmann & Lascara 2000).

A comparison between ice grazing ingestion rates as specified in the Hofmann and Lascara (2000) model and the model fit to scraping ingestion rates obtained in this study reveals that the Hofmann and Lascara (2000) model may underestimate ingestion. We used the average dry weight for larval krill collected during the winter of 2001 to calculate F^{cf} using equation 9. From this I^{ig} was estimated over a range of sea ice algae chl *a* concentrations ($\mu g\ l^{-1}$) and ingestion rates for both their model and our model were normalized to wet mass of krill in g. Thus, ingestion rates are in μg chl *a* $DM^{-1}\ h^{-1}$. Our model fit to scraping ingestion rates measured at winter temperatures indicates larval krill ingestion rates for feeding by scraping the sea ice biota may be 1.5 (at very low chl *a* concentration) to 3 times that assumed in the Hofmann and Lascara (2000) model (Figure 6).

Simulated growth of larval and sub-adult krill based on this model was comparable to observed growth only if ingestion of sea ice biota was included and winter respiration rates were reduced. In contrast to the latter assumption, Meyer at al. (2002) found no reduction in measured oxygen uptake rate or in the digestive enzyme citrate synthase for furcilia III krill between the summer and fall. High clearance rates from feeding experiments showed furcilia III larvae were capable of

exploiting high food concentrations when available (Meyer et al. 2002). Both results indicate larval krill do not reduce metabolic rates at the onset on winter and continue to feed on alternative food sources such as the sea ice algae, heterotrophic organisms or detritus. Results from our scraping experiments suggest larval krill may be able to meet metabolic demands feeding on sea ice biota at concentrations encountered in the field, thus highlighting the importance sea ice biota as a food source for larval krill during winter.

CONCLUSIONS

This study represents the first comparison of quantitative clearance and ingestion rates, daily ration, and the functional response for krill feeding by two different modes, surface scraping and 'water column' filtration. We found a Type III functional response for ingestion by the surface scraping feeding mode that was pronounced for large krill, resulting in lower ingestion rates and daily ration at low amounts of initial food offered. Compared to 'water column' filtration, large krill required 2 times more initial food to meet their basic metabolic functions when feeding by surface scraping, suggesting large krill are more efficient at feeding in the water column at lower food availability. In contrast, small krill had higher ingestion rates and daily ration at low initial amounts when feeding by surface scraping. Small krill required 1.6 times the amount of initial food to meet their basic metabolic needs when feeding by water column filtration, suggesting they are better able to feed by surface scraping when food is scarce. Ingestion by sea ice surface scraping is likely higher than previously thought and estimates of winter ingestion by small krill used to model winter growth must account for this. Small krill may be able to meet their metabolic needs feeding by scraping sea ice surfaces when sea ice is available and not necessarily need to reduce metabolic rates during winter. Results from this study support the idea that smaller krill have fundamentally different over-wintering strategy than larger krill.

Field observations support the idea that size of krill is a factor in under-ice krill distribution during winter. Divers often see larval and early juvenile krill

feeding on the underside of sea ice with low chl *a* concentration during winter, exemplifying their need to feed regardless of predation risk. In contrast, late juvenile and sub-adult krill are found in the water column during winter and do not appear to feed on the sea ice surface until spring (O'Brien, 1987) when algal concentrations in the sea ice are high. These observations support the idea that it is energetically favorable for the smaller stages of krill to feed on sea ice surfaces but is not necessarily so for larger krill who appear to use over-wintering strategies such as lipid utilization (Torres et al. 1994, Hagen et al. 1996), body shrinkage (Ikeda & Dixon 1982), reduced metabolism (Quetin & Ross 1991) and carnivory (Torres et al. 1994). Krill that are mature enough to utilize these strategies may benefit from avoiding visual predators near to the sea-ice surface to water interface, such as seals and penguins, some of which are reported to prey on krill as small as 20 mm (Berrow et al. 1999).

REFERENCES

Aarest AV, Torres JJ (1989) Cold resistance and metabolic responses to salinityvariations in the amphipod *Eusirus antarcticus* and the krill *Euphausiasuperba.* Polar Biol 9:491-497

Alonzo SH & Mangel M (2001) Survival strategies and growth of krill: avoidingpredators in space ad time. Mar Ecol Prog Ser 209:203-217.

Atkinson A, Meyer B, Stübing D, Hagen W, Schmidt K, Bathman UV (2002) Feeding and energy budgets of Antarctic krill *Euphausia superba* at the onset of winter-II. Juveniles and adults. Limol and Oceanogr 47(4): 953-966

Atkinson A, Snÿder R (1997) Krill-copepod interactions at South Georgia, Antarctica, I. Omnivory by *Euphausia superba.* Mar Ecol Prog Ser 160: 63-76

Atkinson D (1994) Temperature and organism size—a biological law for ectotherms? Adv Ecol Res 25: 1–58

Becker K (1998) Detachment studies on microfouling in natural biofilms on substrata with different surface tensions. Int Biodeterior Biodegrad 41:93-100

Begon M, Harper JL, Townsend CR (1990) Ecology: individuals, populations, and communities. Blackwell Scientific Publications, Boston, Massachusetts, USA.

Berman, MS, McVey AL, Ettershank G (1989) Age determination of Antarctic krill using fluorescence and image analysis of size. Polar Biol 9(4): 267-271

Berrow DB, Taylor RI, Murray AWA (1999) Influence of sampling protocol on diet determination of gentoo penguins *Pygoscelis papua* and Antarctic fur seals *Arctocephalus gazella.* Polar Biol 22: 156-163

Bochadansky AB, Bollens SM (2004) Relevant scales in zooplankton ecology: distribution, feeding, and reproduction of copepod *Acartia hudsonica* in response to thin layers of the diatom *Skeletonema costatum.* Limnol and Oceanogr 49(3): 625 -636

Croll DA, Tershy BR (1998) Penguins, fur seals, and fishing: prey requirements and potential competition in the South Shetland Islands, Antarctica. Polar Biol 19: 365-374

Daly K (1990) Overwintering development, growth, and feeding of larval *Euphausia superba* in the Antarctic marginal ice zone. Limnol and Oceanogr 35(7): 1564-1576

Daly KL (2004) Overwintering growth and development of larval *Euphausia superba*: an interannual comparison under varying environmental conditions west of the Antarctic Peninsula. Deep-Sea Res Part II 51 (17-19): 2139-2168

Daly KL, Macaulay MC (1991) Influence of physical and biological mesoscale dynamics on the seasonal distribution and behavior of *Euphausia superba* in the marginal ice zone. Mar Ecol Prog Ser 79: 36-66

DeMott WR, Watson MD (1991) Remote detection of algae by copepods—responses to algal size, odors and motility. J. Plankton Res 13:1203–1222

Dewar WK, Bingham R, Iverson R, Nowacek D, St Laurent L, Wiebe P (2006) Does the marine biosphere mix the ocean? J Mar Res 64:541- 561

Elias MC (1990) Effects of photoperiod, phytoplankton level and temperature on the growth, development and survival of larval *Euphausia superba* (Dana). MA thesis, University of California, Santa Barbara, CA

Ettershank G (1984) A new approach to the assessment of longevity in the Antarctic krill *Euphausia superba.* The Biology of The Antarctic Krill *Euphausia superba* . J Crustac Biol 4: 295-305

Fenchel T (1980) Suspension feeding in ciliated protozoa: functional response and particle size selection. Microb Ecol 6:1-11

Frazer TK (1996) Stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) of larval krill, *Euphausia superba*, and two of its potential food sources. J Plankton Res 18(8):1413-1426

Frazer TK, Quetin LB, Ross RM (1997a) Abundance and distribution of larval krill, *Euphausia superba*, associated with annual sea ice in winter. In: Battaglia B, Valencia J, Walton DWH (eds) Antarctic Communities. Cambridge University Press, Cambridge, p 107–111

Frazer TK, Quetin LB, Ross RM (2002) Energetic demands of larval krill, *Euphausia superba*, in winter. J Exp Mar Biol Ecol 277: 157-171

Frost, BW (1972) Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol and Oceanogr 17(6): 805-979

Gentleman W, Leising A, Frost B, Strom S, Murray J (2003) Functional responses for zooplankton feeding on multiple resources: a review of assumptions and biological dynamics. Deep-Sea Res Part II 50: 2847-2875

Green CH (1986) Patterns of prey selection: implications of predator foraging tactics. Am Nat 128:824–839

Guillard RRL, Ryther JH (1962) Studies of marine planktonic diatoms 1: *Cyclotella nana* Hustedt and *Detonula confervacea* (Cleve) Gran. Can J Microbiol 8:229-245

Gutt J, Siegel V (1994) Benthopelagic aggregations of krill (*Euphausia superba*) on the deeper shelf of the Weddell Sea (Antartica). Deep-Sea Res I 41(1):169-178

Guzman O (1983) Distribution and abundance of antarctic krill (*Euphausia superba*) in the Bransfield Strait. In: Schnack, S. B. (ed.), On the Biology of Krill Euphausia superba. Ber Polarforsch 4. Alfred-Wegener-Institute for Polar Research, Bremerhaven, p 169– 190

Hagen W, Van Vleet ES, Kattner G (1996) Seasonal lipid storage as overwintering strategy of Antarctic krill. Mar Ecol Prog Ser 134(1-3):85-89

Hagen, W, Kattner G, Terbrueggen A, Van Vleet ES (2001) Lipid metabolism of the Antarctic krill *Euphausia superba* and its ecological implications. Mar Biol 139(1):95-104

Hamner WM, Hamner PP, Strand SW, Gilmer RW (1983) Behavior of Antarctic krill, *Euphausia superba*: chemoreception, feeding, schooling, and molting. Science 220 (4595):433-435

Hamner WM, Hamner PP, Obst BS (1989) Field observations on the ontogeny of schooling of *Euphausia superba* furciliae and its relationship to ice in Antarctic waters. Limnol and Oceanogr 34(2):451-456

Hewitt RP, Watkins JL, Naganobu M, Tshernyshkov P, Brierley AS, Demer DS, Kasatkina S, Takao Y, Goss C, Malyshko A, Brandon M, Kawaguchi S, Siegel V, Trathan P, Emery JH, Everson I, Miller D (2002) Setting a precautionary catch limit for Antarctic krill, Oceanography 15(3):26–33

Hill HJ, Trathan PN, Croxall JP, Watkins JL (1996) A comparison of Antarctic krill *Euphausia superba* caught in nets and taken by Macaroni penguins *Eudyptes chrysolophus*: evidence for selection? Mar Ecol Prog Ser 140:1-11

Holling CS (1959a) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Can Entomol 91:293–320

Holling CS (1966) The functional response of invertebrate predators to prey density. Mem Entomol Soc Can 48

Hofmann EE, Lascara CM (2000) Modeling the growth dynamics of Antarctic krill *Euphausia superba.* Mar Ecol Prog Ser 194:219-213

Hopkins TL, Lancraft TM, Torres JJ, Donnelly J (1993) Community structure and trophic ecology of zooplankton in the Scotia Sea marginal ice zone in winter (1988). Deep-Sea Res 40:81-105

Huntley ME, Nordhausen W, Lopez MDG (1994) Elemental composition, metabolic activity and growth of Antarctic krill Euphausia superba during winter. Mar Ecol Prog Ser 107:232–240

Huntley ME, Zhou M (2004) Influence of animals on turbulence in the sea. Mar Ecol Prog Ser 273: 65-79

Ikeda T, Dixon P (1982) Body shrinkage as a possible over-wintering mechanism of the Antarctic krill, *Euphausia superba* (Dana). J Exp Mar Biol Ecol 62(2):143-151

Jeschke JM, Kopp M, Tollrian R (2002) Predator functional responses: discriminating between handling and digesting prey. Ecol Monogr 72:95-112

Jonsson, PR (1986) Particle size selection, feeding rates and growth dynamics of marine planktonic oligotrichous ciliates (*Ciliophora: Oligotrichina*). Mar Ecol Prog Ser 33:265-277

Ju, S-J., Scolardi K, Daly KL, Harvey HR (2004) Understanding the trophic role of the Antarctic ctenophore, *Callianira Antarctica*, using lipid biomarkers. Polar Biol 27:782-792

Kawaguchi K, Ishikawa S, Matsuda O (1986.) The overwintering strategy of Antarctic krill (*Euphausia superba* Dana) under the coastal fast ice off the Ongul Islands in Luetzow- Holm Bay, Antarctica. Proceedings of The Eighth Symposium On Polar Biology, 1985. Mem Natl Inst Polar Res (Japan) (Spec. Iss.) (4):67-85

Kawaguchi S, Nicol S (2007) Learning about Antarctic krill from the fishery. Antarct Sci 19(2):219-230

Kirkwood R, Robertson G (1997) Foraging ecology of female Emperor Penguins in winter. Ecol Monogr 67: 155–17

Kunze E, Dower JF, Beveridge I, Dewey R, Bartlett KP (2006) Science 313:1768-1770

Lam RK, Frost BW (1976) Model of copepod filtering response to changes in size and concentration of food. Limnol and Oceanogr 21:490–500

Lascara, CM, Hofmann EE, Ross RM, Quetin LB (1999) Seasonal variability in the distribution of Antarctic krill, *Euphausia superba*, west of the Antarctic Peninsula. Deep-Sea Res I. 46:951–984

Laws RM (1985) The ecology of the Southern Ocean. Am Sci 73(1):26-40

Lehman JT (1976) The filter-feeder as an optimal forager, and the predicted shapes of feeding curves. Limnol Oceanogr 21:501–516

Ligowski R (2000) Benthic feeding by krill, *Euphausia superba* Dana, in coastal waters off West Antarctica and in Admiralty bay, South Shetland Islands. Polar Biol 23:619-625

Lizotte MP (2001) The contributions of sea ice algae to Antarctic marine primary production. Am Zool 41:57-73

Lowry LF, Testa JW, Calvert W (1988) Notes on winter feeding of crabeater and leopard seals near the Antarctic Peninsula Polar Biol 8:475-478

Makarov R (1980) Larval Development of the Antarctic Euphausiids. BIOMASS Handbook no. 3:6-13

Marin V, Huntley ME, Frost BW (1986) Measuring feeding rates of pelagic hebivores: analysis of experimental design and methods. Mar Biol 93:49-58

Marschall HP (1988) The overwintering strategy of Antarctic krill under the pack-ice of the Weddell sea. Polar Biol 9:129-135

Mauchline J (1980) Measurement of body length of *Euphausia superba* Dana: BIOMASS Handbook, vol. 4, pp. 4–9. SCAR/SCOR

Meyer B, Atkinson A, Blume B, Bathmann UV (2003) Feeding and energy budgets of larval Antarctic krill *Euphausia superba* in summer. Mar Ecol Prog Ser 257:167-177

Meyer B, Saborowski R, Atkinson A, Buchholz F, Bathman UV (2002) Seasonal differences in citrate synthase and digestive enzyme activity in larval and postlarval Antarctic krill, *Euphausia superba*." Mar Biol 141: 855-86

Meyer B, Atkinson A, Stübing D, Hagen W, Oettl B, Bathman UV (2002) Feeding and energy budgets of Antarctic krill *Euphausia superba* at the onset of winter-I. Furcilia III larvae. Limnol Oceanogr 47(4):943-952

Miller DGM, Hampton I (1989) Biology and ecology of the Antarctic krill *Euphausia superba* Dana – a review. Biomass 9:1-166

Morris and Priddle (1984) Observations on the feeding and molting of the Antarctic Krill, *Euphausia superba* Dana, in winter. Br Antarct Surv Bull 65:57–63

Mueller LN, de Brouwer JFC, Almeida JS, Stal LJ, Xavier JB (2006) Analysis of a marine phototrophic biofilm by confocal laser scanning microscopy using the new image quantification software PHLIP. BMC Ecology 6:1-15

Nöthig EM, Bathmann U, Jennings JC, Fahrbach E, Gradinger R, Gordon LI, Makarov R, (1991a) Regional relationships between biological and hydrographical properties in the Weddell Gyre in late austral winter 1989. Mar Chem 35:325-336

O'Brien DP (1987) Direct observations of the behavior of *Euphausia superba* and *Euphausia crystallorophias* (Crustacea: Euphausiacea) under pack ice during the Antarctic spring of 1985. J Crustac Biol 7(3):437-448

Ohman MD (1984) Omnivory by Euphausia pacifica: The role of copepod prey. Mar Ecol Prog Ser 19: 125–131

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

Price HJ, Boyd KR, Boyd CM (1988) Omnivorous feeding behavior of the Antarctic krill *Euphausia superba.*" Mar Biol 97:67-77

Quetin LB, Ross RM (1988) Summary of WinCruise II to the Antarctic Peninsula during June and July 1987. Antarct J US 23:149-151

Quetin LB, Ross RM (1991) Behavioral and physiological characteristics of Antarctica krill, *Euphausia superba.* Am Zool 31:49-63

Quetin LB, Ross RM, Clarke A (1994) Krill energetics: seasonal and environmental aspects of the physiology of Euphausia superba. In: El-Sayed SZ (ed) Southern Oceanecology. Cambridge University Press, Cambridge, pp 165–184

Quetin LB, Ross RM, Frazer TK, Haberman KL (1996) Factors affecting the distribution and abundance of zooplankton, with an emphasis on Antarctic Krill, *Euphausia superba*. In: Ross RM, Hofmann EE, Quetin LB (eds) Foundations for Ecological Research West of the Antarctic Peninsula. American Geophysical Union, Washington D.C.

Quetin LB, Ross RM, Frazer TM, Amsler M, Wyatt-Evens C, Oakes, SA (2003) Growth of larval Antarctica krill in fall and winter west of the Antarctic Peninsula. Mar Biol 143:833-843

Ross RM, Quetin LB (1991) Ecological physiology of larval euphausiids, *Euphausia superba* (Euphausiaceae). Mem Queensl Mus 31:321–333

Ross RM, Quetin LB, Newberger T, Oakes SA (2004) Growth and behavior of larval krill (*Euphausia superba*) under ice in late winter 2001 west of the Antarctic Peninsula. Deep Sea Res II: Spec Top Oceanogr 51(17-19):2169-2184

Sarnelle O (2003) Non-linear effects of an aquatic consumer: causes and consequences. Am Nat 161:478-496

SiegelV (1988) A concept of seasonal variation of krill (Euphausia superba) distribution and abundance west of the Antarctic Peninsula. In: Sahrhage D (ed) Antarctic ocean and resources variability. Springer Verlag, Berlin, Heidelberg, p 219-230

Smetacek V, Scharek R, Nöthig EM (1990) Seasonal and regional variation in the pelagical and its relationship to the lifecycle of krill. In: Kerry KL, Hempel G (eds). Antarctic Ecosystems, Ecological Change and Conservation, Springer-Verlag, Berlin

Solomon ME (1949) The natural control of animal populations" J Anim Ecol: 18 1–45

Stammerjohn SE, Smith RC (1997) Opposing southern ocean climate patterns as revealed by trends in regional sea ice coverage. Clim Chang 37(4):617-639

Stretch JJ, Hamner PP, Hamner WM, Michel WC, Cook J, Sullivan CW (1988) Foraging behavior of Antarctic krill *Euphausia superba* on sea ice microalgae. Mar Ecol Prog Ser 44:131-139

Stuart V (1989) Observations on the feeding of *Euphausia lucens* on natural phytoplankton suspensions in the southern Benguela upwelling region. Cont Shelf Res 9(11):1017-1028

Tarling GA and Johnson ML (2006) Satiation gives krill that sinking feeling. Curr Biol 16: 83–84

Tinbergen L (1960) The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by song birds. Arch Neerl Zool 13:265-343

Tiselius P (1992) Behavior of *Acartia Tonsa* in patchy food environments. Limnol and Oceanogr 37:1640-1651

Torres J J, Aarset AV, Donnelly J, Hopkins TL, Lancraft TM, Ainley DG (1994) Metabolism of Antarctic micronektonic Crustacea as a function of depth occurrance and season. Mar Ecol Prog Ser 113(3):207-219

Torres JJ, Donnelly J, Hopkins T L, Lancraft TM, Aarset AV, Ainley DG (1994) Proximate composition and overwintering strategies of Antarctic micronektonic Crustacea. Mar Ecol Prog Ser 113(3):221-232

Werner I (1997) Grazing of Arctic under-ice amphipods on sea ice algae. Mar Ecol Prog Ser 160:93-99

Table 1. Comparison of winter water column and sea ice chlorophyll concentrations from various studies. Sources in parentheses: water depth and type of sea ice. No Data: -.

Study	Year	Chlorophyll ($\mu g\ l^{-1}$)	
		Sea Water	Sea Ice
Daly (2004)	2001	0.001- 0.05 (0-100m)	0.02-0.48 (surface)
Daly (2004)	2002	0.001-0.18 (0-100m)	0.016-3.14 (surface)
Daly (2004)	2002	-	0.601-50 (1^{st}, 2^{nd} yr)
Quetin et al. (2003)	1991	0.001 (5m)	0.012 (scoop)
Quetin et al. (2003)	1993	0.209 (0-50m)	2.71, 1.09 (soft, hard)
Quetin et al. (2003)	1994	0.068 (20m)	0.103 (surface)
Garrison and Buck (1989)	1987	-	~3 (new)
Garrison and Buck (1989)	1987	-	~5 (core, surface)
Marschall (1988)	1986	>0.02 (0-200m)	0.27-36.2 (core)
Kottmeier and Sullivan (1987)[a]	1985	0.02-0.13 (0-100m)	1.2-30 (not given)
Brightman and Smith (1989)[a]	1987	0.04-0.3 (0-100m)	-
Lizotte and Sullivan (1992)[a]	1987	-	0.8-260 (floe)
Lizotte and Sullivan (1992)[a]	1987	-	1.2-2.4 (new)
Lizotte and Sullivan (1992)[a]	1988	-	0.1-91 (floe)
Lizotte and Sullivan (1992)[a]	1987	-	0.22-18 (new)
Cota et al. (1992)[a]	1988	<0.05-0.33 (0-100m)	-
Nothig et al. (1991a)[a]	1989	<0.01-0.02 (0-100m)	-
Dieckmann et al. (1998)[a]	1989	-	0.4-78 (not given)

[a] summarized in Lizotte (2001)

Table 2. *Euphausia superba.* Summary of feeding experiments: *Euphausia superba* size group, experiment type, experiment volume, mean temperature (temp) range, initial chlorophyll (chl) concentration range, and food type. Endemic phytoplankton (phyto) and *Fragilariopsis curta* (*F. curta*).Values in parentheses: number of experiments.

Size	Experiment		Range		Food Type
	Type	Volume	Temp (°C)	Chl ($\mu g\ tank^{-1}$)	
Large	Filtering (12)	20-l	-1.1 to –1.8	10.2 to 189	endemic phyto
Large	Scraping (16)	2.5-1	-1.7 to –1.8	0.8 to 32	endemic phyto
Small	Filtering (12)	20-1	-1.2 to –1.9	4.5 to 113	*F. curta*
Small	Scraping (17)	2.5-1	-1.3 to –1.9	3.4 to 25	*F. curta*

Table 3. *Euphausia superba.* Total length (TL) to telson length (TelL) and wet mass (WM) to telson length relationships for two size groups of *Euphausia superba* in feeding experiments. Values in parentheses: regression coefficient and number of measurements.

Size Group	Total Length to Telson Length Equation	Wet Mass to Telson Length Equation
Large	TL = 5.328 * TelL + 0.5586 (0.85, 24)	WM = 7E-4 * $TelL^{3.2267}$ (0.88, 24)
Small	TL = 5.7721 * TelL – 3.3597 (0.95, 71)	WM = 4E-4 * $TelL^{3.645}$ (0.92, 30)

Table 4. *Euphausia superba.* Comparison of clearance and daily ration rates for similar stage or size krill in late summer and fall from other studies to winter values from this study. Experimental temperature (temp) and carbon concentration of food source (carbon). No data: -.

Study	Stage or Size	Temp (°C)	Carbon ($\mu g\ l^{-1}$)	Clearance Rate (ml $mgWM^{-1}\ h^{-1}$)	Daily Ration (%bodyC d^{-1})
Ross and Quetin	furcilia II	-1.5	0-200[a]	2.5-19	-
Unpublished	furcilia IV	-1.5	0-360[a]	1.0-4.4	-
	Furcilia VI	-1.5	0-320[a]	0-10	-
Daly	8mm	-0.5	6	20[b] (max)	-
(1990)	8mm	-0.5	259	0.3[b] (min)	-
Atkinson et al.	juvenile	-1[c]	0-300	0-0.45[c]	0-0.8
(2002)	juvenile	-1[c]	0-100	0-0.34[c]	0-0.5
Meyer et al.	furcilia III	0	2.7-4.7	1.0-4.9 [d]	0.4-1.3
(2002)	furcilia III	0	35-216	1.8-3.6 [d]	2-28
Meyer et al.	furcilia I	0	125-440[e]	1.2-2.4 [e]	18-31[e]
(2003)	furcilia II	0	215-440[e]	0.75-1.1[e]	11-16[e]
Pakhomov	calyptosis III	-1	0-200	-	17.6-29.2[f]
(2004)	to furcilia II				
	furcilia III	-1	0-200	-	21.5-44.5[f]
	to furcilia V				
This study					
scraping	small	-1.8	50-492	0.5-4.1[i]	0-16[g]
filtering	small	-1.5	42-1389	0.08-3.3	0.13-84[g]
scraping	large	-1.7	13-525	0-2.3[i]	0-13.1[h]
filtering	large	-1.5	22-406	2.4-12	1.6-35[h]

[a] feeding incubations, *Thalassiosira sp.*, assuming c:chl a ratio of 40

[b] gut fluorescence, autotrophic carbon in water and ice, for 8-mm krill, $WW=1.02 \times 10^{-3}L^{3.49}$, WW(wet weight in mg) and L(length in mm) from Daly (1990)

[c] feeding incubation, natural and enriched sea water, 28-38-mm krill for algae at 1-2°C adjusted to -1°C (Atkinson et al.,2002), DM(dry mass)=0.226WM(wet mass) from Quetin and Ross (2004)

[d] feeding incubation, natural or enriched sea water, C(carbon)=0.357DM (Meyer et al., 2002), DM=0.12WM (Elias, 1990)

[e] feeding incubation, natural sea water, mean carbon, mean clearance rate and daily ration estimated from Meyer et al.(2003) Figure 3, C=0.386DM for FII and C=0.375DM for FI (Meyer et al. 2003), DM=0.14WM (Ross and Quetin, unpublished data)

[f] gut fluorescence, natural sea water

[g] feeding incubations, *Fragilariopsis curta*

[h] feeding incubations, endemic phytoplankton

[i] units are $cm^2\ mgWM^{-1}\ h^{-1}$

Figure 1. Total length frequency for *Euphausia superba* used in grazing experiments in 2001 and 2002. Black bars indicate the 2001 group, predominately late juvenile and sub-adult krill (large krill). Grey bars indicate the 2002 group, dominated by furcilia and juvenile krill (small krill).

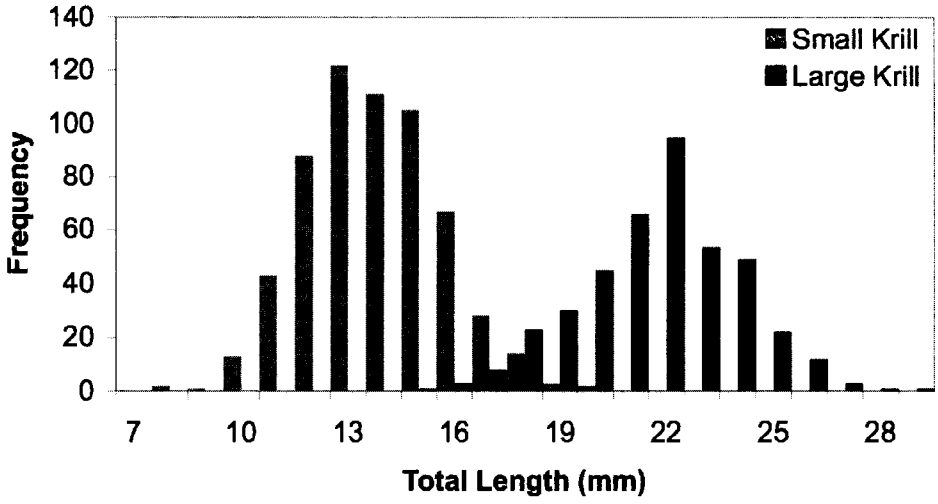
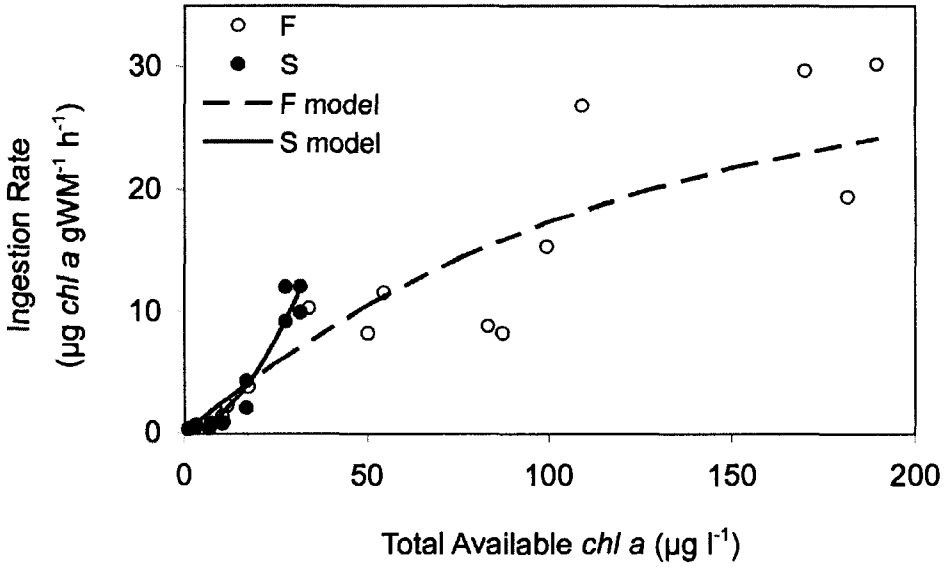

140
120
100
80
60
40
20
0
Frequency
Small Krill
Large Krill
7
10
13
16
19
22
25
28
Total Length (mm)

Figure 2. Ingestion rates for *chl a* ($Ing_{[chl\ a]}$) by *Euphausia superba* grazing on diatoms by surface scraping (S, closed circles) and by water-column filtration (F, open circles) for (a) large krill (late juvenile and sub-adults) and (b) small krill (furcilia and juveniles) plotted as a function of initial absolute *chl a* (μg). Black dashed line is a Type II non-linear fit to the data using Ivlev's Equation (1961): $Ing_{[chl\ a]} = Ing_{max} * (1- e^{-a*[chl\ a]})$. Black Solid line is a Type III non-linear fit to the data using a modified form of the Gompertz curve (1825): $Ing_{[chl\ a]} = [Ing_{min} * (e^{(R * (1-e^{\wedge}(r * [chl\ a]))})]- Ing_{min}$. a) Feeding response of large krill. Maximum ingestion (Ing_{max}) = 30. Parameter a = 0.00862 determined by iteration ($r^2 = 0.77$). Minimum ingestion (Ing_{min}) = 0.4. Parameters R = 4.613 and r = 0.0426 determined by iteration ($r^2 = 0.95$). b) Feeding response of small krill. Maximum ingestion (Ing_{max}) = 26. Parameter a = 0.0109 determined by iteration ($r^2 = 0.77$). Minimum ingestion (Ing_{min}) = 0.92. Parameters R = 2.892 and r = 0.1193 determined by iteration ($r^2 = 0.78$).

a)


F
S
F model
S model
Ingestion Rate
(µg chl a gWM-1 h-1)
30
20
10
0
0
50
100
150
200
Total Available chl a (µg l-1)

b)

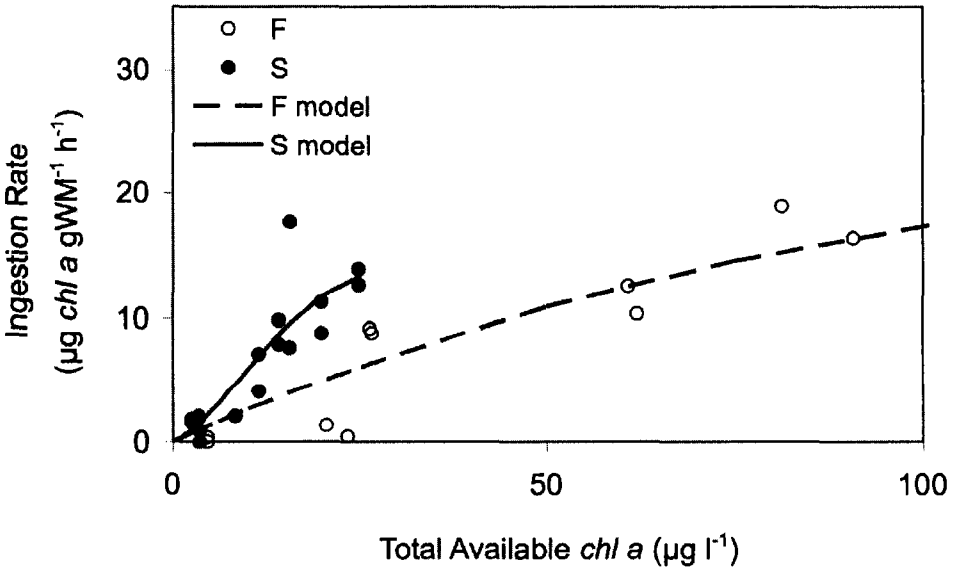
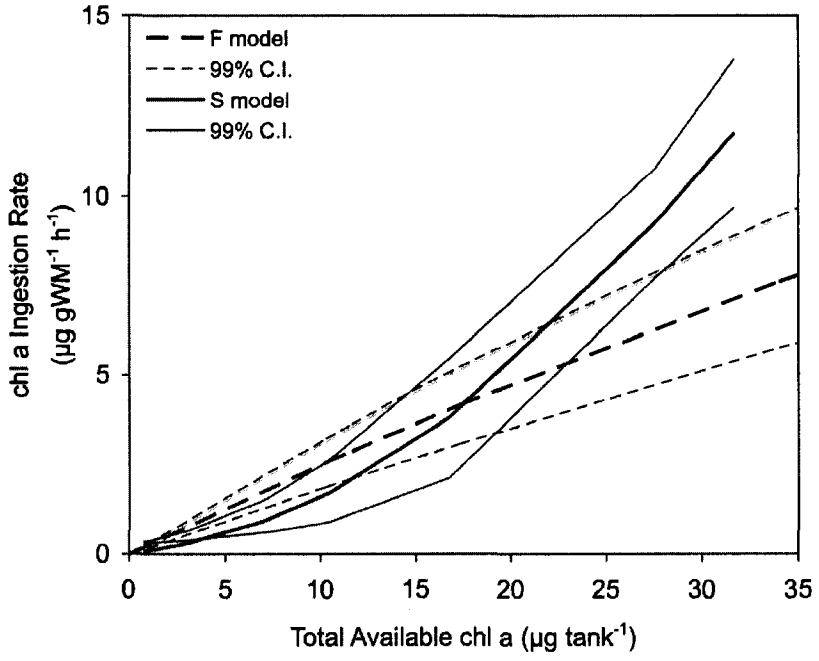

F
S
F model
S model
Ingestion Rate
(µg chl a gWM-1 h-1)
30
20
10
0
0
50
100
Total Available chl a (µg l-1)

Figure 3. 99% confidence bands (C.I.) for parameters of non-linear equations (solid and dashed lines) fit to ingestion rate data presented in Fig. 2 at low initial amounts. Ingestion rate model for *chl a* by *Euphausia superba* grazing on diatoms by water-column filtration (bold dashed line) and by surface scraping (bold black line) and for (a) large krill (late juvenile and sub-adults) and (b) small krill (furcilia and juveniles) plotted as a function of initial *chl a* ($\mu g\ tank^{-1}$). Models are significantly different if one model does not fall within the confidence band of the alternative model.

a)


F model
99% C.I.
S model
99% C.I.
chl a Ingestion Rate
(µg gWM-1 h-1)
Total Available chl a (µg tank-1)
0
5
10
15
20
25
30
35

b)

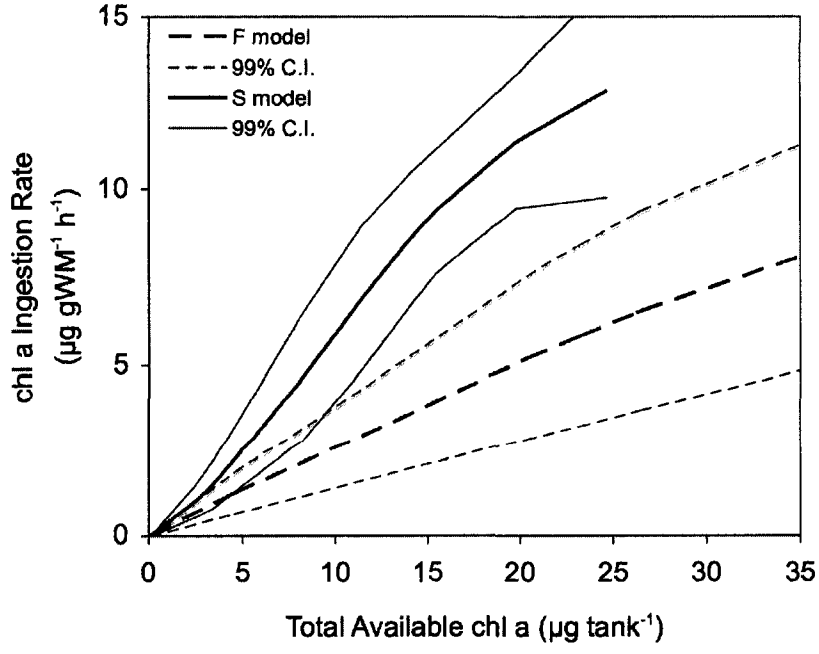
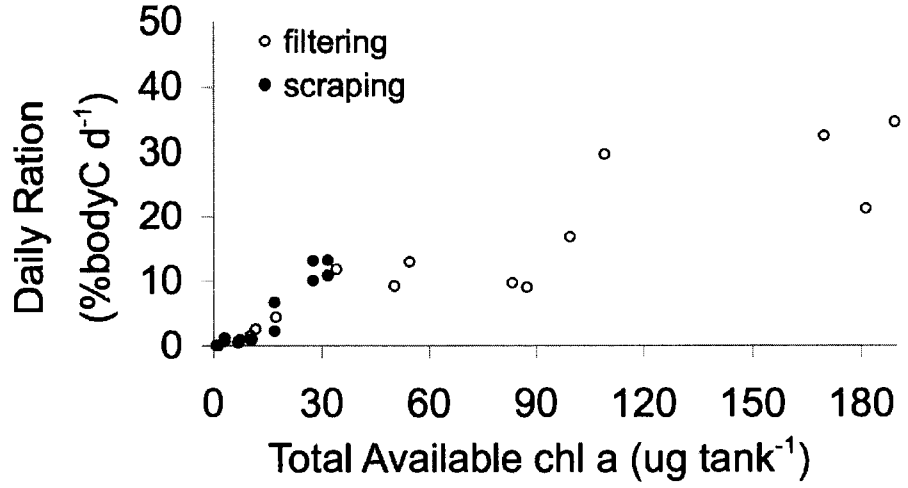

F model
99% C.I.
S model
99% C.I.
chl a Ingestion Rate
(µg gWM-1 h-1)
Total Available chl a (µg tank-1)
0
5
10
15
20
25
30
35

Figure 4. Daily ration (%bodyC d^{-1}) of *Euphausia superba* feeding on diatoms as a function of initial *chl a* (μg $tank^{-1}$). Open circles are water-column filtration experiments and closed circles are surface scraping experiments. a) Large krill (surface n = 16, water n = 12). b) Small krill (surface n = 17, water n = 12).

a)


Daily Ration
(%bodyC d-1)
50
40
30
20
10
0
filtering
scraping
0
30
60
90
120
150
180
Total Available chl a (ug tank-1)

b)

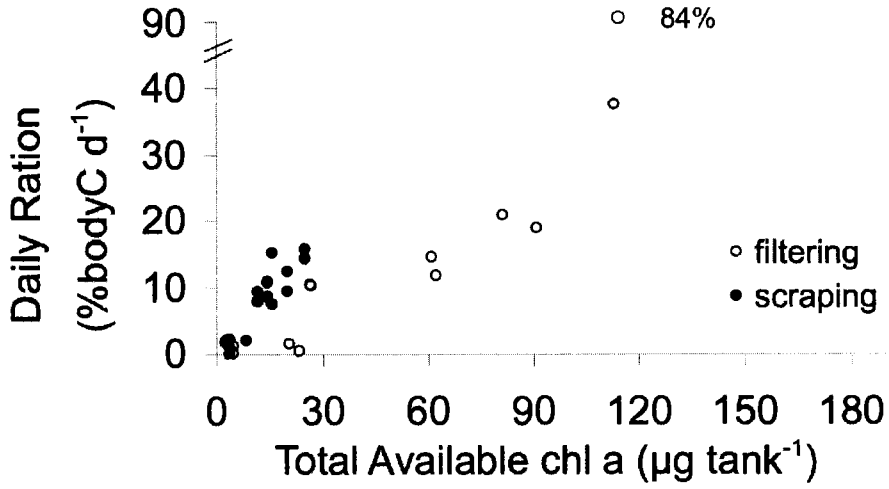
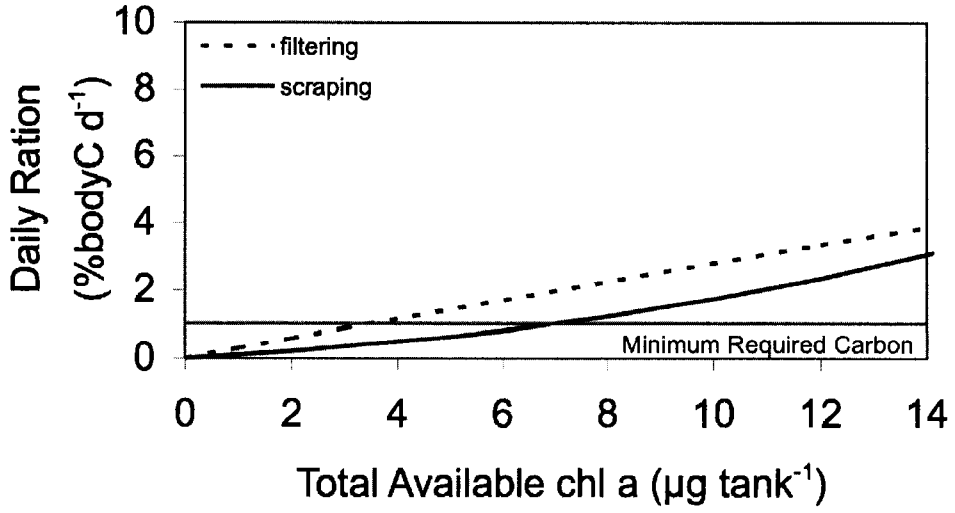

Daily Ration
(%bodyC d-1)
90
40
30
20
10
0
84%
filtering
scraping
0
30
60
90
120
150
180
Total Available chl a (µg tank-1)

Figure 5. Ability of *Euphausia superba* to meet minimum carbon requirements. Krill feeding by the water column filtration (dashed black line) and feeding by surface scraping (solid black line). a) Daily ration (%body C d^{-1}) with *chl a* (μg $tank^{-1}$) for large krill modeled with median value for average krill size in large krill experiments. Estimated carbon requirements of approximately 1% for sub-adult krill (grey line) near winter temperatures (Atkinson et al., 2002). b) Daily ration (%body C d^{-1}) with *chl a* (μg $tank^{-1}$) for small krill modeled with value for average krill size in small krill experiments. The range of standard winter daily ration values for larval krill, 1.34% to 1.80% (grey box), represent the amount of carbon required to maintain basic metabolic functions during winter (Frazer et.al., 2002).

a)


filtering
scraping
Minimum Required Carbon
Daily Ration (%bodyC d-1)
Total Available chl a (µg tank-1)
0
2
4
6
8
10
12
14

b)

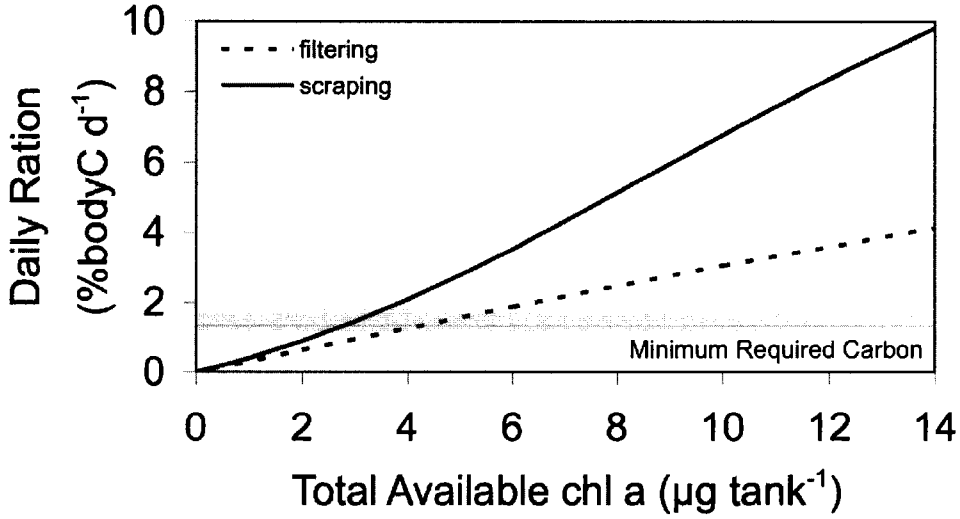
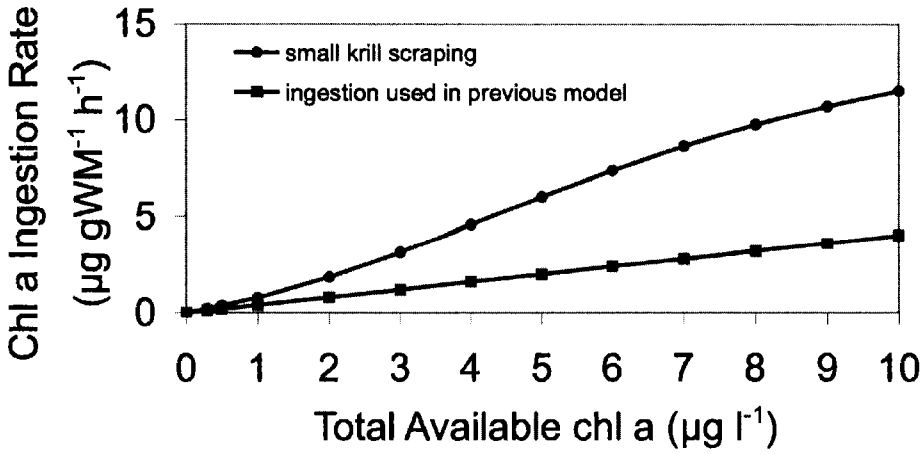

filtering
scraping
Minimum Required Carbon
Daily Ration (%bodyC d-1)
Total Available chl a (µg tank-1)
0
2
4
6
8
10
12
14

Figure 6. Model comparison for larval *Euphausia superba* ingestion rates. Solid circles represent estimate of larval krill ingestion rate based on model fit to data from small krill surface scraping experiments in this study. Solid squares represent estimate of larval krill ingestion rate based on model of Hofmann and Lascara (2000) for larval krill < 12 mm.


Chl a Ingestion Rate
(µg gWM-1 h-1)
15
10
5
0
small krill scraping
ingestion used in previous model
0 1 2 3 4 5 6 7 8 9 10
Total Available chl a (µg l-1)

CHAPTER 2:

GRAZING OF LARVAL AND JUVENILE ANTARCTIC KRILL, *EUPHAUSIA SUPERBA*, ON THE NATURAL COMMUNITY OF SEA ICE BIOTA

ABSTRACT

Grazing experiments were conducted on the RVIB N.B. Palmer during an austral winter cruise along the Western Antarctic Peninsula (September and October 2001) to determine whether feeding in winter by larval and juvenile Antarctic krill (*Euphausia superba*) was selective and to examine the relative importance of autotrophic versus heterotrophic food sources in their diet. Larval and juvenile krill were kept at winter temperatures (-1.1 to -1.8°C) and fed endemic sea ice microorganisms, collected from sea ice or brine pits in order to determine whether clearance rates and ingestion rates on autotrophic and heterotrophic microorganisms were affected by total food availability and/or community composition. Wet mass (WM) specific maximum clearance rates for larval and juvenile krill (6-12mm) were 3.8 ml $mgWM^{-1}\ h^{-1}$, 4.0 ml $mgWM^{-1}\ h^{-1}$, and 4.7 ml $mgWM^{-1}\ h^{-1}$ for total, autotrophic and heterotrophic microorganisms, respectively. Maximum ingestion rates on total, autotrophic and heterotrophic carbon were 166 $\mu gC\ gWM^{-1}\ h^{-1}$, 105 $\mu gC\ gWM^{-1}\ h^{-1}$, and 48 $\mu gC\ gWM^{-1}\ h^{-1}$, respectively. Total and autotrophic carbon ingestion rates increased with increasing carbon concentration until a critical carbon concentration of 45 $\mu g\ l^{-1}$ and 43 $\mu g\ l^{-1}$, respectively, was reached. Heterotrophic carbon ingestion rates were not correlated with carbon concentration. Daily rations calculated for total, autotrophic and heterotrophic carbon were 17%, 11% and 4.1% body C d^{-1}, respectively. Larval and Juvenile krill were usually able to meet their minimum winter daily carbon requirement of 1.34 to 1.80% body C d^{-1} (Frazer et. al., 2002) when total carbon was as low as 12 $\mu g\ l^{-1}$. Daily rations suggest that

during winter larval and juvenile krill ingestion, at comparable food concentrations, is similar to ingestion in fall and spring. This suggests seasonal reduction of metabolism in winter in larval and juvenile krill is a function of temperature or limited food intake rather than a physiological adaptation for winter survival. Krill exhibited selectivity that depended on the availability of food and the sea ice microbial community composition. Krill exhibited a higher degree of selectivity when carbon concentrations were higher. Autotrophic food items were important sources of carbon. Among the autotrophic sources *Phaeocystis sp.* and autotrophic *Gymnodinium sp.* were often dominant and were usually readily consumed. Ingestion of heterotrophic food items was much more variable. In some cases, cells identified as autotrophic *Gymnodinium sp.* were rejected and suggested the presence of undesirable species of autotrophic dinoflagellates may inhibit krill feeding.

INTRODUCTION

The Antarctic krill *Euphausia superba*, henceforth referred to as krill, is an important grazer in the Southern Ocean. Given its substantial biomass and feeding modes, krill are an important food source for higher trophic levels and play an important role in carbon export in the region. Gravid females spawn during the summer, between December and February (Ross and Quetin, 1986) producing larval krill that must continue to feed during the winter in order to survive and develop into juveniles and subadults the following spring. However, during winter phytoplankton concentrations in the water column are usually too low to support krill metabolic requirements (Daly, 1990; Frazer et al., 2002; Meyer et al., 2002). An alternative food source for larval krill is the sea ice microbial community that develops in the annual sea ice (Stretch *et al.*, 1988; Daly, 1990; Smetacek et al., 1990). Larval krill are associated with pack ice (Guzman, 1983; Daly and Macauly, 1988; Marschall, 1988; Daly, 1990; Smetacek, 1990) and larval krill survival and recruitment depend on the presence of sea ice (Siegel and Loeb, 1995; Quetin and Ross, 2003) of appropriate duration to provide sufficient production in the sea ice microbial community (SIMCO) (Quetin et al., 2003, 2007).

As sea ice formation progresses a variety of processes (scavenging of phytoplankton, snow loading and rafting) influence SIMCO structure and hence its suitability as a food source for larval krill. The SIMCO is not always dominated by diatoms, which are high quality food, but may include significant numbers of bacteria, heterotrophic protozoans, and metazoans (Garrison 1991b). Some or all of

these taxonomic groups may constitute an alternative to phytoplankton in the water column as a food source for krill.

At present quantitative estimates of winter clearance and ingestion rates for larval and juvenile krill feeding on these microorganisms are lacking. Feeding on the SIMCO by larval krill in winter is not well documented and it is not clear whether larval and juvenile krill feed selectively within SIMCOs (Daly, 1990). Previous research on feeding selectivity in more mature stages of krill has centered on phytoplankton cell size (Quetin and Ross 1985, Haberman et al. 2003a,b) or food quality (Stuart 1989, Haberman et al. 2003a,b) and suggests preferences may be expected in younger krill. Additionally, studies have been conducted predominantly in the summer and fall seasons (Quetin and Ross 1985, Price 1988, Atkinson and Snÿder 1997, Atkinson et al. 2002, Meyer et al. 2002, Haberman et al. 2003a,b) and focus on organisms found in the pelagic community (Quetin and Ross 1985, Price 1988, Atkinson and Snÿder 1997, Haberman et al. 2003a,b). Adult krill feed on copepods (Price 1988, Atkinson and Snÿder 1997, Atkinson et al. 2002) and have similar clearance rates on phytoplankton and copepods in feeding incubations (Price 1988). During summer, juvenile krill at South Georgia were found to have the highest median clearance rates on copepods followed by protozoans and algae (Atkinson and Snÿder 1997). Conversely, juvenile krill collected from the southwest Lazarev Sea in the autumn fed equally among groups of algae, protozoans and copepods offered in incubations with organisms contained in natural seawater, seawater enriched with SIMCOs from multiyear sea ice and copepods (Atkinson et

al. 2002). Larval krill collected during the same study showed no feeding preference based on cell type or size (Meyer et al. 2002).

Food preferences may be explained in terms of optimal foraging theory, by which a consumer engages in feeding behavior that will maximize net nutritional gain (De Mott 1989). Various copepods display preferences based on food quality by selecting more nutritional cells within mixtures (Cowles et al. 1988) and avoiding low quality items such as dead phytoplankton and digestion resistant species (Donaghay and Small 1979; De Mott 1989), polystyrene spheres (De Mott 1989), and toxic cells (Huntley et al. 1986). Copepods, in accordance with optimal foraging theory, exhibited stronger discrimination against larger low-quality algae at high food concentrations and preferred to ingest smaller high-quality algae (DeMott 1989). However, copepods ingested the larger, low-quality cells when offered alone or in mixtures at low overall food concentrations (De Mott 1989). It is possible young krill would show similar preferences feeding on the SIMCO in winter.

Feeding experiments with larval krill feeding on the SIMCO were conducted on board the RVIB N.B. Palmer during a sea ice cruise along the Western Antarctic Peninsula, during September and October of 2001. This study compares the clearance rates and ingestion rates of larval krill fed sea ice microbes, including both autotrophic and heterotrophic organisms. Our hypotheses were that feeding selectivity by larval krill on sea ice microbes is dependent on community composition, including the proportion or composition of the heterotrophic component of the community, and that the degree of selectivity is dependent on the

total amount of food available. Selective feeding has implications for the ability of the SIMCO to sustain larval krill in winter.

MATERIALS AND METHODS

The RVIB N.B. Palmer encountered exceptional ice conditions (Massom et al. 2006) during September and October of 2001 along the Antarctic Peninsula. Average daily sea ice measured by SSMI satellite during this time ranged from 60 to 100% concentration (Hyatt 2006) and sea ice thickness estimated by scuba divers reached ~20m (Massom et al. 2006). The ship was beset and confined to a limited geographic area on the continental shelf bounded by 67° 38.50′ to 68° 14.80′ S and 69° 36.90′ to 70° 37.00′W (Table 1) when material for the feeding experiments was collected resulting in low variability in the sea ice microbial community composition.

Collection and Maintenance of Krill

During September and October 2001 late larval stage and juvenile krill were collected from beneath the ice by divers with aquarium nets (~1000-μm mesh). Once captured, krill were placed in insulated buckets of seawater, transferred back to the ship and approximately 30 each were placed in 2-l glass jars filled with 0.45-μm-filtered seawater. The seawater in the jars was kept at near-ambient water temperature (-1.1 to -1.8°C) in flow-through seawater racks. Krill were kept 2 to 12 d before use. Only actively swimming krill were used in experiments.

Grazing Material Sources and Maintenance

Sea ice microorganisms (SIMCOs) were collected from brine pits, ice blocks, ice cores or slush. Brine pits were drilled into the snow-cleared sea ice surface with 13-cm augers and were allowed to fill with brine overnight. If the salinity of the brine was above 35 ppt, 0.45-μm-filtered seawater was used to reduce the salinity. Sea ice blocks where removed from consolidated first year pack ice with chain saws or sea ice cores were taken with a 10-cm hand auger. Pieces of ice were measured to estimate their volume and placed in filtered seawater at a ratio of approximately 1:3 and left to melt at 0°C. Occasionally, a visible slushy green layer was apparent in the sea ice just beneath the accumulated surface snow (see Massom et al. 2006). This green layer was cleared of fresh snow, shoveled into buckets and transported to the ship. Filtered seawater was added to this higher salinity material in an approximate ratio of 1:1 and the resulting "slush" was allowed to melt. The resulting salinities for all of the collections after melting or dilution ranged from 32 ppt to 35 ppt. Each collection method produced a type of SIMCO that becomes available to larval krill as pack ice buckles under compression and is submerged by over-rafted floes. All SIMCOs collected were kept at 0°C in dim light prior to use in experiments (Table 1).

Feeding Experiments

Seventeen feeding experiments were conducted. Samples of the grazing material were filtered and extracted in 90% acetone (12 hours) prior to each

experiment to estimate the approximate *chl a* concentration. Grazing material (0.5 to 19.5 l) was diluted in a total volume of 20-l with 0.45-μm-filtered seawater to reach a pre-determined *chl a* concentration. After mixing well, a series of sub-samples were taken from the 20-l for analysis. One hundred ml sub-samples (n = 6) were filtered (HAWP filters) for determination of initial *chl a* concentration. Sub-samples (n = 3) of varying volumes between 25 and 200 ml were filtered (13-mm A/E filters) for carbon and nitrogen (CHN) analysis. A separate 500-ml sub-sample (n = 1) was preserved in a final concentration of 1% gluteraldehyde and stored at 4°C until slides for determining community composition were made. Experimental buckets with krill (n = 2-3) and control buckets without krill (n = 2) were filled with 3-l of grazing material. The experimental and control buckets were cooled from ~0 °C to ambient temperature (between –1.1 to -1.8°C). Krill (n = 20) were then added to each experimental bucket. Krill were allowed to feed for approximately 12 h. The experimental and control buckets were gently shaken at least one time during each experiment. At the end of the experiment the krill were removed from the experimental buckets. The sub-sample routine described above was repeated for each experimental and control bucket at the end of each experiment.

Morphometric Analysis

The developmental stages of krill were determined by examining the telson under a dissecting microscope (Markarov 1980). Total length (TL) was measured from the tip of the rostrum to the end of the uropods (standard measure 1, Maucline,

1980). Telson length (TelL) was measured from mid-bump at the insertion point to the abdomen to the tip of the telson. When only TelL was measured the total length and wet mass of krill were estimated from the relationships TL = 5.09 TelL - 1.4391 (R^2 = 0.98, n= 30) and WM = 0.365 $TelL^{3.412}$ (R^2 = 0.96, n = 31) given in Ross et al. (2004). Depending on other post-experiment uses for the larvae and juvenile krill not reported here, either the TL was measured directly or TelL was measured and used to calculate TL.

Community Characteristics from Microscopic Analysis

One each of DAPI (4',6-Diamidino-2-phenylindole) and acridine orange stained slides were made by filtering SIMCO sub-samples fixed with 4% gluteraldehyde onto black 0.8-μm and 5.0-μm polycarbonate membrane filters backed by either A/E glass fiber filters or HAWP filters following the methods of Coleman (1980) and Verity and Sieracki (1993), respectively. Slides were frozen and stored at -40°C until analysis. In order to determine autotrophic and heterotrophic cells, cells stained with DAPI were enumerated with light microscopy at 400x magnification. For all experiments, cells counted were contained within a 0.25 mm x 0.25 mm ocular grid. For 5 experiments, initial examination of the slides indicated that cells were not randomly dispersed and were more concentrated on the outer edge of the filter area. In this case the non-overlapping grids were counted along either one strip or two perpendicular strips. For 12 experiments random distribution of the cells on the slide was not a concern and grids counted were

selected randomly to save time and increase precision (Venrick 1978a). Cells more than half outside the grid were not included. Between 36 and 196 grids were counted for each experimental slide resulting in 345 to 3828 total cells or colonies counted. One concern was the reliability of abundance estimates for rare cell types. The variability of the cell counts was examined by comparing the running abundance estimate for each cell type compared to the total number of grids counted. For rare cells we found that as few as five cells produced a good degree of precision so long as approximately 45 grids were counted.

Cells were classified into groups based on genus such as *Gymnodinium sp.* or *Phaeocystis sp.* unless the species could be identified. In cases where cells could not be identified, general taxonomic categories such as heterotrophic and autotrophic monad were used. Linear length and width measurements were made for all cells of each type to estimate biovolume (Hillebrand et al. 1999) and carbon content (Menden-Deuer and Lessard 2000). Carbon concentration in sea ice is often elevated by large amounts of detritus and by the production of carbohydrate rich compounds by nitrogen-limited phytoplankton. Based on CHN analysis (Control Equipment Corporation CEC 440HA automated organic elemental analyzer by Dumas combustion method at the Marine Science Institute Analytical Laboratory, University of California Santa Barbara) bulk particulate organic carbon (POC) in the initial and each experimental and control bucket was estimated by linear regression of POC and sample volume (n = 3-4 variable volumes). We found the carbon concentration based on cell volumes approximately 20% of the POC

concentration (Figure 1). To make a gross estimate of potential micrograzer impacts, copepod abundance was estimated from counts (n = 3) of the initial and control sub-samples with variable volumes of 40 – 100 ml.

Ingestion Rate Calculations

Phytoplankton growth rates and krill grazing rates were calculated according to the equations of Frost (1972) as modified by Marin et al. (1986). The phytoplankton growth coefficient k (h^{-1}) for selective grazing experiments was calculated from phytoplankton controls

$$(1) \qquad k = \ln ([C]_t/[C]_o)*t^{-1}$$

where $[C]_t$ was the carbon concentration ($\mu g\ l^{-1}$) with time t (h) and $[C]_o$ was the initial carbon concentration. The experimental phytoplankton loss coefficient b (h^{-1}) was calculated as

$$(2) \qquad b = \ln ([C]_t/[\ C]_o)*t^{-1}$$

where $[C]_t$ was the final carbon concentration ($\mu g\ l^{-1}$) in the krill grazing buckets at time t and $[C]_o$ was the initial carbon concentration. The grazing coefficient g (h^{-1}) was calculated using k and b.

(3) $g = k-b$

The clearance rate F (ml gWM^{-1} h^{-1}) was calculated multiplying g by the ratio of the experimental volume V (ml) and the wet mass WM (g) of the krill.

(4) $F = g * V/WM$

From the clearance rate, the ingestion rate, I_c, of carbon was calculated with equation

(5) $I_c = F * [C]_0$

where $[C]_0$ is the initial concentration of carbon.

Daily Ration Calculation

Daily ration was calculated as the percent of krill body carbon ingested per day. Average body carbon of krill in the experiment was calculated from the relationship between wet mass and carbon content derived by Quetin and Ross (unpublished data) as reported by Elias (1990)

(6) $C = -113.185 + 92.882 * WM$

where C was carbon (μg) and WM was wet mass (mg) ($r^2 = 0.98$).

RESULTS

Krill Developmental Stage and Total Length

Krill were furcilia VI and juvenile stage with total length ranging from 6 to 12 mm. The range of calculated WM of krill was 1.40 to 22.5 mg with a median value of 5.6 mg.

Microbial Community Characteristics

Linear length and width measurements of cells were converted to volume. Cell volumes ranged from 2.0×10^0 to 1.2×10^6 μm^3 (Table 2) or an equivalent spherical diameter of 1.3 to 102 μm. Most experiments had the greatest percent of cell volumes falling in the 10 to 40 μm^3 or 2 to 4 μm equivalent spherical diameter (ESD) range with few larger cells, as illustrated by experiment 11 (Figure 2a). In some experiments, for example experiment 3 (Figure 2b), there were a substantial percent of cells with volumes from 100 to 6000 μm^3 (3 to 22 μm ESD). Four experiments had a high percent of small heterotrophic cells with volumes ranging from 2 to 8 μm^3 as exemplified in experiment 16 (Figure 2c). Cell volumes were used to calculate the carbon content of cells and the carbon content was subsequently used to estimate the total, autotrophic and heterotrophic carbon concentration for each experiment.

The initial total living carbon concentration ranged from 12 to 201 $\mu g\ l^{-1}$. The total community was divided into 3 main groups depending on the relative amount of autotrophic (AUT C) and heterotrophic (HET C) carbon present; 1) AUT

C ≥ 90%, HET C ≤ 9%, 2) AUT C 78 to 83%, HET C 17 to 22% and 3) AUT C 51 to 71%, HET C 29 to 49% (Table 3). Heterotrophic carbon was a significant form of carbon (29-49%) in only 5 experiments (expt. 5-7, 16, 17) (Table 3). In 4 experiments (13-15, 17) there were abundant small heterotrophic cells of 4 to 34 μm^3 (Table 2) that were absent or found only in low concentrations in the remaining experiments. In 12 experiments autotrophic carbon was the major form of carbon (Table 3).

The autotrophic community composition was further divided into 5 taxonomic groups; autotrophic *Gymnodinium sp.*, colonial and solitary *Phaeocystis sp.*, diatoms, autotrophic monads and cryptomonads, accounting for 6 to 52%, 13 to 81%, 2 to 17%, <1 to 17% and <1 to 8%, respectively, of the total carbon (Table 3). Autotrophic *Gymnodinium sp.* comprised the highest percent of total carbon (34 – 81%) in 9 experiments (expt. 1-4, 7-10, 13) and the second highest (24 – 38%) in 7 experiments (expt. 5, 6, 11, 12, 14, 17). The cells classified as autotrophic *Gymnodinium sp.* were dominated by two morphologies; one round with a premedian cingulum and another oblong with a medial displaced cingulum. The linear length to width ratio distribution for *Gymnodinium sp.* was bimodal centered on ~1.5 and ~2. *Phaeocystis sp.* occurred both in solitary and colonial forms with colonial forms usually dominant (51 – 92%) except for 4 (expt. 4-7) of the 17 experiments in which colonial cells constituted ≤ 4% of the total *Phaeocystis sp.* present. Colonial forms were especially dominant in 3 experiments (expt. 15-17) and represented ≥86%. *Phaeocystis sp.* dominated the total carbon (36 - 52%) in

only 4 experiments (expt. 11,12,14,15) and was the second most dominant form of carbon (9 - 39%) in 9 experiments (expt. 1-4, 8-10, 13, 16). Together *Phaeocystis sp.* and autotrophic *Gymnodinium sp.* accounted for >62% of total carbon in 12 of 17 experiments (expt. 1-4, 8-15) and between 30 – 60% in the remaining 5 experiments (Table 3). Diatoms and autotrophic monads only accounted for the third highest amount of total carbon in 3 experiments each, for diatoms (expt. 1-3) and autotrophic monads (expt. 6,8,9), and were never greater than 17% of total carbon (Table 3). Cryptomonads never reached higher than 8% of total carbon (Table 3).

Krill Feeding and Functional Response

Krill were fed at initial living carbon concentrations that ranged from 12 to 201 $\mu g l^{-1}$. Maximum mass-specific clearance rates were similar for all carbon types and ranged from 3.8, 4.0 and 4.7 ml $gWM^{-1} h^{-1}$ for total, autotrophic and heterotrophic carbon, respectively. The maximum mass-specific ingestion rate of 166 $\mu gC\ gWM^{-1} h^{-1}$ was highest for total carbon. Mass-specific ingestion reached a maximum of 105 $\mu gC\ gWM^{-1} h^{-1}$ for autotrophic carbon and 48 $\mu gC\ gWM^{-1} h^{-1}$ for heterotrophic carbon.

When feeding on total and autotrophic carbon, krill exhibited a Type II functional response (Holling 1966) (Figure 3a, 3b), with ingestion increasing non-linearly with increasing carbon. There was no clear relationship between mass-

specific ingestion and heterotrophic carbon concentration (Figure 3c). Total mass-specific carbon ingestion increased with increasing percent autotrophic carbon until the total carbon concentration reached 36 $\mu g\ l^{-1}$, but above this concentration ingestion rates did not correlate with percent autotrophic carbon (Figure 4a). No relationship between total carbon mass-specific ingestion and percent heterotrophic carbon was found (Figure 4b).

Our hypothesis was that krill would ingest selectively at higher total carbon concentrations. Ingestion rates, negative and positive, were considered significantly different from zero if zero was not contained within one standard errors (SE) of the mean rate. Ingestion rates were considered of higher significance if zero was not contained within 2 SE of the mean rate. Negative ingestion rates, possible indications of selection against a cell type, were found for at least one of the 5 taxonomic groups in 10 of 17 experiments (Table 3) usually when total carbon was above 46 $\mu g\ l^{-1}$. Only 9 ingestion rates that fell between -0.6 and -51 $\mu gC\ gWM^{-1}\ h^{-1}$ were significant to two SE, 4 that fell between -2.2 and -70 $\mu gC\ gWM^{-1}\ h^{-1}$ were significant to one SE (Table 3). Experiments for which significant negative ingestion rates were obtained had initial total carbon concentrations ranging from 45 to 201 μgl^{-1}, and those for which only positive ingestion rates were obtained ranged from 12 to 53 μgl^{-1} (Table 3), suggesting krill are less selective when feeding at low total living carbon concentrations.

One experiment (expt. 2) had one high negative ingestion rate for total carbon that was significant to one SE (-70 μgC gWM^{-1} h^{-1}) and one negative ingestion rate for autotrophic carbon that was significant to two SE (-35 μgC gWM^{-1} h^{-1}). Another experiment (expt. 3) had a negative ingestion rate for autotrophic carbon significant to one SE (-24 μgC gWM^{-1} h^{-1}). The two experiments that had significant negative ingestion rates for autotrophic carbon were dominated by *Gymnodinium sp.* suggesting this taxonomic group may influence feeding behavior.

Phytoplankton growth coefficients (k) were often different from zero. Positive values of k ranged from 0.0004 to 0.48 d^{-1} indicating possible growth of cells. Negative values of k ranged from -0.001 to -0.25 d^{-1} suggesting possible micrograzer activity, differential settling of cells, or other sub-sampling variability. We included the k values in the ingestion calculation to account for any significant change in cell concentrations not the result of krill grazing.

Daily Ration

Daily rations calculated from these experiments were compared both to daily rations from other studies and to the minimum daily carbon requirement for comparable sized krill at winter temperatures. Maximum daily rations of 17% and 11% body C d^{-1} for total and autotrophic carbon (Table 4), respectively, were reached when total carbon was highest (201 μg l^{-1}). The daily ration for

heterotrophic carbon reached a maximum of 4.1% body C d^{-1} (Table 4) when total carbon was only 44 $\mu g\ l^{-1}$ but heterotrophic carbon was at a maximum 49% of total carbon. Krill were usually able to meet their minimum daily carbon requirement of 1.34 to 1.80% body C d^{-1} (Frazer et. al., 2002) when total carbon was as low as 12 $\mu g\ l^{-1}$.

Selective Feeding

To determine if krill were feeding selectively on autotrophic or heterotrophic carbon, we created a selection index by subtracting the initial ratio of each carbon type to total carbon (initial carbon ratio) from the ratio of mass-specific carbon ingestion for each type of carbon to mass-specific total carbon ingestion (ingestion ratio). The rationale was that if krill were eating a carbon type in the same proportion as the carbon type was available in the experiment, the difference between the initial carbon ratio and the ingestion ratio would be zero. If the carbon type was 1) selected, the selection index for that carbon type would be positive and 2) not selected, the selection index would be negative. If the ingestion ratio was greater than the initial carbon ratio (above the horizontal line in Figure 5), the krill were ingesting a particular carbon type in a proportion greater than would be expected given the initial carbon ratio. Ingestion rates were considered significantly different from zero if zero was not contained within two standard errors (Figure 5).

In 14 of 17 experiments with autotrophic carbon the selection index was positive and all ingestion rates were significantly different from zero to one or two standard errors (Figure 5a). In one of the three experiments where autotrophic carbon was not selected, the ingestion rate was not significantly different from zero (closed circle) (Figure 5a). In 9 of 17 experiments with heterotrophic carbon the selection index was positive and in 5 experiments ingestion rates were not significantly different from zero (closed circle) (Figure 5b).

The same process was used to determine selectivity among the various cell types or groupings. Autotrophic *Gymnodinium sp.* carbon was the greatest percent of the total carbon in 9 experiments (Table 3). In 14 of 17 experiments with autotrophic *Gymnodinium sp.* the selection index was positive and 8 out of 14 of these experiments had selection indexes significantly different from zero (Figure 5c). Autotrophic *Gymnodinium sp.* carbon was not selected in the same 3 experiments in which autotrophic carbon was not selected (Figure 4a). *Phaeocystis sp.* was the highest percent of total carbon in 4 experiments (Table 3) and in 15 of 17 experiments with *Phaeocystis sp.* the selection index was positive (Figure 6b) significantly different from zero in 6 experiments.

Diatoms, autotrophic monads and cryptomonads were always < 18% of the total carbon source (Table 3). In 17 experiments with diatoms the selection index was not significantly different from zero (figure 6c).

Autotrophic monads comprised <1% of total carbon in 4 experiments and were never greater than 17% of the total carbon (Table 3). Ingestion ratios for autotrophic monads in 13 experiments were positive and significantly different from zero (Figure 5f). Cryptomonads were not present in 7 experiments and were <1% of total carbon in 3 experiments (Table 3).

DISCUSSION

The results of these feeding experiments allow us to draw some general conclusions about young krill feeding on the SIMCO in winter. Additionally, we were able to address the hypotheses that selective feeding in young krill would depend on the SIMCO composition and the total amount of food available in the context of many of the factors that are known to influence feeding selectivity.

Krill Developmental Stage and Total Length

Krill used in our experiments were of a similar stage (furcilia VI and Juvenile), total length (6 to 12 mm) and wet mass (1.40 to 22.5 mg) to those reported to feed on the sea ice microbial community in winter (Guzman, 1983; Quetin et al., 1988; Marschall, 1988; Stretch et al., 1988; Daly, 1990, 2004; Quetin et al., 1994; Frazer, 1996; Frazer et al., 1997a, 2002; Ross et al., 2004). The results of these experiments are applicable to young krill feeding on the SIMCO in winter.

Microbial Community Composition from Microscopy

The SIMCO, due to physical factors, is heterogeneous in abundance and occurrence at local and large-scales as well as with vertical depth in the ice (Garrison 1991b). Pennate diatoms belonging to *Fragilariopsis* and some centric genera usually dominate the SIMCO (Garrison 1991b). Other genera that often dominant in the SIMCO include the diatoms from the genera *Nitzschia,*

Chaetocerous, Thalassiosira and *Coscinodiscus* (Lizotte 2001). Autotrophic nano- and microflagellates may dominate at times but are difficult to identify and *Phaeocystis sp.* can reach levels as high as 5 x 10^7 cell l^{-1} (Garrison 1991b). Autotrophic dinoflagellates from the genera *Gymnodinium*, *Gyrodinium* and *Amphidinium* can be abundant at times, and heterotrophic flagellates and ciliates can comprise a significant portion of the biotic community (Garrison 1991b).

The composition of the sea ice microorganisms collected for these experiments were consistent with observed species reviewed in Garrison (1991b) and Lizotte (2001). While autotrophic gymnodiniods and *Phaeocystis sp.* often dominated the biomass, larger diatoms such as often found in the SIMCO were rarely observed. We observed larger diatoms from the genera *Plagiotropis, Corethron, Chaetocerous, Eucampica* and *Odentella* but rarely and in low numbers. However, small pennate diatoms *Fragilariposis sp.* and *Navicula sp.* sometimes occurred in high numbers.

Spatial coverage of the winter cruise of 2001 was limited by heavy sea ice conditions resulting from anomalous atmospheric conditions (Massom et al. 2006). Despite the limited geographic coverage of the cruise, the community composition of feeding material collected during the cruise was variable but did not represent all possible SIMCOs that krill may encounter during winter in this region.

Krill Feeding

Our clearance rates were in general agreement with those documented in other studies with two approaches: laboratory or ship-based experiments with either cultured or natural phytoplankton assemblages or the field ingestion technique that depends on the decrease in gut fluorescence in freshly caught krill (Table 4). However, comparisons with other studies need to consider variations in food, temperature, krill size and krill stage. Our maximum clearance rates for furcilia VI and juvenile krill feeding on total, autotrophic and heterotrophic carbon agreed well with those obtained for furcilia VI and juvenile krill fed *Fragilariopsis curta* on surfaces and in the water column at winter temperatures of -1.8 to -1.1°C (Chapter 1), and for furcilia IV fed *Thalassiosira sp.* at -1.8 to -1.5°C, but were only 38 to 47% of that for fucilia VI (Ross and Quetin unpublished data). These rates for older furcilia and juveniles also agreed well with maximum clearance rates for furcilia III fed microorganisms in natural and SIMCO enriched seawater at 0°C (Meyer et. al. 2002). Atkinson et al. (2002) obtained maximum clearance rates, adjusted to -1°C, for juvenile krill (28 – 38 mm) that were approximately 10% of those obtained in our experiments, as would be expected for larger size krill. The highest maximum clearance rate, estimated with the field ingestion protocol, for furcilia feeding under or near the ice during winter but measured at -0.5°C (Daly, 1990) was 4 to 5 times higher than the maximum in our feeding experiments. This difference could result from differences in techniques used to measure ingestion.

Ingestions rates for late furcilia and juvenile krill feeding at winter temperatures indicate that they are able to feed at rates comparable to late summer and fall rates when food concentrations are greater than those typically found in the water column during winter (Table 4). The few reported measurements of *chl a* contained in the sea ice microbial community in samples collected during September in the same geographic region as our study were 5 to 350 times higher in concentration in the sea ice than in the water column (Kottmeier and Sullivan 1987, Quetin et al. 2003). Larval and juvenile krill are poised to exploit these dense patches of food, when they are encountered, by scraping cells from the sea water-ice interface or feeding on cells released into the water column by over-rafting of the pack ice or through drainage of brine channels.

Negative ingestion rates obtained for particular cell types and for overall carbon consumption are difficult to interpret. Mathematically, they result when the concentration of carbon in the final feeding incubation is greater than that measured initially or relative to the control. We obtained some significant negative ingestion rates, corrected with controls, for krill grazing on both autotrophic and heterotrophic organisms. Ingestion rates were considered significantly different from zero if zero was not contained within one or two standard errors of the mean rate. There are two main theoretical explanations for why negative ingestion rates arise in feeding incubations with natural communities, 1) the release of micrograzer feeding pressure and 2) nutrient enrichment from grazers. In the case that no micrograzers are present, negative ingestion rates could result when macrograzers discriminate

against a cell type and growth of that cell type is fueled by nutrient enrichment from grazers not present in the controls.

The presence of micrograzers in natural phytoplankton incubation experiments can lead to significant "apparent" negative mesozooplankton ingestion rates if mesozooplankton feed on micrograzers and release micrograzer pressure on food items that is greater than mesozooplankton grazing pressure on the same food (Nejstgaard et al. 2001). Three species of copepods are associated with the sea ice, *Paralabidocera antarctica, Drescheriella glacialis,* and *Stephos longipes. P. Antarctica* are present in sea ice during winter as naupliar stages (NIV to NV) and exhibited slow development as winter progressed indicating possible reduced but active feeding on sea ice algae throughout the winter (Tanimura et al. 1996). *D. glacialis* lives in the sea ice for its entire lifecycle and the main reproductive season is in winter (Dahms et al. 1990). The life strategy of *S. longipes* consists of overwintering of adults and nauplii in the sea ice and the overwintering of late copepedite stages at depth in the water column (Schnack-Schiel et al. 1995). Microscopic analysis of the initial community composition in our experiments indicated that naupliar to copepodite stage copepods from 0.1 to 1 mm size were present in the grazing material of 12 experiments but in numbers too low to enumerate reliably. However, we estimated the concentration and calculated a conservative estimate of the potential grazing impact with summer clearance rates for *S. longipes* and *P. Antarctica* nauplii and copepodites (Swadling et al. 1997). Even if feeding at summer rates, the copepods would clear on average a maximum

of 3% of the experimental volume. We considered this too small for copepod micrograzers to be a factor.

Nutrient enrichment resulting from zooplankton feeding and excretion may spur growth of phytoplankton during feeding incubations with natural communities. Our experiments lasted for 12 h and were kept in the dark. The shortest generation times measured for Antarctic phytoplankton during late winter, approximately 91 h, correspond to a doubling of 0.18 d^{-1} (Kristiansen et. al, 1992). Growth rates measured for ice associated phytoplankton communities in early spring and early fall range from 0.05 to 0.6 d^{-1} depending on light levels and salinity (Sakshaug and Holm-Hansen 1986, Vargo et al. 1986, Smith and Nelson 1990, Garrison and Buck 1991) but may reach as high as 1 d^{-1} for individual species. The positive phytoplankton growth coefficients from the phytoplankton controls ranged from 0.0004 to 0.48 d^{-1}. Some k values from our experiments are too low to indicate possible phytoplankton growth but many fall within the low end of reported growth rates for ice-associated phytoplankton. Autotrophic cells from incubations were observed to be actively dividing at the time they were preserved. Feeding material was keep at 0°C in dim light for up to several days prior to use in incubations and may have provided an environment that favored autotrophic cell growth sufficient to produce cell doubling during the experiment in some cases.

Daily Ration

Krill are usually found in a limited thermal range (-1.8 to 4°C) and relatively small differences in temperature affect rates of physiological processes such as metabolism (Frazer et al. 2002). Most feeding studies for krill of similar size fed at temperatures closest to the temperature of our experiments have reported ingestion rates in terms of daily ration or percent of body carbon ingested per day. We converted our ingestion rates into daily ration for comparison (Table 4). Our daily ration estimates for total carbon fell within the range obtained for furcilia III fed sea ice microbes at 0°C (Meyer et. al., 2002) at similar carbon concentrations. At maximum carbon concentrations 2 to 7 times higher than that of this study (Chapter 1) daily ration estimates were the same or fell within the range documented in this study. Our maximum daily ration estimates were 20 to 30 times higher those obtained for juvenile krill fed in natural and SIMCO enriched seawater at -1°C (Atkinson et. al, 2002) and similar carbon concentrations. Although described as juveniles, the krill used in their fall study were much larger (28 to 38 mm) than our winter juvenile krill (≤ 12 mm) and would have been entering their second winter, sufficiently developed to adopt an over wintering strategy of reduced metabolism as is seen in adult krill (Kawaguchi t al. 1986, Quetin and Ross 1991, Torres et al. 1994).

Our daily ration estimates from autotrophic carbon ingestion fell just below the range measured by gut fluorescence for furcilia III-V fed natural biota from the seawater at -1°C (Pakhomov et al. 2004) but were 3 to 6 times higher than those

obtained by the same methods but measured at -0.5°C (Daly 1990) despite similar maximum carbon values. One would expect our estimate of daily ration to be lower given the low temperature of our experiments.

Selective Feeding Factors

The overall carbon concentration available for krill in the feeding experiments was expected to influence the degree of selectivity in krill feeding behavior based on optimal foraging theory (De Mott 1989) and because larval krill with little food available likely cannot energetically afford to be selective. The results suggested a critical concentration of ~ 36 $\mu g\ l^{-1}$ total carbon. In this context 75% of experiments with negative ingestion rates of at least one taxonomic group had a mean concentration above 36 $\mu g\ l^{-1}$ total carbon, and 78% of the experiments with positive ingestion rates for all taxonomic groups were below 36 $\mu g\ l^{-1}$ total carbon. Assuming the negative ingestion rate indicates a lower grazing pressure for a given taxonomic group, this would generally suggest that when food is scarce krill feed on what is available. Autotrophic carbon was generally greater than heterotrohic carbon and high positive ingestion rates for 14 of 17 experiments indicate the importance of autotrophic sea ice microbes in winter diet of young krill. Heterotrophic carbon was ingested in 11 experiments suggesting heterotrophic organisms are also a part of the winter diet of larval and juvenile krill. Negative ingestion rates were obtained in 6 experiments with heterotrophic carbon 3 - 42% of

available carbon. However, only one negative ingestion rate was significantly different from zero (expt 3).

Krill ingestion rates in this study were affected by the composition of the sea ice microbial community. Community composition was linked to a reduction in krill grazing in a previous study. Habermann et al. (2003b) found grazing rates of adult *E. superba* on all phytoplankton was severely reduced when krill were fed natural phytoplankton assemblages dominated by cryptophytes. However, cryptophytes were ingested in low quantities when diatoms were sufficiently available. Cryptophyte-dominated communities are considered a poor food source relative to those dominated by diatoms and may signal krill to search for a better food source.

The presence of phytoplankton that produce toxins may also inhibit krill grazing. When fed the toxin producing diatom *Pseudo-nitzchia multiseries,* the temperate species *Euphausia pacifica* was found to alternate between 6-h feeding/non-feeding intervals over a 24 h period (Bargu et al. 2003). *E. pacifica* fed constantly on non-toxic *Pseudo-nitzchia pungens* at a rate that declined with decreasing food concentration over time (Bargu et al. 2003). The authors suggest that discontinuous feeding may allow animals to exploit toxic food sources avoiding high levels of toxin in the digestive tract.

Determining which potentially toxic strains of phytoplankton may inhibit feeding or alter feeding behavior is not simple and must be tested directly. An investigation of the palatability of 16 autotrophic dinoflagellate species to 6 larval crab species revealed a complex pattern of discrimination that was independent of

taxonomic affinity, size or toxicity (Perez and Sulkin 2005). However, saxitoxin producing *Gymnodinium catenatum* was never ingested and non-toxic *G. catenatum* was only ingested by 2 of 6 species crab larvae. The presence of toxic *G. catenatum* has also been implicated in reduced grazing of Mediterranean mesozooplankton on microbial communities (Calbet et al. 2002).

Three experiments in which large negative ingestion rates were obtained for autotrophic carbon ingestion (Table 3) contained high amounts of what we identified as autotrophic *Gymnodinium sp.* A recent study found seawater and slush samples from the pack ice in the Ross Sea contained a novel autotrophic dinoflagellate whose closest genetic relations are from the genera *Karenia* and *Karlodinium* (Gast et al. 2006). Species from these genera have been cited in marine fish and invertebrate kills, though such events have yet to be recorded for Antarctic waters. The potential toxicity of the novel dinoflagellate has yet to be determined (Gast et al. 2006). Some species of *Gymnodinium,* such as *G. catenatum* are known to have toxic strains. *Gymnodinium sp.* are difficult to identify and have a range of morphologies (McMinn and Scott 2005). We observed two distinct morphs, one near round with a premedian cingulum and another oblong with a medial displaced cingulum, that were classified as *Gymnodinium sp.* Our grouping of autotrophic *Gymnodinium sp.* may have contained unidentified species that are harmful to krill or inhibit their feeding response. High concentrations of suboptimal or noxious autotrophic gymnodimniod dinoflagellates may have reduced overall ingestion in some of our experiments.

Other than the three experiments discussed above, autotrophic *Gymnodinium sp.* group was readily ingested by krill. *Phaeocystis sp.* was ingested in all experiments except the one (expt 2) containing 81% autotrophic carbon as autotrophic *Gymnodinium sp.* in which the krill apparently did not feed.

Diatoms were ingested readily if they were available in high enough concentrations. The only study that has been published on the selectivity of larval *E. superba* fed on field-collected phytoplankton indicates larval krill are not selective when fed a mixture. Meyer et al. (2002) found furcilia III larvae showed no feeding preference based on phytoplankton cell type or size (range 10 to 220 μm). In their study, conducted in autumn, diatoms constituted 83 to 98% of the particles counted. Autotrophic monads and cryptomonads generally represented a low proportion of the total carbon concentration but were usually ingested. During the winter, when light is further limited, the sea ice community may shift to include a higher proportion of species that are adapted to lower light (i.e. *Phaeocystis sp.*) or are heterotrophic (i.e. bacteria or protozoans). This may influence the feeding behavior of larval krill when diatoms are not the dominant particle.

CONCLUSIONS

This study looked at the relative importance of food availability and composition within the sea ice microbial community as influences in selective feeding behavior in young krill during winter. We hypothesized that selectivity would depend on the overall food concentration and the microbial community composition within the sea ice. Krill exhibited a higher degree of selectivity when carbon concentrations were higher. Ingestion of heterotrophic food items was much more variable than ingestion of autotrophic food items and autotrophic food items were generally the most important sources of carbon. Among the autotrophic sources *Phaeocystis sp.* and autotrophic *Gymnodinium sp.* were often dominant and were usually readily consumed. Some cells identified as autotrophic *Gymnodinium sp.* were distinctly rejected and indicated that the presence of unpalatable species of autotrophic dinoflagellates may suppress krill feeding behavior however, this could not be determined definitively in this study.

Young krill offered naturally collected sea ice microbes exhibited flexibility in food choice depending on overall food availability and community composition. Clearance and ingestion rates indicate that with this flexible behavior they are often able to meet their minimum energetic requirements during winter. Daily rations are comparable to those measured in young krill during late summer and fall suggesting they do not need reduce their metabolism to cope with winter conditions in the water column. This study further supports the idea that during winter young krill are

coupled to the sea ice and receive energetic benefits from feeding on the sea ice microbial community.

REFERENCES

Atkinson A, Meyer B, Stübing D, Hagen W, Schmidt K, Bathman UV (2002) Feeding and energy budgets of Antarctic krill *Euphausia superba* at the onset of winter-II. Juveniles and adults. Limol and Oceanogr 47(4): 953-966

Atkinson A, Snÿder R (1997) Krill-copepod interactions at South Georgia, Antarctica, I. Omnivory by *Euphausia superba*. Mar Ecol Prog Ser 160: 63-76

Bargu S, Marinovic B, Mansergh S, Silver MW (2003) Feeding responses of krill to the toxin-producing diatom *Pseudo-nitzschia*. J Exp Mar Biol Ecol 284: 87–104.

Calbet A, Broglio E, Saiz E, Alcaraz M (2002) Low grazing impact of mesozooplankton on the microbial communities of the Alboran sea: a possible case of inhibitory effects by toxic dinoflagellate *Gymnodinium catenatum*. Aquat Microb Ecol 26: 235–246

Coleman A (1980) Enhanced staining of bacteria in natural environments by fluorochrome staining of DNA." Limnol and Oceanogr 25: 948-951

Cowles TJ, Olson RJ, Chisholm SW (1988) Food selection by copepods: discrimination on the basis of food quality. Mar Biol 100: 41–49

Dahms H-U, Bergmans M, Schminke HK (1990) Distribution and adaptations of sea ice inhabiting Harpacticoida (Crustacea, Copepoda) of the Weddell Sea (Antarctica). PSZN I: Mar Ecol 11:207–226.

Daly K (1990) Overwintering development, growth, and feeding of larval *Euphausia superba* in the Antarctic marginal ice zone. Limnol and Oceanogr 35(7): 1564-1576

Daly KL (2004) Overwintering growth and development of larval *Euphausia superba*: an interannual comparison under varying environmental conditions west of the Antarctic Peninsula. Deep-Sea Res Part II 51 (17-19): 2139-2168

Daly KM, Macauly MC (1988) Abundance and distribution of krill in the ice edge zone of Weddell Sea, austral spring 1983. Deep-Sea Res 35:21–41

DeMott WR (1988) Discrimination between algae and detritus by freshwater and marine zooplankton. Bull. Mar. Sci. 43: 486–499

Donaghay PL, Small LF (1979) Food selection capabilities of the estuarine copepod *Acartiaclausii*. Mar Biol 52: 137–146

Elias MC (1990) Effects of photoperiod, phytoplankton level and temperature on the growth, development and survival of larval *Euphausia superba* (Dana). MA thesis, University of California, Santa Barbara, CA

Frazer TK (1996) Stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) of larval krill, *Euphausia superba*, and two of its potential food sources. J Plankton Res 18(8):1413-1426

Frazer TK, Quetin LB, Ross RM (1997a) Abundance and distribution of larval krill, *Euphausia superba*, associated with annual sea ice in winter. In: Battaglia B, Valencia J, Walton DWH (eds) Antarctic Communities. Cambridge University Press, Cambridge, p 107–111

Frazer TK, Quetin LB, Ross RM (2002) Energetic demands of larval krill, *Euphausia superba*, in winter. J Exp Mar Biol Ecol 277: 157-171

Frost, BW (1972) Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol and Oceanogr 17(6): 805-979

Garrison DL (1991b) The biota of Antarctic sea ice. Am Zool 31: 17-33

Garrison DL, Buck KL (1991) Surface layer assemblages in Antarctic pack ice during Austral spring: environmental conditions, primary production. Mar Ecol Prog Ser 75: 161–172

Gast RJ, Moran DM, Beaudoin DJ, Blythe JN, Dennett MR, Caron DA (2006) Abundance of a novel dinoflagellate phylotype in the Ross Sea, Antarctica. J Phycol 42: 233–242

Guillard RRL, Ryther JH (1962) Studies of marine planktonic diatoms 1: *Cyclotella nana* Hustedt and *Detonula confervacea* (Cleve) Gran. Can J Microbiol 8:229-245

Guzman O (1983) Distribution and abundance of antarctic krill (*Euphausia superba*) in the Bransfield Strait. In: Schnack, S. B. (ed.), On the Biology of Krill Euphausia superba. Ber Polarforsch 4. Alfred-Wegener-Institute for Polar Research, Bremerhaven, p 169– 190

Haberman K L, Quetin LB, Ross RM (2003a) Diet of the Antarctic krill (*Euphausia superba* Dana): I. Comparisons of grazing on *Phaeocystis antarctica* (Karsten) and *Thalassiosira antarctica* (Comber). J Exp Mar Biol Ecol 283(1-2): 79-95.

Haberman K L, Quetin LB, Ross RM (2003b) Diet of the Antarctic krill (*Euphausia superba* Dana): II. Selective grazing in mixed phytoplankton assemblages. J Exp Mar Biol Ecol (283): 97-113

Hillebrand H, Dürselen C, Kirschtel D, Pollingher U, Zohary T (1999) Biovolume calculation for pelagic and benthic microalgae. J Phycol 35: 403-424

Holling CS (1966) The functional response of invertebrate predators to prey density. Mem Entomol Soc Can 48

Huntley M, Sykes P, Rohan S, Marin V (1986) Chemically mediated rejection of dinoflagellate prey by the copepods *Calanus pacificus* and *Paracalanus parvus*: mechanism, occurrenceand significance. Mar Ecol Prog Ser 28: 105–120

Huntley ME, Tande K, Eilersten HC (1987b) On the trophic fate of *Phaeocystis pouchetii* (Hariot) II. Grazing rates of *Calunus hyperboreus* (KryØr) on diatoms and different sizecategories of *Phaeocystis pouchetii.* J Exp Mar Biol Ecol 110: 197-212

Hyatt J (2006) Wind, sea ice, inertial oscillations and upper ocean mixing in Marguerite Bay, Western Antarctic Peninsula: Observations and Modeling. Dissertation, Massachuesetts Institute of Technology and Woods Hole Oceanographic Institution.

Ikeda T, Dixon P (1982) Body shrinkage as a possible over-wintering mechanism of the Antarctic krill, *Euphausia superba* (Dana). J Exp Mar Biol Ecol 62(2):143-151

Kawaguchi K, Ishikawa S, Matsuda O (1986.) The overwintering strategy of Antarctic krill (*Euphausia superba* Dana) under the coastal fast ice off the Ongul Islands in Luetzow-Holm Bay, Antarctica. Proceedings of The Eighth Symposium On Polar Biology, 1985. Mem Natl Inst Polar Res (Japan) (Spec. Iss.) (4):67-85

Kottmeier ST, Sullivan CW (1987) Late winter primary production and bacterial production in sea ice and seawater west of the Antarctica Peninsula. Mar Ecol Prog Ser 36: 287–298

Kristiansen S, Syvertsen EE, Farbrot T (1992) Nitrogen uptake in the Weddell Sea during late winter and spring. Polar Biol 12: 245-251

Lizotte MP (2001) The contributions of sea ice algae to Antarctic marine primary production. Am Zool 41:57-73

Makarov R (1980) Larval Development of the Antarctic Euphausiids. BIOMASS Handbook no. 3:6-13

Marin V, Huntley ME, Frost BW (1986) Measuring feeding rates of pelagic hebivores: analysis of experimental design and methods. Mar Biol 93:49-58

Marschall HP (1988) The overwintering strategy of Antarctic krill under the pack-ice of the Weddell sea. Polar Biol 9:129-135

Massom RA, Stammerjohn SE, Smith RC, Pook MJ, Iannuzzi RA, Adams N, Martinson DG,Vernet M, Fraser WR, Quetin LB, Ross RM, Massom Y, Krouse HR (2006) Extremeanomalous atmospheric circulation in the West Antarctic Peninsula region in AustralSpring and Summer 2001/02, and its profound impact on sea ice and biota. J Clim, 19: 3544–3571

Mauchline J (1980) Measurement of body length of *Euphausia superba* Dana: BIOMASS Handbook, vol. 4, pp. 4–9. SCAR/SCOR

Menden-Deuer S, Lessard EJ (2000) Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnol Oceanogr 45: 569–579.

Meyer B, Atkinson A, Stübing D, Hagen W, Oettl B, Bathman UV (2002) Feeding and energy budgets of Antarctic krill *Euphausia superba* at the onset of winter-I. Furcilia III larvae. Limnol Oceanogr 47(4):943-952

McMinn A, Scott FJ (2005) Dinoflagellates. In: Scott FJ, Marchant HJ (Eds) Antarctic marineprotists. Australian Biological Resources Study, Australian Antarctic Division, Canberra Hobart, pp. 202-250.

Nejstgaard JC, Naustvoll LJ, Sazhin A (2001) Correcting for underestimation of microzooplankton grazing in bottle incubation experiments with mesozooplankton. Mar Ecol Prog Ser 221: 59–75.

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

Perez M, Sulkin S (2005) Palatability of autotrophic dinoflagellates to newly hatched larval crabs. Mar Biol 146:771–780

Price HJ, Boyd KR, Boyd CM (1988) Omnivorous feeding behavior of the Antarctic krill *Euphausia superba*." Mar Biol 97:67-77

Quetin LB, Ross RM (1985) Feeding by Antarctic Krill, *Euphausia superba*: Does size matter? In: Siegfried WR, Condy PR, Laws RM (eds) Antarctic Nutrient Cycles and Food Webs. Springer-Verlag Berlin Heidelberg, pp 372-377

Quetin LB, Ross RM (1988) Summary of WinCruise II to the Antarctic Peninsula during June and July 1987. Antarct J US 23:149-151

Quetin LB, Ross RM (1991) Behavioral and physiological characteristics of Antarctica krill, *Euphausia superba.* Am Zool 31:49-63

Quetin LB, Ross RM, Clarke A (1994) Krill energetics: seasonal and environmental aspects of the physiology of Euphausia superba. In: El-Sayed SZ (ed) Southern Oceanecology. Cambridge University Press, Cambridge, pp 165–184

Quetin LB, Ross RM, Frazer TK, Haberman KL (1996) Factors affecting the distribution and abundance of zooplankton, with an emphasis on Antarctic Krill, *Euphausia superba*. In: Ross RM, Hofmann EE, Quetin LB (eds) Foundations for Ecological Research West of the Antarctic Peninsula. American Geophysical Union, Washington D.C. pp 357-371

Quetin LB, Ross RM (2003) Episodic recruitment in Antarctic krill *Euphausia superba* in the Palmer LTER study region. Mar Ecol Prog Ser 259:185–200

Quetin LB, Ross RM, Frazer TM, Amsler M, Wyatt-Evens C, Oakes, SA (2003) Growth of larval Antarctica krill in fall and winter west of the Antarctic Peninsula. Mar Biol 143:833-843

Quetin LB, Ross RM, Fritsen CH, Vernet M (2007) Ecological responses of Antarctic krill to environmental variability: can we predict the future? Antarct Sci 19: 253–266

Ross RM, Quetin LB (1986) How productive are Antarctic krill? BioScience 36:264-269

Ross RM, Quetin LB, Newberger T, Oakes SA (2004) Growth and behavior of larval krill (*Euphausia superba*) under ice in late winter 2001 west of the Antarctic Peninsula. Deep Sea Res II: Spec Top Oceanogr 51(17-19):2169-2184

Siegel V, Loeb S (1995) Recruitment of antarctic krill *Euphausia superba* and possible causes for its variability. Mar Ecol Prog Ser 123(1-3): 45-56

Smetacek V, Scharek R, Nöthig EM (1990) Seasonal and regional variation in the pelagical and its relationship to the lifecycle of krill. In: Kerry KL, Hempel G (eds). Antarctic Ecosystems, Ecological Change and Conservation, Springer-Verlag, Berlin pp 103-114

Schnack-Schiel SB, Thomas D, Dieckmann GS, Eiken H, Gradinger R, Spindler M, Weissenberger J, Mizdalski E, Beyer K (1995) Life cycle strategy of the Antarctic calanoid copepod *Stephos longipes*. Prog Oceanogr 36:45-75

Sakshaug E, Holm-Hansen O (1986) Photoadaptation in antarctic phytoplankton: variations in growth rate, chemical composition and *P* versus *I* curves. J Plankton Res 8:459–473

Smith Jr WO, Nelson DM (1990) Phytoplankton growth and new production in the Weddell Sea marginal ice zone in the austral spring and autumn. Limnol Oceanogr 35:809–821

Stretch JJ, Hamner PP, Hamner WM, Michel WC, Cook J, Sullivan CW (1988) Foraging behavior of Antarctic krill *Euphausia superba* on sea ice microalgae. Mar Ecol Prog Ser 44:131-139

Stuart V (1989) Observations on the feeding of *Euphausia lucens* on natural phytoplankton suspensions in the southern Benguela upwelling region. Cont Shelf Res 9(11):1017-1028

Swadling KM, Gibson JAE, Ritz DA, Nichols PD, Hughes DE (1997) Grazing of phytoplankton by copepods in eastern Antarctic coastal waters. Mar Biol, 128:39–48

Torres J J, Aarset AV, Donnelly J, Hopkins TL, Lancraft TM, Ainley DG (1994) Metabolism of Antarctic micronektonic Crustacea as a function of depth occurrence and season. Mar Ecol Prog Ser 113(3):207-219

Vargo GA, Fanning K, Heil C, Bell L (1986) Growth rates and the salinity response of an Antarctic ice microflora community. Polar Biol 5: 241-247

Venrick EL (1978a) How many cells to count? In: Sournia, A. (ed.), Monographs on Oceanographic Methods 6: Phytoplankton Manual. United Nations Educational, Scientific and Cultural Organization, Paris, pp 167–180

Verity PG, Sieracki ME (1993) Use of color-image analysis and epifluorescence microscopy to measure planktonic biomass. In: Kemp PF, Sherr BF, Cole JJ (Eds) Handbook of Methods in Aquatic Microbial Ecology, Lewis Boca Raton, 327-338

Table 1. Experiment grazing material source, presence or absence of copepods, latitude and longitude of grazing material collection, date collected, volume of grazing material, volume of seawater dilution and date of experiment.

Experiment	Grazing Material Source	Copepods (copepod L^{-1})	Latitude (°S)	Longitude (°W)	Date Collected	Volume Grazing Material (L)	Filtered Sea Water Added (L)	Experiment Run Date
1	Core	4[a]	67° 38.500'	70° 37.000'	18-Sep-01	4.0	13	20-Sep-01
2	Core	4[a]	67° 38.500'	70° 37.000'	18-Sep-01	4.0	16	23-Sep-01
3	Core	13[a]	67° 38.500'	70° 37.000'	18-Sep-01	10	10	24-Sep-01
4	Ice	3[b]	67° 54.360'	69° 36.900'	24-Sep-01	2.0	18	25-Sep-01
5	Ice	0[c]	67° 54.360'	69° 36.900'	24-Sep-01	0.9	19.1	27-Sep-01
6	Brine	8[a]	68° 03.600'	69° 50.900'	27-Sep-01	20	0	28-Sep-01
7	Brine	12[c]	68° 03.600'	69° 50.900'	27-Sep-01	12.5	7.5	29-Sep-01
8	Slush	4[c]	68° 15.700'	69° 48.500'	30-Sep-01	2.0	18	30-Sep-01
9	Slush	4[c]	68° 15.700'	69° 48.500'	30-Sep-01	1.1	19	1-Oct-01
10	Slush	7[c]	68° 10.700'	69° 41.650'	3-Oct-01	2.8	17	3-Oct-01
11	Slush	6[c]	68° 10.700'	69° 41.650'	3-Oct-01	2.0	18	4-Oct-01
12	Slush	0[c]	68° 10.700'	69° 41.650'	3-Oct-01	1.3	18.7	5-Oct-01
13	Slush	18[c]	68° 10.700'	69° 41.650'	3-Oct-01	1.5	18.5	6-Oct-01
14	Ice	0[c]	68° 06.700'	70° 15.400'	6-Oct-01	0.8	19.2	7-Oct-01
15	Ice	7[b]	68° 14.800'	70° 16.700'	12-Oct-01	3.0	17	13-Oct-01
16	Ice	0[b]	68° 14.800'	70° 16.700'	12-Oct-01	6.0	14	14-Oct-01
17	Ice	0[b]	68° 14.800'	70° 16.700'	12-Oct-01	0.5	19.5	15-Oct-01

[a] grazing material poured through 500 μm mesh
[b] grazing material not poured through 500 μm mesh
[c] no record of whether grazing material was poured through mesh

Table 2. Initial cell volume distribution for grazing experiments based on taxomonic groupings. Solitary *Phaeocystis sp.* (SPHAEO), colonial *Phaeocystis sp.* (CPHAEO), all diatoms (DIATOM), autotrophic *Gymnodinium sp.* (GYMNO), cryptomonad (CRYPTO), and autotrophic monad (MONAD), rare and large heterotrophs (HET), and common small heterotrophs (SMALL HETERO). Min is minimum, Max is maximum, and Med is median cell volume.

		Experiment								
Group	Vol (μm^3)	1	2	3	4	5	6	7	8	9
SPHAEO	Min	14	14	96	14	14	14	14	14	14
	Max	34	113	-	34	48	34	34	34	34
	Med	22	14	-	14	22	14	14	14	14
CPHAEO	Min	268	524	576	1357	-	2145	2945	131	268
	Max	294,524	220,893	705,217	-	-	3054	32,070	220,893	104,720
	Med	11,454	33,510	30,024	-	-	-	2945	8181	6283
GYMNO	Min	245	245	226	402	385	2	503	105	335
	Max	3901	2945	6283	13,450	3780	6283	8181	11,454	13,090
	Med	1131	1047	1412	2294	1230	1131	1508	1230	2225
DIATOM	Min	4	4	5	3	1997	5	5	13	47
	Max	57,467	12,528	163,625	46,121	7210	4038	57,596	3927	11,520
	Med	158	97	131	21	2312	382	94	165	141
CRYPTO	Min	79	92	92	105	118	79	79	-	-
	Max	628	257	2945	1593	785	995	1047	-	-
	Med	131	170	188	244	268	257	257	-	-
MONAD	Min	79	151	23	231	283	131	785	180	226
	Max	4241	4241	628	16,493	5236	34,407	-	11,454	16,493
	Med	396	2288	180	2985	4241	12,788	-	11,454	2719
	Min	50	10	19	50	13	2	34	92	113
HET	Max	14,137	6283	25,918	42,412	32,070	19,085	23,562	4189	1357
	Med	524	231	113	231	98	681	832	302	188
SMALL	Min	-	-	-	-	-	-	-	-	-
HET	Max	-	-	-	-	-	-	-	-	-
	Med	-	-	-	-	-	-	-	-	-

Table 2. Continued

		Experiment							
Group	Vol (μm^3)	10	11	12	13	14	15	16	17
SPHAEO	Min	14	34	14	14	4	14	14	4
	Max	34	65	48	34	48	14	65	65
	Med	14	34	22	14	14	14	34	14
CPHAEO	Min	268	84	188	67	151	65	180	65
	Max	523,599	220,893	368,155	220,893	220,893	113,097	1,227,185	791,943
	Med	8181	2945	8181	5236	5131	785	1767	8378
GYMNO	Min	207	67	157	503	257	402	402	603
	Max	5937	5429	5445	4241	3902	5089	8378	11,454
	Med	973	1357	942	1131	942	2386	1884	2356
DIATOM	Min	15	8	13	38	63	2	2	3
	Max	641	654	737	2279	838	524	13,500	589
	Med	165	99	151	123	151	94	94	53
CRYPTO	Min	-	-	92	50	-	-	151	-
	Max	-	-	369	942	-	-	628	-
	Med	-	-	308	-	-	-	207	-
MONAD	Min	4241	50	84	28	28	42	3	2
	Max	9817	8378	7658	15,708	9163	226	10,137	180
	Med	-	228	382	170	89	123	6283	50
	Min	19	14	24	50	28	3	10	19
HET	Max	6283	4712	22,907	11,454	2945	5236	530,144	5236
	Med	141	131	157	188	151	207	335	65
SMALL	Min	-	-	-	14	8	4	-	4
HET	Max	-	-	-	-	34	-	-	14
	Med	-	-	-	-	13	-	-	9

Table 3.Total initial carbon concentration (μl^{-1}), Ingestion rates for *Euphausia superba* feeding on carbon type and taxonomic groupings of sea ice biota and percent of initial total carbon for each grouping. Total initial carbon (TOTAL C), ingestion rates (ING) in μgC gWM^{-1} h^{-1} +/- standard error (STERR) and percent of total initial carbon (% C) for total, autotrophic (AUT C), heterotrophic (HET C), autotrophic *Gymnodinium sp.* carbon (GYMNO), solitary and colonial *Phaeocystis sp.* carbon (PHAEO C), diatom carbon (DIATOM C), cryptomonad carbon (CRYPTO C), and autotrophic monad carbon (MONAD C). Ingestion rates in bold are considered significantly different from zero because zero is not contained within 2 standard errors (sterr) of the mean. Ingestion rates that do no contain zero within 1 standard error of the mean are possibly significant.

	CARBON TYPE					
EXPT	**TOTAL C**		**AUT C**		**HET C**	
	($\mu g\ l^{-1}$)	**ING +/- (STERR)**	**% C**	**ING +/- (STERR)**	**% C**	**ING +/- (STERR)**
1	62	-21 (30.0)	92	-9 (14)	8	-6.6 (9.5)
2	45	**-70 (25)**	97	**-35 (3.3)**	3	**-4.4 (2.1)**
3	68	**16 (6.4)**	93	-24 (20)	7	13 (7.3)
4	21	**28 (2.8)**	79	**23 (3.4)**	21	**5.9 (2.3)**
5	15	**24 (4.4)**	58	**20 (4.2)**	42	-0.8 (1.8)
6	44	**98 (36)**	51	**53 (12)**	49	48 (31)
7	17	12 (9.5)	71	**16 (3.8)**	29	-3.3 (4.3)
8	33	**82 (23)**	92	**80 (21)**	8	**3.6 (1.7)**
9	23	**62 (15)**	97	**67 (22)**	3	0.9 (0.66)
10	36	37 (21)	97	**46 (16)**	11	-1.7 (4.4)
11	53	**42 (11)**	95	**44 (14)**	5	2.7 (2.6)
12	34	**82 (6.9)**	79	**61 (5.8)**	21	**23 (1.5)**
13	73	**54 (6.5)**	83	**44 (3.3)**	17	**11 (4.4)**
14	13	14 (11)	78	11 (8.7)	22	2.5 (2.2)
15	29	**61 (6.7)**	83	**48 (5.5)**	17	**14 (1.2)**
16	201	166 (94)	58	105 (56)	42	-3.0 (26)
17	12	**26 (1.5)**	62	**22 (0.33)**	38	**4.3 (0.67)**

Table 3 continued.

	AUTOTROPHIC CARBON TYPE									
EXPT	**GYMNO C**		**PHAEO C**		**DIATOM C**		**MONAD C**		**CRYPTO C**	
	% C	**ING +/- (STERR)**	**% C**	**ING +/- (STERR)**	**% C**	**ING +/- (STERR)**	**% C**	**ING +/- (STERR)**	**% C**	**ING +/- (STERR)**
1	53	-14 (9.4)	23	4.2 (3.8)	13	**6.0 (1.6)**	2	13 (7.2)	2	**-0.9 (0.01)**
2	81	**-22 (7.9)**	9	-2.9 (1.9)	4	**-2.5 (0.84)**	2	**-2.4 (0.60)**	1	0.4 (0.25)
3	47	**-51 (12)**	26	**44 (12)**	17	**6.1 (3.0)**	<1	-0.1 (0.18)	2	**0.7 (0.36)**
4	41	**21 (3.8)**	22	**3.2 (0.80)**	3	**2.7 (0.47)**	7	2.6 (4.0)	7	-0.3 (0.39)
5	26	**7.6 (2.3)**	15	3.6 (3.2)	3	-0.1 (0.49)	6	2.7 (1.6)	8	1.1 (0.74)
6	24	**24 (9.6)**	6	**3.6 (0.74)**	<1	**1.5 (0.47)**	17	**29 (4.6)**	4	**3.3 (0.49)**
7	34	**15 (0.82)**	22	1.6 (1.4)	6	**7.7 (2.5)**	<1	0.1 (0.07)	8	**0.3 (0.13)**
8	53	**77 (24)**	25	**12 (5.6)**	2	-0.3 (0.40)	12	**32 (8.3)**	0	-
9	59	**54 (28)**	27	**14 (0.03)**	2	0.4 (0.31)	9	**11 (5.5)**	0	-
10	45	**21 (9.3)**	36	**23 (3.1)**	2	**1.2 (0.12)**	5	2.2 (2.3)	0	-
11	38	**11 (3.5)**	52	**32 (11)**	1	**1.3 (0.36)**	3	1.6 (1.1)	0	-
12	29	**18 (1.5)**	47	**40 (5.6)**	3	**2.0 (0.15)**	3	**4.2 (1.7)**	<1	**0.15 (0.05)**
13	43	**23 (3.9)**	33	**23 (2.9)**	3	-0.2 (0.46)	3	-2.2 (1.8)	<1	**-0.6 (0.0)**
14	27	3.8 (4.4)	36	**4.9 (1.8)**	7	**0.9 (0.06)**	8	4.7 (2.9)	0	-
15	35	**23 (6.5)**	40	**23 (8.9)**	8	**2.3 (0.48)**	<1	**0.6 (0.02)**	0	-
16	13	**36 (13)**	39	72 (45)	2	**2.7 (0.09)**	3	**-19 (0.08)**	<1	0.1 (0.09)
17	34	2.3 (1.7)	26	**9.1 (1.3)**	2	**1.0 (0.29)**	<1	0.05 (0.09)	0	-

Table 4. Comparison of clearance rate and ingestion in terms of daily ration for similar stage *Euphausia superba* in spring, summer and fall to winter values from this study. Krill stages are furcilia 3 (F III) , furcilia 4 (FIV), furcilia 5 (FV) and furcilia 6 (F VI). Total carbon (TOTAL C) Autotrophic carbon (AUT C), heterotrophic carbon (HET C), natural seawater (NSW), enriched seawater (ESW), *Nitzchia curta* (*N. curta*), wet mass (WM).

Study	Krill Stage or Size	Month	Experiment Type	Food Type	Carbon (ug l^{-1})	Temperature °C (ave)	Clearance Rates (ml mgWM^{-1} h^{-1}) Max	Min	Daily Ration (% body C d^{-1})
Ross and	F IV	Mar.	Feeding	*Thalassiossira sp.*	~0-360[a]	-1.5	4.4	1.0	-
Quetin unpub.	F VI		Incubation		~0-320[a]	-1.5	10	0	
Daly 1990	8mm	Jun. –	Gut	AUT C in water	6	-0.5	20[b]	-	3.2
	8mm	Aug.	Fluorescence	AUT C in sea ice	259	-0.5	-	0.3[b]	2.0
Atkinson et al.	Juvenile	Apr.	Feeding	NSW	~0-300	-1[b]	0.45[c]	0[c]	0-0.8
2002	28-38 mm		Incubation	ESW	~0-100	-1[b]	0.34[c]	0[c]	0-0.5
Meyer et al.	F III	Apr.	Feeding	NSW	2.7-4.7	0	4.9[d]	1.0[d]	0.4-1.3
2002			Incubation	ESW	35-216	0	3.6[d]	1.8[d]	2-28
Pakhomov et	F III-F V	Apr.	Gut	NSW	~0-200	-1	-	-	17.8-29.2
al. 2004			Fluorescence						
Oakes	FVI –	Nov. –	Feeding	*N. curta* on surface	50-492	-1.8	4.1	0.5	0-16
(chapter 1)	Juvenile	Dec.	Incubation	*N. curta* in water	42-1389	-1.5	3.3	0.08	0.13-84[e]
This Study	FVI-	Sep. –	Feeding	Sea ice TOTAL C	12-201	-1.5	3.8	0	0-17
	Juvenile	Oct.	Incubation	Sea ice AUT C	7.4-116	-1.5	4.0	0	0-11
	6-12 mm			Sea ice HET C	0.75-85	-1.5	4.7	0	0-4.1

[a]assuming c:chl a ratio of 40

[b]For 8-mm krill, $WW=1.02 \times 10^{-3} L^{3.49}$, WW(wet weight in mg) and L(length in mm) from Daly (1990)

[c]28-38-mm krill for algae at 1-2°C adjusted to -1°C (Atkinson et al.,2002), DM(dry mass)=0.226WM(wet mass) from Quetin and Ross (2004)

[d]C(carbon)=0.357DM (Meyer et al., 2002), DM=0.12WM (Elias, 1990)

[e]high c:chl a ratio of 113

Figure 1. Comparison of carbon estimated from cell volume and from particulate organic carbon (POC) analysis. Solid line is linear fit to data ($y=0.168 x -5.61$, $R^2=0.376$). Linear fit is significant (ANOVA $\alpha=0.05$, $p<<0.002$).

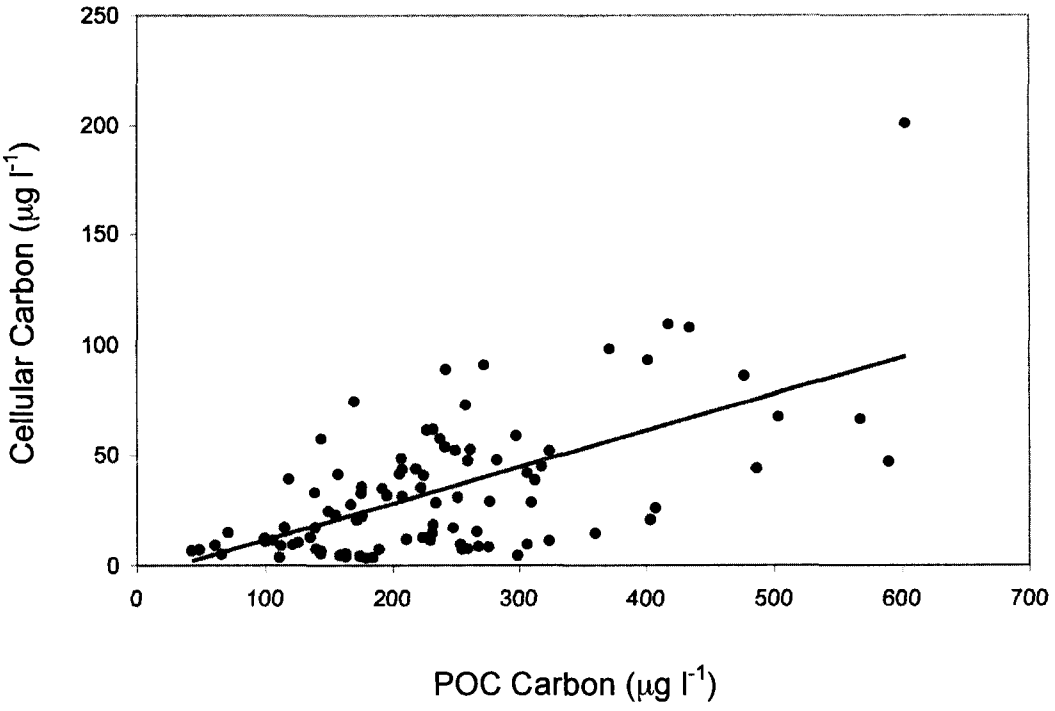
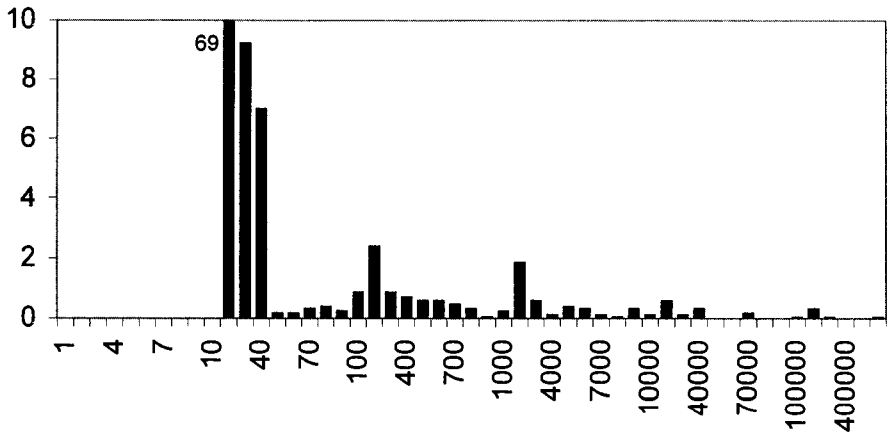
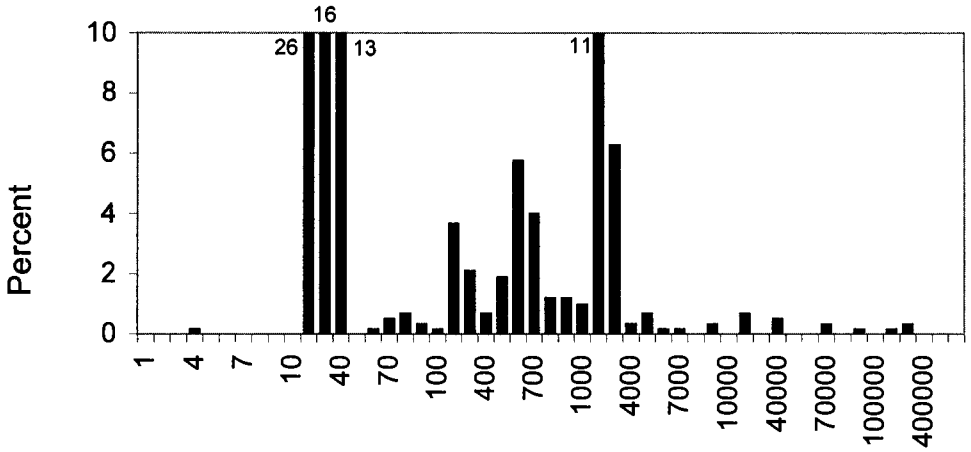

250
200
150
100
50
0
Cellular Carbon (µg l-1)
0
100
200
300
400
500
600
700
POC Carbon (µg l-1)

Figure 2. Cell volume distribution as a percent of total cells. a) typical - expt. 11, b) larger cells present - expt. 3, and c) small heterotrophic cells present - expt. 16

a) Experiment 11



b) Experiment 3



c) Experiment 16

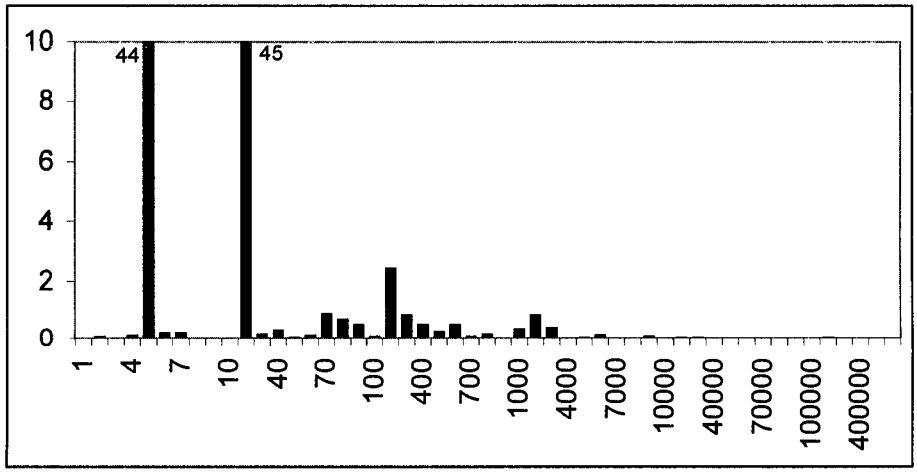


Figure 3. Carbon ingestion rates by *Euphausia superba* grazing on sea ice microbial communities for total carbon (a), autotrophic carbon (b) and heterotrophic carbon. Solid line is a Type II non-linear fit to the data (closed circles) with Ivlev's Equation (1961): $Ing_C=Ing_{max}*(1-e^{-a*C})$. Three experiments with high percent of autotrophic dinoflagellate carbon were not included in the equation. a) Feeding response to total carbon. Maximum ingestion (Ing_{max}) = 166 µgC gWM^{-1} h^{-1}. Parameter a=0.0149 determined by iteration (R^2=0.671). b) Feeding response to autotrophic carbon. Maximum ingestion (Ing_{max}) = 105µgC gWM^{-1} h^{-1}. Parameter a=0.022 determined by iteration (R^2=0.560). c) Feeding response to heterotrophic carbon. No trend detected. Error bars are standard error.

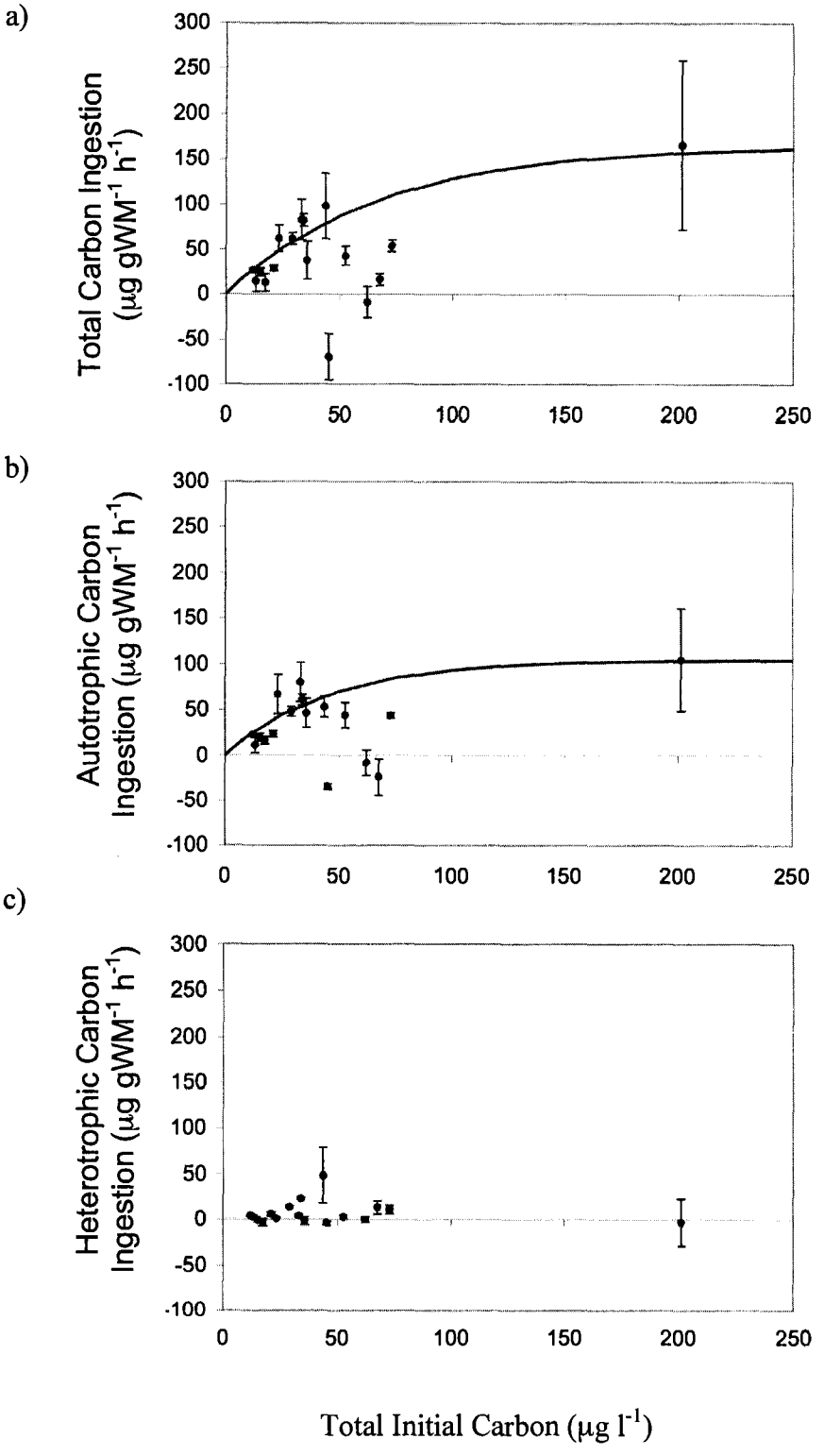

a)
Total Carbon Ingestion (µg gWM-1 h-1)
300
250
200
150
100
50
0
-50
-100
0
50
100
150
200
250
b)
Autotrophic Carbon Ingestion (µg gWM-1 h-1)
c)
Heterotrophic Carbon Ingestion (µg gWM-1 h-1)
Total Initial Carbon (µg l-1)

Figure 4. Total carbon ingestion rates by *Euphausia superba* grazing on sea ice microbial communities with total carbon compared to the percent of autotrophic (a) and percent of heterotrophic (b) carbon. a) Total carbon ingestion rate (circle) and percent autotrophic carbon (open diamond). b) Total carbon ingestion (circle) and percent heterotrophic carbon (open diamond). Error bars are standard error.

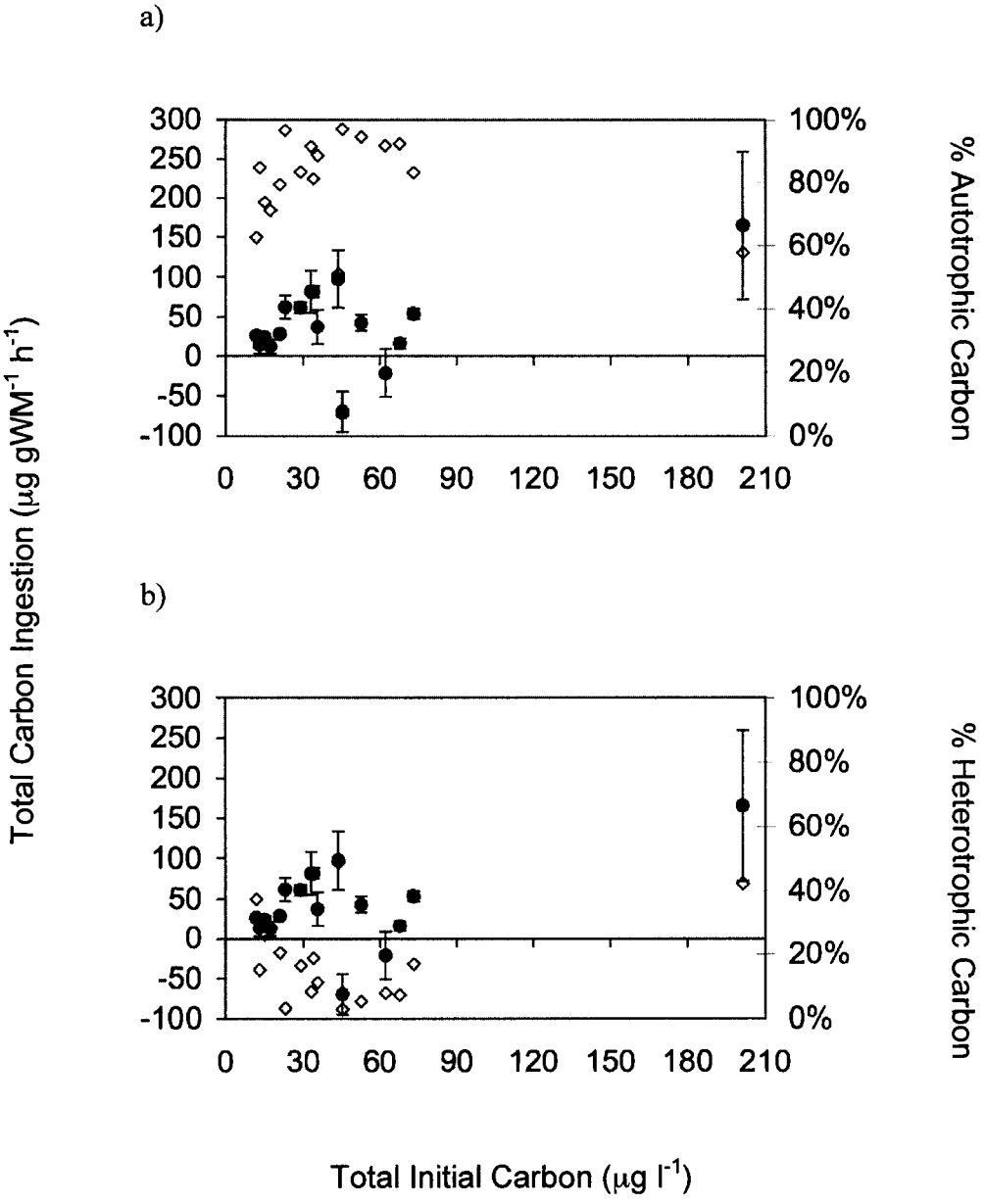
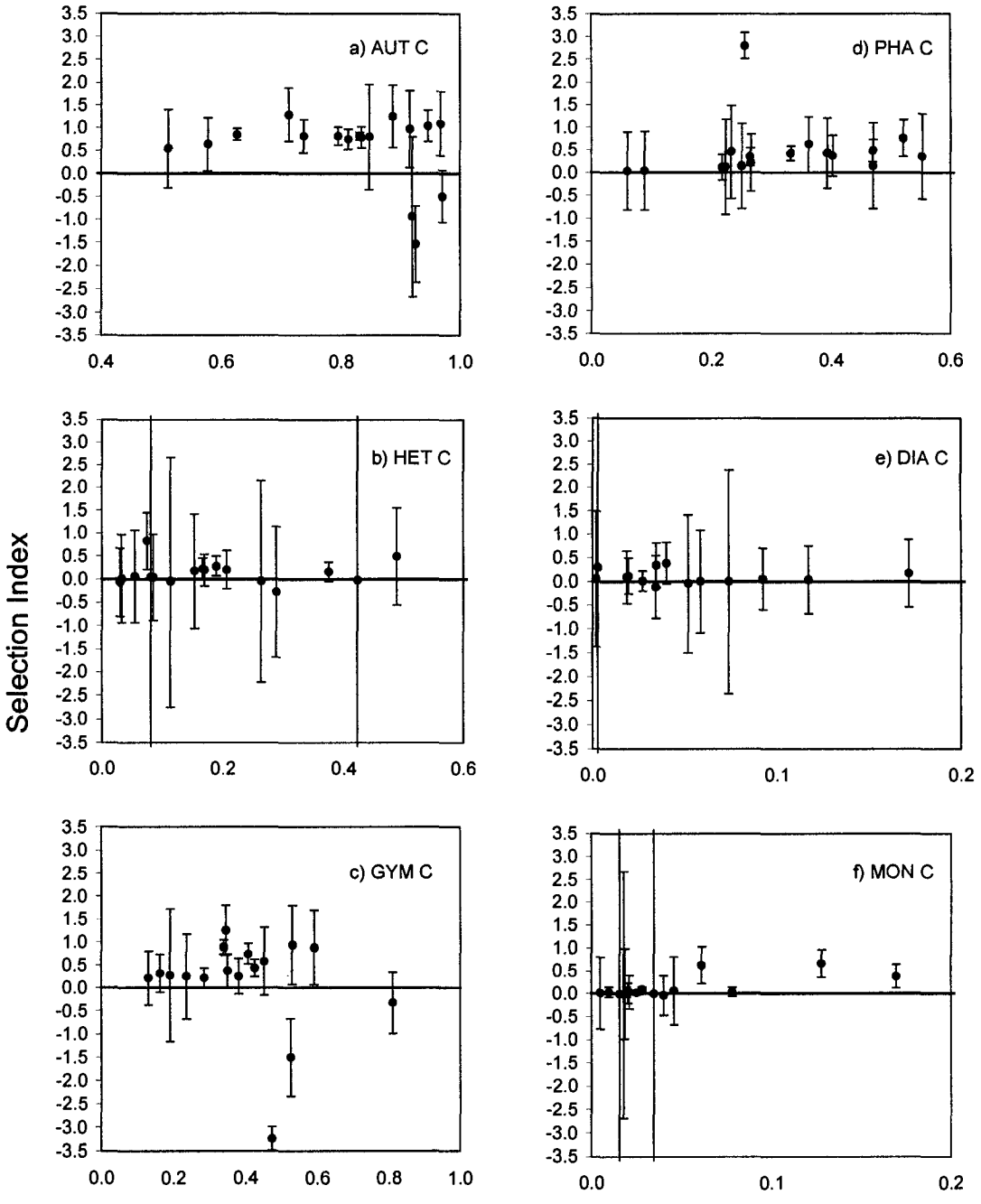

a)
b)
300
250
200
150
100
50
0
-50
-100
0
30
60
90
120
150
180
210
100%
80%
60%
40%
20%
0%
% Autotrophic Carbon
% Heterotrophic Carbon
Total Carbon Ingestion (μg gWM-1 h-1)
Total Initial Carbon (μg l-1)

Figure 5. The selection index of autotrophic (a), heterotrophic (b) *Gymnodinium sp.* (c), *Phaeocystis sp.* (d), diatom (e) and autrotrophic monad (f) carbon ingestion compared to the proportion of initial autotrophic (a), heterotrophic (b), *Gymnodinium sp.* (c), *Phaeocystis sp.* (d), diatom (e), and autrophic monad (f) carbon. Horizontal line represents 1:1 response in the ratio of ingestion to the ratio of carbon type. Points falling above the line indicate accelerated ingestion on carbon type. Points falling below the line indicate decelerated or no ingestion on carbon type. Error bars are standard error.


a) AUT C
b) HET C
c) GYM C
d) PHA C
e) DIA C
f) MON C
Selection Index
Initial Proportion Carbon Type Available

CHAPTER 3:

A PHYSIOLOGICALLY BASED MODEL OF LARVAL AND SUB-ADULT KRILL (*EUPHAUSIA SUPERBA*) GROWTH IN WINTER

ABSTRACT

Possible changes in sea ice conditions in the western Antarctic peninsula (timing of formation, shift to more southerly latitudes) that impact the development of the sea ice microbial community, raise questions as to the ability of sea ice-dependant organisms to adapt to regional warming. A physiologically-based model was constructed to examine the effect of food conditions and feeding behavior on the growth of larval and sub-adult Antarctic krill (*Euphausia superba*) during winter. The model incorporated (1) assimilation efficiencies (70 to 91%) measured for larval krill feeding on sea ice microbes during late winter 2001; (2) winter ingestion for larval and juvenile krill feeding both in the simulated water column and on simulated sea ice surface (Chapter 1); and (3) winter respiration for larval and adult stage krill. Feeding behavior was budgeted daily based on observations of krill behavior and correlations between day length and growth. Thus, day length with latitude was a driver of krill foraging behavior. Winter growth (julian day 140 to 230) was simulated for krill of initial wet mass 2, 5, and 100 mg, representing larval krill from March and January spawnings, and sub-adult krill entering their second winter, respectively. Model results indicate that many conservative combinations of water column and sea ice chl *a* (indicators of food quantity), and C:chl *a* ratios (indicator of food quality) sustain krill during winter. Older larvae required the same C:chl *a* ratios as sub-adult krill but needed higher chl *a* concentrations to survive. Younger larvae required higher chl *a* and C:chl *a* ratios $\geq$ 40 to survive. To survive, sub-adult krill needed the lowest chl *a* concentrations for

a given C:chl *a* ratio. Model-derived growth increments (GI) and daily growth rates (DGR) agreed with field-based and laboratory measurements. GIs and DGRs higher than reported values may indicate that larval krill from a late season spawning are not physically mature enough to reach maximum length (15 mm) by the end of winter. GIs and DGRs for sub-adult krill that reached maximum allowed length (30 mm) were higher than those reported but comparative measurements of winter growth for sub-adult krill are few. Our model predicts krill survival and growth under chl *a* and C:chl *a* conditions that krill are likely to encounter during winter.

INTRODUCTION

Antarctic krill, *Euphausia superba,* has long been considered an important species in the Antarctic marine ecosystem. Krill directly link primary production to higher predators and sequester carbon to the deep sea via rapidly sinking fecal pellets (Tarling and Johnson 2006, Swadling 2006). Understanding the growth of krill is important for the management of stocks, and models that project total length with age are important for assessing stock yields (Candy and Kawaguchi 2006). Gravid females spawn during the summer, mainly during January and February (Quetin and Ross 1986). Depending on latitude and sea ice conditions (Ross and Quetin 2000), female krill may spawn as early as late November (Spiridonov 1995) and as late as early April (Quetin et al. 1994, personal observation). Embryos released over deep water hatch and larvae progress through naupliar and calyptosis stages to furcilia by fall (Fraser 1936). By mid-winter later stage furcilia (FV and FVI) usually dominate but earlier stages (FI – FIV) are also found (Frazer 2002). A critical period for larval krill is the first winter (Ross and Quetin 1991, Quetin et al. 1996), due to low starvation tolerance (Ikeda and Dixon 1982) and limited food supply (Smith et al. 1996). It is generally accepted that larval krill must continue to feed during the winter in order to survive and mature to young-of-year the following spring (Daly 1990, Meyer et al. 2002).

Previous models of krill growth include individual-based phenomenological models (Astheimer et al. 1985) and models based on energetic and physiological parameters measured for adults in the laboratory (Huntley et al. 1994, Hofmann and

Lascara 2000). More recently, empirical models to predict growth trends for krill with sex, length, season, and region or maturity stage have been constructed based on instantaneous growth rate (IGR) measurements (Atkinson et al. 2006) with linear mixed models (Kawaguchi et al. 2006, Candy and Kawaguchi 2006).

Only a few models have included growth in larval and or sub-adult stage krill. Astheimer et al. (1985) used a 'black box' pre-defined growth function and did not attempt to model complicated processes individually. Huntley et al. (1994) focused on winter growth of 20, 30, and 40 mm krill under three scenarios: 1) no ingestion and reduced winter metabolism, 2) no ingestion and summer metabolism and 3) winter ingestion with growth efficicency of 0 or 0.25. Hofmann and Lascara (2000) simulated growth of 2, 22 and 45 mm krill from Julian dat3 32 to 500. They found the larval krill growth cycle best-fit observational data when reduced winter metabolism and an additional food source (sea ice algae) were included. Prior to Oakes (Chapter 1) no studies had quantified krill ingestion by sea ice surface grazing. Estimates of ingestion by this feeding mode were assumed to be 5% of ingestion by water column filtration (Hofmann and Lascara 2000) and may have underestimated energetic inputs from this feeding mode.

More recent experimental evidence suggests metabolism in larval krill is not reduced and ingestion is maintained over winter. From summer to fall neither oxygen uptake rates (Meyer et al. 2002a, 2002b) nor the level of the digestive enzyme citrate synthase (Meyer et al. 2002b) were reduced in furcilia III larvae. Feeding experiments showed furcilia III larvae maintained high clearance rates and

were capable of exploiting high food concentrations if available (Meyer et al., 2002). Thus, larval krill may not reduce metabolic rates at the onset on winter as a physiological necessity and continue to feed.

Several aspects of previous models can now be substantially improved. First, no models have included measured estimates of winter ingestion for both water column filtration and sea ice surface scraping, both known feeding modes (Hamner 1983, summarized in Quetin et al. 1996). Second, assimilation efficiencies for larval krill during winter have not previously been available. Results reported here on the effect of day length on krill feeding behavior have not been considered, so time budgets for feeding have been based on assumptions about behavior. We present here a physiologically-based model that incorporates ingestion rates for two feeding modes, assimilation efficiencies, and respiration rates, all measured during winter or at winter temperatures. Also, we distinguish between time spent on water column filtration and sea-ice scraping based on observations of krill behavior under ice floes (Quetin et al. in prep). The relative amount of time spent in either environment may depend on day length, and as a consequence may vary with latitude. Thus, we have included day length with latitude as a driver of diel migration that influences krill foraging behavior.

The aim of this model was to explore the general food conditions (combinations of chl *a* concentration in the sea ice and the water column and C:chl *a* ratio) that are suitable for survival and/or growth of larval and sub-adult krill, during the winter. Specifically, we were interested in exploring the possible impacts

of conditions ultimately driven by changing sea ice dynamics. If seasonal sea ice is restricted to the high latitudes (ie. 70 °S), if the sea ice forms late and a strong autotrophic component of the sea ice microbial community (SIMCO) fails to develop (ie. low chl *a* and high C:chl *a*), or if spawning is delayed (ie. larvae are from a March spawning), how could winter growth be impacted? The paper will be structured in two sections. First, I will describe the methodology and report the experimentally determined assimilation efficiencies. Second, I will describe the growth model and discuss the results. The ensuing discussion will incorporate elements from the experimental results and implication of the model results.

MATERIALS AND METHODS OF ASSIMILATION EFFICIENCY EXPERIMENTS

Assimilation efficiency (AE) can be calculated from simultaneous measurement of ingestion and egestion rates (ie. AE = ingestion – egestion). Fecal pellet production was measured in conjunction with experiments for larval krill feeding on the sea ice microbial community (SIMCO) on board the RVIB Nathaniel B. Palmer west of the Antarctic Peninsula during September and October of 2001, as described in detail (Chapter 2).

Feeding Experiments

During September and October 2001, late larval stage and early juvenile krill were collected from beneath the ice, with aquarium nets (~1000-μm mesh) by SCUBA divers. Once captured, krill were placed in insulated buckets of seawater and transferred back to the ship where they were placed in 2-l glass jars filled with filtered seawater. The jars were kept in tanks with flowing seawater to keep them near ambient water temperature (-1.5 ± 0.16 °C). Krill were kept 2 to 12 d prior to use in experiments and only actively swimming krill were used in experiments.

The SIMCO was collected from brine pits, ice blocks or ice cores and diluted with 0.45 μm-filtered seawater to a pre-determined chlorophyll *a* (chl *a*) concentration with a total volume of 20 l. Experimental (n = 2-4) and phytoplankton control (n = 2) buckets were filled with 3 l of well-mixed grazing material. The experimental and control buckets were cooled to ambient seawater temperature (-

1.5°C) before adding 20 krill to each experimental bucket. Krill were allowed to feed at -1.5 ± 0.16 °C for approximately 12 h.

Sub-samples of 100 ml (n = 6) were filtered (Millipore 0.45 μm HAWP filters) for determination of initial and final chl *a* concentration in all treatments. Sub-samples (n = 3) of varying volumes between 25 and 200 ml were filtered (13-mm A/E filters) for carbon and nitrogen (CHN) analysis in all treatments.

Ingestion Rate

Ingestion rate (μgC gWM^{-1} h^{-1}) based on chl *a* for calculating assimilation efficiency was calculated from phytoplankton growth rates and krill grazing rates according to the equations of Frost (1972) as modified by Marin (1986).

Fecal Pellet Production

Fecal pellet production was measured for krill from 6 experiments. To determine fecal pellet production, krill were transferred to shallow rectangular containers with mesh basket inserts and filled with 0.45 μm-filtered seawater. Since fecal pellets sink rapidly, the mesh baskets served to isolate krill from the fecal pellets. The containers were sealed and floated in flow-through seawater tanks at ambient temperature (-1.5 ± 0.16 °C) for 30 to 41 min, because fecal pellets egestion rates were found to decline after 30 to 40 min (Clark et al. 1988), then krill were removed.

The mesh baskets were shaken to dislodge any fecal pellets into the filtered seawater and the baskets removed. Fecal pellets were removed from each container with a glass pipette, placed in a small petri dish, cleaned of debris under a dissecting microscope, rinsed with 0.2 μm-filtered seawater, and transferred to a pre-combusted (500 °C, 1 h) 13-mm A/E filter with a dropper. A control filter was prepared with the same number of filtered seawater drops as required to transfer the fecal pellets to the A/E filter. The samples were subsequently dried for approximately 4 hours before being placed in pre-combusted (450 °C, 24 h) alumninum sleeves and plates. Samples were stored in a drying oven at 60 °C prior to elemental analysis.

Egestion rate (μgC gWM^{-1} h^{-1}) was calculated from the total carbon mass (μg) of fecal pellets for each container divided by the total wet mass (WM, g) of the krill in each container and the egestion time (h). The total carbon mass of the fecal pellets was the carbon mass of the fecal pellets on the experimental filter minus the control.

The krill from experimental containers were placed in filtered seawater until they could be measured and staged. The developmental stages of krill were determined by examining the telson under a dissecting microscope (Markarov 1980). Measured total length (TL) was standard measure 1 (Maucline 1980) and the relationship $WM = 0.180\ e^{(1.53\ TelL)}$ ($r^2 = 0.96$, $n = 31$) derived from data reported in Ross et al. (2004).

Chlorophyll a and Carbon Analysis

Chl *a* in HAWP filters was stored frozen at –70 °C in 20-ml glass scintillation vials prior to extraction in 90% acetone for 24 h at –20 °C. The extract was decanted into a test tube and then the fluorescence was read on a Turner Designs 10-AU-005 digital fluorometer.

Both fecal pellet and grazing material samples were analyzed for particulate organic carbon and nitrogen with a Control Equipment Corporation CEC 440HA automated organic elemental analyzer (Dumas combustion method) at the University of California Marine Science Institute Analytical Laboratory.

Assimilation Efficiency Calculation

Assimilation efficiency was calculated as

(1) $A_c = (I_c - E_c) / I_c$

where I_c is carbon ingestion and E_c is carbon egestion.

ASSIMILATION EFFICIENCY EXPERIMENTAL RESULTS

Results from experiments with krill feeding on SIMCOs based on microscopic examination can be found in Oakes (Chapter 2). Krill with an average wet mass of 6.6 mg fed SIMCOs at a range of particulate organic carbon concentration from 135 to 602 $\mu C\ l^{-1}$ had average egestion rates from 7 to 54 $\mu gC\ gWM^{-1}\ h^{-1}$. Mean assimilation efficiency calculated from these egestion rates and ingestions rates from the same krill ranged from 0.70 to 0.91 (Figure 1) and were not correlated with POC concentration (Spearman's Rank, $r_s = 0.257$, $P = 0.943$, $\alpha = 0.01$).

MODEL DESCRIPTION

The growth model was based on the physiological parameters of ingestion, assimilation efficiency and respiration. Growth was represented by an equation balancing carbon gain and loss.

(2) $Growth_c = Ingestion_c * Assimilation\ Efficiency_c - Respiration_c$

Other carbon loss terms such as reproductive output, molts and excretion were not considered. Loss due to reproductive output was zero because krill are not reproductively mature until their third summer (Seigel and Loeb 1995). Carbon lost as molts was not included because it represents a very small portion of body carbon (see discussion). Excretion of organic carbon has been suggested for zooplankton under nutrient limitation, but estimates of organic carbon excretion are problematic (Anderson et al. 2005) and were not included in our model. The choice of model parameters will be introduced in order, e.g. inputs based on experimental data reported in this paper or recent work by the authors will be first, followed by inputs based on the literature.

Ingestion

Ingestion has been found to have an allometeric relationship to size of the form $I = aWM^b$, where WM is wet mass and a, a constant, and b, the weight

coefficient, are estimated from data (Moloney and Field 1989). An analysis of maximum ingestion rate as a function of krill wet mass from grazing experiments reported in Chapter 1 and 2 estimated that b = 1, but there may have been an insufficient size range for an accurate estimate of b. Ross (1982a) found a weight coefficient of 0.910 for *Euphausia pacifica* which, when considered with our measurements, led to a choice of b =1. The parameter a was estimated by the measured mass specific chl *a* ingestion equations (equations 3 – 6 below, ie $I = I_{[chl\ a]} * WM^1$) for two size classes of krill feeding in two modes, water column filtration or surface scraping (Chapter 1). The small size krill represent larvae entering their first winter and the large size krill represent sub-adult krill entering their second winter. Ingestion by water column filtration is:

(3) $I_{[chl\ a]} = 26 * (1- e^{-0.0109*[chl\ a]})$, larval krill

(4) $I_{[chl\ a]} = 30 * (1- e^{-0.0086*[chl\ a]})$, sub-adult krill

Ingestion by surface scraping is:

(5) $I_{[chl\ a]} = [0.92* (e^{(2.892 * (1-e^{\wedge}(0.1193 * [chl\ a])})]- 0.92$, larval krill

(6) $I_{[chl\ a]} = [0.40* (e^{(4.613 * (1-e^{\wedge}(0.0426 * [chl\ a])})]- 0.40$, sub-adult krill

Ingestion is thus a function of both the chl *a* concentration and the wet mass of the krill and is converted to carbon for calculation via the C:chl *a* ratio.

Assimilation Efficiency

Mean assimilation efficiencies, as described in the assimilation efficiency results section, ranged from 0.70 to 0.91 (Figure 1). We used the mean value of 0.8 in all simulations.

Chlorophyll and Carbon to Chlorophyll Ratios

Along the Western Antarctic peninsula, chl *a* values ranged from 0.02 to 0.5 $\mu g\ l^{-1}$ in the winter water column (Stewart and Fritsen 2004, Daly 2004, Lizotte 2001) and from 1 to 610 $\mu g\ l^{-1}$ in sea ice (Stewart and Fritsen 2004, Lizotte 2001). In the model water column chl *a* values ranged from 0 to 1 $\mu g\ l^{-1}$, in increments of 0.1, and sea ice chl *a* ranged 0 to 15 $\mu g\ l^{-1}$, in increments of 0.5. We used C:chl *a* ratios of 10 -100 in increments of 10 to convert chl *a* ingestion to carbon ingested in each scenario. A C:chl *a* ratio of 10 might indicate a low-light adapted phytoplankton community, 40 a healthy phytoplankton-dominated community, and 100 a community with a significant heterotrophic component. We used conservative Chl *a* concentrations and C:chl *a* ratios (see discussion) that were fixed in each model simulation.

Feeding Time Budget Based on Day Length Variation with Latitude

In a study of in situ growth rates from multiple winter cruises Quetin et al. (2003) found that the growth increment of larval krill in most winters was linearly

related to day length at the time of the experiment ($r^2 = 0.74$, n = 49). Analysis of larval krill collected in drift nets deployed beneath the sea ice surface at multi-day ice camps suggests larval krill migrate to the sea ice surface during the day and descend the upper water column at night (Quetin et al. in prep). We incorporated day length as a driver of the habitat in which feeding occurred, ie. krill fed at the ice surface during day and in the water column during night. Krill were allowed to feed 24 h per day based on visual observations of gut fullness that indicate larval krill feed both night and day (Daly 1990). Day length was estimated by fitting second order polynomial equations to winter day length from Julian date 110 to 260 at three latitudes 64 °S, 66 °S and 70 °S (http://www.qpais.co.uk/modb-iec/dayleng.htm, March 2007). Krill would experience a period of total darkness at 70 °S and no feeding at the sea ice surface would occur.

Respiration Rates

Respiration rates were based on measurements of oxygen consumption at winter temperatures (-1.5°C) for larval krill held 1-2 days prior to respiration measurements (Frazer et al. 2002) and sub-adult krill (Quetin & Ross 1991). Respiration for larval krill in their first winter (R_1) were based on oxygen consumption of 2 – 14 mg (wet mass) krill

(7) $R_1 = VO_2\ (\mu l\ mg\ WM^{-1}\ h^{-1}) = 0.667 * WM^{-1.13}$

where WM is wet mass in mg. Starved krill had respiration rates approximately half of that of fed krill (Ikeda and Dixon 1984). Similarly, respiration rates for furcilia IV larval krill decreased approximately 23% over three days of starvation (Meyer and Oettl 2005).

Respiration rates for sub-adult krill (R_2) at winter temperature (-1.5°C) were based on rates of oxygen consumption for 30 – 55 mm krill (Quetin & Ross 1991)

(8) $R_2 = \log VO_2(\text{ml } h^{-1}) = 0.0285*TL(\text{mm})-2.7873$

where TL is total length. Oxygen consumption rates were converted to carbon respiration with the relation 1 mg C respired = (12/22.4) ml O_2 assuming an RQ of 0.72 for lipid metabolism (Ikeda & Bruce 1986).

Carbon Mass and Total Length

To convert among the carbon units in the model, initial input of krill wet mass, and the desired outputs in terms of total length and linear growth increment, the following conversions were used. The carbon mass of krill was estimated by the relationship between wet mass and carbon content

(9) $C = (92.884 * WM) - 113.185$

where C is carbon (μg) and WM is wet mass (mg) derived by Quetin and Ross (unpublished data) as reported by Elias (1990) ($R^2 = 0.98$).

Length was estimated from wet mass (mg) and length (mm) regression

(10) $TL = 5.6125 * WM^{0.3156}$

from krill data reported in Quetin et al. (2004) expanded with measurements of fresh krill in spring of 2002 (n=122, $R^2 = 0.9719$).

The model was initialized in late-May (Julian date 140) and iterated daily for 90 days within the MATLAB platform (version 7.4.0). Model krill of starting wet mass 2, 5 and 100 mg were exposed to 3400 combinations of constant conditions of C:chl *a*, chl *a* in sea ice and chl *a* in the water column under day length at 3 latitudes, and final carbon mass, total length, growth increment (mm d^{-1}) and growth per inter-molt period (% IMP^{-1}) were recorded.

MODEL RESULTS

Total Length at the End of 90-day Simulation

The initial total lengths of krill with a wet mass of 2 mg, 5 mg and 100 mg were 7.0 mm, 9.3 mm and 24 mm, respectively. The total length of a krill at the end of the 90-day simulation was a based on the balance between carbon mass lost through respiration as a function of body mass and the gain in carbon mass through assimilation of ingested chl *a* converted carbon via the C:chl *a* ratio. Ingestion was dependant on the concentration of chl *a* in the sea ice and sea water and the amount of time krill spend feeding in each environment based on day length with latitude.

Realistic combinations of environmental food conditions were defined by a minimum and maximum krill size. Larval and sub-adult krill were considered viable if they lost no more than approximately 50% of their original carbon mass (Ross and Quetin 1989, Meyer and Oettl 2004). This was equivalent to a minimum total length ≥ to 8 mm for 5 mg larval krill, ≥ 6.5 mm for 2 mg larval krill and ≥ 19 mm for sub-adult krill. Larval krill that were greater than 15 mm by winter's end were considered to be unrealistically large. Sub-adult krill were considered unrealistically large if they grew to more than 30 mm during the 90-day simulation. None of the results presented included combinations of environmental conditions that resulted in a krill that lost >53% carbon mass or grew unrealistically large (15 mm larvae or 30 mm sub-adult).

General Conditions Suitable for Winter Growth

Larval krill were initialized on Julian date 140 at two sizes: 5 mg WM (9 mm), representing older krill spawned in January, and 2 mg WM (7 mm), representing younger krill spawned in March. Of the 5 mg WM larval krill (8-15 mm) that survived the 90-day simulation, the majority were found at C:chl *a* ratios of 20 to 40 provided krill were exposed to high chl *a* in the sea ice and the water. Larval krill initialized at 2 mg only survived the simulation if C:chl *a* ratio was 40 or greater regardless of the chl *a* level as specified in the model. The majority of surviving sub-adult krill were found at C:chl *a* ratios between 10 and 30 and at high chl *a* levels in ice and water. As C:chl *a* levels increased viable krill were produced at progressively lower chl *a* levels in the ice and water.

Chl a Conditions Suitable for Larval and Sub-adult Krill

The range of C:chl *a* specified in the model all represented a high quality food source with little detritus or refractory carbon. As C:chl *a* increased, the amount of carbon assimilated by krill for a given chl *a* concentration increased. For each given C:chl *a* ratio viable krill were produced under a variety of chl *a* concentrations in the sea ice and in the water column. The total length of a simulated krill was a function of the day length, C:chl *a* ratio and the concentration of chl *a* in the sea ice and the water column.

Possible combinations of chl *a* concentration in the sea ice and the water column defined in the model that produced viable krill, as constrained by mass and

length in the model, are shown at a C:chl *a* ratio of 40 or 80 (colored circles, Figures 2–4) with krill foraging migration based on day length at a given latitude (64 °S, 66 °S or 70 °S). Shifting latitude to the south decreased the day length and altered the time budget of feeding. At higher latitudes, krill spent relatively less time feeding at the sea ice surface and relatively more time in the water column than at lower latitudes. Diel foraging migration to the sea ice surface stopped for a period at 70 °S. Additionally, each figure indicated combinations of sea ice and water column chl *a* that produced krill that are either too small to survive (empty lower left region) or are unrealistically large (empty upper right region).

Overall, graphs of the combinations of chl *a* in the sea ice versus chl *a* in the water column at a particular C:chl *a* ratio, that are suitable for krill survival, took two forms: diagonal bands or filled corners (Figures 2 – 4). When all graphs for modeled C:chl *a* ratios were combined , the general trend with C:chl *a* and chl *a* in the sea ice and water column became apparent (Figures 5, 6).

In graphs for older larval krill, at a given C:chl *a* level, suitable conditions formed a diagonal band spread between mid to high chl *a* values in the sea ice and water (Figure 2). At higher C:chl *a* ratios, the band was narrower and shifted towards lower values of chl *a* in the sea ice and water (Figure 2).

For example, when the food source had a C:chl *a* of 40, older larval krill undergoing diel foraging migration based on day length at 64°S (Figure 2a) would, on average, need access to chl *a* concentrations of 0.5 to 1 $\mu g\ l^{-1}$ in the water column if no sea ice were present. Conversely, if there were no chl *a* in the water column,

older larval krill could survive and/or grow so long as they had access to sea ice chl *a* concentrations between 4 and 15 $\mu g\ l^{-1}$, on average. However, if the larvae stopped migrating to the sea ice surface for a period due to light conditions at 70 °S and C:chl *a* concentration were 40 (Figure 2e), there would have to be a low level of chl *a* in the water column (0.1 $\mu g\ l^{-1}$) for the older larval krill to survive, even when sea ice chl *a* concentration was above 9 $\mu g\ l^{-1}$ on average (ie. water column more important when winters days go to 24 hour darkness).

At a C:chl *a* ratio of 80 (Figure 2b, 2d, and 2f), fewer combinations of sea ice and water column chl *a* values support older larval krill survival or growth given the conditions and behavior of krill specified in the model. Sea ice and water column chl *a* concentrations, on average, do not need to be higher than 6 $\mu g\ l^{-1}$ and 0.6 $\mu g\ l^{-1}$, respectively, with diel foraging migrations at 64 °S (Figure 2b). Even if migration to the sea ice surface stopped for part of the simulation at 70 °S (Figure 2f), older larval krill survived so long as sea ice chl *a* was above 6 μgl^{-1} regardless of water column chl a concentration.

Young larval krill would be half the size of older larvae from entering the winter months. Model results suggest that younger larvae need increased food concentrations and quality compared to older larval krill and a narrower range of food conditions would be suitable. This was apparent in the two general graphical forms. When C:chl *a* was lower the suitable combinations of chl *a* were confined to the upper right corner indicating a need for higher food levels and when C:chl *a* was

higher, suitable combinations of chl *a* formed a diagonal band that encompassed a broader range of conditions.

Under diel foraging migration patterns at 64 °S and when C:chl *a* was 40 (Figure 3a), younger larval krill required water column chl *a* values to be at least 0.5 $\mu g\ l^{-1}$ regardless of chl *a* concentrations in the sea ice. When more limited time spent at the sea ice surface at 66 °S (Figure 3c) younger larval krill did not survive if sea ice chl *a* was less than 7.5 $\mu g\ l^{-1}$ or if water column chl *a* was less than 0.7 $\mu g\ l^{-1}$. The maximum size of surviving krill was less than 12 mm. Further south, at 70 °S, younger larval krill from a late season spawn did not survive under any of combination of sea ice and water column chl *a* used in model runs.

With younger larval krill and food with a C:chl *a* ratio of 80, both chl *a* in the ice and in the water column took any value in their respective range of values but were inversely related. With diel foraging migration driven by day length at 64 °S (Figure 3b) combinations of high chl *a* concentration for both sea ice and water column produced krill that were unrealistically large and combinations with low values produced krill that were too small. This pattern was repeated for 66 °S (Figure 3d) but require slightly higher chl a concentrations. When diel migration ceased for a period at 70 °S (Figure 3e) no younger krill survived until water column chl a concentrations reached 0.4 $\mu g\ l^{-1}$.

The graphical pattern of chl *a* concentration for sub-adult krill indicated that sub-adult krill did not need chl *a* concentrations in the sea ice and the water column to be as high as did larval krill. The suitable chl *a* and C:chl *a* combinations,

conducive to survival and growth as specified by krill feeding behavior in the model, were generally found in the lower left hand corner (Figure 4).

Sub-adult krill in their second winter generally survived and/or grew under many combinations of chl *a* concentration in the sea ice and water column that were lower than those that support larval krill. When C:chl *a* was 40 and with diel foraging migrations for 64 °S, 66 °S and 70 °S sub-adult krill survived and/or grew without sea ice so long as water column chl *a* concentrations were 0.1 to 0.4 $\mu g\ l^{-1}$ (Figures 4a, 4c, and 4e). At these three latitudes, when water column chl *a* was zero, sub-adult krill needed, on average, access to sea ice with minimum chl *a* concentrations 3.5, 4 and 6 $\mu g\ l^{-1}$, respectively (Figures 4a, 4c, and 4e).

With a C:chl *a* of 80, the limited number of sea ice and water column combinations that yielded surviving sub-adult krill in the size range specified by the model were confined to a small envelope in the lower left corner (Figures 4b, 4d, 4f). With sea ice surface versus water-column foraging migration driven by day length at 64 °S and 66 °S, sub-adult krill grew if sea ice were absent and water column chl *a* was as low as 0.2 $\mu g\ l^{-1}$ (Figures 4b and 4d). Even at 70 °S sub-adult krill could survive without sea ice so long as they had access to water column chl *a* of 0.1 $\mu g\ l^{-1}$ on average (Figure 4f).

When all C:chl *a* layers were displayed simultaneously, the general trend in condition required for survival or growth was apparent (Figures 5, 6). For older larval krill and sub-adult krill, a larger set of sea ice and water column chl *a* combinations supported krill survival and/or growth to a reasonable size at lower

C:chl *a* ratios (10-40) than at higher ratios. As C:chl *a* ratio increased, there was a general shift towards lower maximum concentrations of sea ice and water column chl *a* required for krill to survive and/or grow. In contrast, younger larval krill did not survive with diel foraging patterns dictated by day lengths at 64 °S and 66 °S (Figure 5d and 5e) until C:chl *a* ratios were ≥ 40 and at 70 °S they do not survive until C:chl *a* reached 50 (Figure 5f). Younger larval krill (Figures 5d, 5e, and 5f) also generally required higher levels of chl a both in the sea ice and water column for a given C:chl *a* ratio than older larval krill or sub-adult krill. Overall, the sub-adult krill did better than the larvae with the least chl *a* available (Figure 6).

Carbon Mass

Older larval krill began at a carbon mass of 351 mg (TL = 9.3 mm) and reached total length from 8 to 15 mm within the conditions allowed. The minimum carbon mass of a "viable" krill (8 mm) decreased to 171 to 175 μgC, slightly less at lower latitudes, representing a loss of 51% to 53 % of initial body carbon (Table 1). The median size krill (11.3 mm) more than doubled in carbon content at all tested latitudes (Table 1). For the largest krill (15 mm) at the end of the simulation total body carbon had increased more than 4 times to 1987, 1999 and 1958 μg at 64 °S, 66 °S, and 70 °S, respectively (Table 1).

Younger larval krill had an initial carbon mass of 73 μg (TL = 7.0 mm) and reached 6.5 to 15 mm in total length within the conditions allowed. The body carbon of a viable krill (6.5 mm) decreased 45% to 49% to a minimum weight of 38 to 37

μg at all latitudes tested (Table 1). These krill would have to make gains in body carbon 9 to 11 times initial carbon mass, at 64 °S, 66 °S, and 70 °S to reach the median length of 11.1 mm and a carbon mass similar to the older larvae (Table 1). Even larger gains in body carbon, 28 to 40 times initial carbon mass, were required for younger larvae to reach the same maximum length (15.0 mm) as older larvae (Table 1).

Sub-adult krill, at the beginning of the simulation, were 9175 μg in carbon mass (24 mm) and reached total lengths of 19 to 30 mm within the conditions allowed. The minimum carbon mass of a "viable" krill (19 mm) decreased to 53 % of initial body carbon at all latitudes (Table 1). The median size krill (24.6 mm) increased by 7.7% to 8.5% of body carbon to 9883 to 9954 μg carbon mass (Table 1). The largest krill (30 mm) doubled total body carbon to 18700 to 1899 μg carbon mass at 64 °S, 66 °S, and 70 °S (Table 1).

Daily Growth Rate

Older larval and sub-adult krill that decreased to the minimum viable carbon mass had negative growth throughout the 90-day simulation with feeding migrations for all three latitudes (Table 2). In contrast, younger larvae had negative minimum growth rates and positive maximum growth rates but the average growth rate was negative for the 90-day simulation (Table 2). Larval and sub-adult krill that reached median and maximum length had positive growth rates over the 90-day simulation for all three latitudes (Table 2).

The average simulated growth rates for all krill that reached the minimum size were negative at all latitudes (Table 2). Sub-adult krill had the highest negative growth rate (-0.056 mm d^{-1}). The final median size of krill in each category all had positive average growth rates and growth rates were highest for the younger larvae (0.05 mm d^{-1}) and lowest for sub-adult krill (~0.06 mm d^{-1}). The average simulated growth rates for all krill that reached maximum size were positive at all latitudes but younger larvae had growth rates ~ 1.3 times higher (0.092 mm d^{-1}) than growth rates for older larvae and sub-adults (Table 2).

Growth Increment

The growth increment or percent growth per inter-molt period (% IMP^{-1}) was calculated assuming an inter-molt period of 30 days (Quetin et al. 2003). The average simulated growth increment was negative (-2.1 to -7.5 % IMP^{-1}) at all latitudes for all larval and sub-adult krill that reached the minimum viable size (Table 2). The average growth increment for younger larvae that reached median size, was 17 to 25 times higher than that of sub-adult krill that reached median size (Table 2). The average simulated growth for larvae and sub-adult krill that reached the maximum size was high (7.8 to 31 % IMP^{-1}) at all latitudes (Table 2).

DISCUSSION OF EXPERIMENTAL AND MODEL RESULTS

Experimental Assimilation Efficiency and Fecal Pellet Production

Assimilation efficiency based on simultaneous measurement of ingestion and egestion via fecal pellet production are critical for formulating individual energy budgets. Egestion rates for larval krill are not yet reported in the literature but have been reported for adults in austral summer (Clarke et al. 1988) and winter (Huntley et al. 1994). Assimilation efficiencies have been reported for larval krill in austral summer and adult krill.

The measured egestion rates of our larval krill were more similar to rates measured for adult krill collected during summer than rates for adult krill collected during winter. Our laboratory-fed larval krill had average egestion rates from 18.6 to 143 $\mu gC\ h^{-1}$, normalized to a 6.7 mg krill. Egestion rates of 60 to 560 $\mu gC\ h^{-1}$ were measured during January for laboratory held and freshly collected krill of 600 mg fresh weight (Clarke et al. 1988). Krill collected during July and August of size 24 to 28 mm (17 to 30 mg DW) had egestion rates of 0.28 to 0.38 $\mu gC\ h^{-1}$ (Huntley et al. 1994).

Assimilation efficiencies measured for adult *E. superba* during summer were generally in the range of 72 to 94% (Kato 1982 in Clarke 1988) although when feeding on *Phaeocystis antarcticum* assimilation efficiencies were 65 to 97% (Haberman 1998). The only measurement of larval krill assimilation efficiency for comparison to our results was measured by a different technique. During February and March estimated carbon assimilation efficiencies, calculated as the ratio of the

proportional decrease in chl *a* to that of POC in grazing and control bottles, for calyptopis III to furcilia II stage krill were 70 to 92% for krill fed at 0°C (Meyer et al. 2003). Our carbon assimilation efficiencies of 70 to 91%, measured in September for furcilia VI and juvenile krill at winter temperatures, were in the same range as rates measured during summer.

Chl a Conditions Suitable for Krill Survival and Growth

The chl *a* concentrations in sea ice (0 to 15 $\mu g\ l^{-1}$) and water column chl *a* concentrations (0 to 1 $\mu g\ l^{-1}$) used in our model to estimate growth in winter were within the range of chl *a* concentrations measured during winter in either habitat (Chapter 1). Chl *a* concentration in sea ice has been reported as low as 0.012 $\mu g\ l^{-1}$ (Quetin et al. 2003, Daly 2004) and as high as 610 $\mu g\ l^{-1}$ (Sterwart and Fritsen 2004). Chl *a* in the water column varies from 0.001 $\mu g\ l^{-1}$ (Quetin et al. 2003, Daly 2004) to 1.3 $\mu g\ l^{-1}$ (Kottmeier and Sullivan 1987). Excessive growth of krill predicted by the model at the highest chl *a* specified in the model (upper right hand corner of Figures 2 – 5) may indicate that krill do not often encounter the highest chl *a* concentrations or do not have prolonged access to such high concentrations during winter. Carbon to chl *a* ratios measured in the sea ice and water column have been greater than the range specified in our growth model (10-100). However, extremely high C:chl *a* ratios likely indicate substantial amounts of detrital material or the production of carbohydrate rich compounds by nitrogen-limited phytoplankton, carbon rich food sources that may not support krill growth in winter.

The energetic benefit of ingesting detrital material is equivocal for marine zooplankton (Pechen-Finenko 1987). Detritus may be used by zooplankton in low-food environments (DeMott 1988) and dead material can support growth at reduced levels (Roman 1984). Studies with marine copepods have shown that they ingest and assimilate significant amounts of dead cell particles (Pavlovskaya 1975, Pechen-Finenko 1975 as cited in Pechen-Finenko 1987; Poulet 1976). However, detrital material has been shown to influence of ingestion and viability in copepods. In *Calanus sp.* feeding on dead material, reproduction rates were ten-fold lower than in copepods fed on living material, and with long term feeding the level of nitrogen and phosphorus in the copepods fell below initial values (Corner 1974). In another copepod, *Acartia clausi* exhibited longer gut transit times were longer when fed detritus derived from *Thalassiosira weissflogii* culture than when fed the living cells (Tirelli and Mayzaud 2005). Fed detritus of the brown alga (*Fucus vesiculosus*), *A. tonsa* ceased growth and suffered 100% mortality after ten days (Roman 1977). Age of detritus also has been linked to assimilation efficiency, with younger detrital material being more efficiently incorporated than older material, dropping from 75% after one day of decomposition to 14% after 60 days (Pavlovskaya, 1976, Ostapenya 1976, Pavlyutin 1979; all as cited in Pechen-Finenko 1987).

Studies on the efficacy of detritus as a food source for krill in winter have not been done. Investigations into the isotopic composition of larval krill indicated that by early winter larval krill are depleted in $\delta^{15}N$, a shift inconsistent with a shift to carnivory or detrital consumption (Frazer 1996). As winter progresses, seasonal

succession in the SIMCO may lead to higher C:chl *a* ratios and which enable krill to deal with lower chl *a* concentrations. However, with very high ratios (1000), much of the carbon in sea ice may be detrital material, depleted in nitrogen and phosphorus required for growth. When somatic growth ceases the need for essential nutrients (nitrogen, phosphorus, macromolecules) decreases and the primary demand of maintenance metabolism is carbon (Anderson et al. 2007). This suggests that if krill continue to grow throughout the winter, they are consuming food of high quality.

Preliminary model runs with C:chl *a* ratios indicative of high detrital carbon produced unrealistically large krill even at very low chl *a* concentrations unless we specified physiologic parameters inconsistent with current knowledge (ie. small weight coefficient or reduced respiration rate in larvae). It has been suggested that ingestion rates based on high particulate organic carbon to chl *a* ratios are likely overestimates (Daly 1990). Thus, we chose not to include the high C:chl *a* values measured in sea ice that indicate high detrital or refractory carbon in our model and opted for more conservative estimates of ingestion.

Feeding Time Budget Based on Day Length Variation with Latitude

Time spent feeding on the sea ice surface versus in the water column based on day length with latitude did not produce a uniform effect. In fact, changes in the diel feeding pattern with latitude did not necessarily prevent krill from reaching maximum allowed sizes at each latitude but altered the conditions (chl *a* and C:chl *a*

ratio) required to reach those sizes. For older larval krill, decreased migration to the sea ice surface at latitude 70 °S required that a small amount of chl *a* (0.1 μg l^{-1}) be present in the water column when C:chl *a* ratio was 40. At latitude 70 °S younger larval krill could not survive under any combination of chl *a* concentration in the sea ice and water until C:chl *a* reached 50. Sub-adult krill grew well with a C:chl *a* ratio of 40 at latitude 70 °S with lower chl *a* concentrations in the water column and sea ice chl *a* concentrations similar to 64 °S and 66 °S.

If regional warming restricts sea ice to latitudes that have periods of total darkness, limiting migration to the sea ice surface to feed, the impact on larval krill would likely be greater than on sub-adult krill

Carbon Mass

The percent of body carbon released in a molt was eliminated as a term in this model. Krill molts were between 1.4 and 2.3% of body carbon (Ikeda and Dixon 1982). Based on these data, the calculated the carbon loss at molt for an adult male krill was only 1.58% of body carbon (Clarke and Morris 1983). The surface area to volume ratio for larval krill is higher than that of post-larval krill and the percent of body carbon estimated for larger krill may under-estimate that of our larvae. However, regardless of mass, the molt of *Euphausia pacifica* represented the same percent of body carbon over 200 to 2500 μg ranged in body carbon (Ross 1982), suggesting that estimates for post-larval krill can be used for larval krill.

Several studies that estimate the IMP for larval krill in winter were available to estimate carbon lost due to molting. From a series of cruises, estimated IMP for larval krill fall, early winter and late winter had median values of 23.4, 30.5, and 23.0 d respectively (Quetin et al. (2003). These IMPs were confirmed by two more recent studies. The IMP during winter 2001 had a median of 30.6 d (Ross et al., 2004) and during winters 2001 and 2002, a median of 40 d (Daly, 2004). Given these estimates of IMP, larval krill would molt 2 to 4 times over the 90-day model iteration and would only lose up to 0.05 % body carbon per day by molting (i.e. average of 3 times 1.58% of body carbon over 90 d).

Daily Growth Rate

Daily growth rates for larval krill, both negative and positive, have been measured by a variety of techniques. High positive growth rates during winter were estimated, 0.047 mm d^{-1} (Hosie and Stolpe 1989) and 0.07 mm d^{-1} for larval krill in winter from length-frequency distributions of krill populations sampled at two geographically distinct sites based on the assumption that the two populations are the same (Daly 1990). More recently, the instantaneous growth rate (IGR) method has been considered a preferred method for measuring in situ growth of krill (Nicol 2000, Ross et al. 2004, Atkinson et al. 2006, Candy and Kawaguchi 2006, Kawaguchi et al. 2006). Seasonal variation in growth rates for larval krill measured over multiple cruises, from austral fall and winter, ranged from as low as -0.015 to as high as 0.055 mm d^{-1} (Quetin et al. 2003). Growth rates based on IGR

experiments conducted in the field during winter were negative, -0.001 to -0.006 mm d^{-1} (Ross et al. 2004) and positive, 0 and 0.013 mm d^{-1} (Daly 2004). Similar growth rates, 0.017 to 0.02 mm d^{-1}, were measured in the laboratory under winter conditions (Elias 1990 cited in Ross and Quetin 1991, Ross et al. 2004). The range of average daily growth rates from our model, for larval krill from a January and March spawning, ranged from -0.015 to 0.092 mm d^{-1}, in the range of rates reported in the literature.

Few estimates of daily growth are reported for post-larval krill in winter. Positive daily growth based on length frequency, 0.01 to 0.048 mm d^{-1}, was measured for krill during winter (McClatchie 1988). Summer growth rates measured in the laboratory were 0.02 to 0.025 mm d^{-1} for krill of mean length 32 mm (Buchholz et al. 1989) and 0.047 mm d^{-1} for juveniles (Ikeda and Thomas 1987). These values that fall between the simulated daily growth of our average and maximum sized krill. The average daily growth output for sub-adult krill obtaining the maximum allowed length was 0.067 mm d^{-1}. This value falls within the low end of the range of daily growth estimated by IGR of 0.0480 to 0.305 mm d^{-1} for krill (30 to 33 mm) in summer (Atkinson et al. 2006).

Growth Increment

We compared our simulated growth increment to measurements of growth increment reported from larval and sub-adult krill during the winter months. The average simulated growth increment for larval krill in our model ranged from -5 to

17% IMP^{-1} for older larvae and -2 to 30 % IMP^{-1} for younger larval krill. Historical mean growth increments for larval krill during June to September ranged from -3 to 12 % IMP^{-1} (Quetin et al. 2003). Growth increments from two recent austral winter studies were negative (Ross et al. 2004) and zero or slightly positive (Daly 2004). Our model may overestimate the ingestion of larval krill resulting from a late or delayed spawning. These larvae, entering winter as calyptopis or furcilia I and II, may not be capable of scraping the sea ice surface efficiently and a may constitute a portion of larval population that is not coupled to the sea ice surface (Frazer et al. 2002). Inclusion of ingestion from sea ice scraping in the model in this case would over-estimate ingestion.

Few estimates of growth increment have been measured for sub-adult krill to compare to our results that ranged from -7.5 to 7.8 IMP^{-1} average growth increment for sub-adult krill during their second winter. Based on data presented in Buchholz et al. (1989), during winter, a 32-mm krill would have a growth increment of 0.069 % IMP^{-1} assuming an increase in size of 3.8% at molt and an IMP of 55 days. From a study of in situ growth rates of adult krill during January (Atkinson et al. 2006), the krill closest in size to our krill (30 to 33 mm) showed growth increments ranging from 1.94 to 13.7 % IMP^{-1} at environmental temperatures of -0.85 to 0.49 °C (Atkinson et al. 2006). Thus, our model may over-estimate both negative and positive growth increments for sub-adult krill. For example, sub-adult krill are not generally found at the sea ice surface in winter but are observed feeding in this manner in late winter and early spring (C. Boch, D. Martin, and L. Quetin, personal

observation). Allowing sub-adult krill to feed at the sea ice surface over the full 90-day simulation may over estimate growth rates. However, given the paucity of measurements of winter growth increments for sub-adult krill, we cannot say this conclusively.

CONCLUSIONS

Our measurements of egestion and assimilation efficiency for larval krill feeding on SIMCOs in winter are an important addition to the sparse data on larval krill ecology. Assimilation efficiencies similar to those measured for larval krill in summer suggest larval krill may be eating a similar quantity and quality of food in both summer and winter. We have been able to incorporate these measurements into our model and reduce the need to make assumptions about winter physiological rates (ie. ingestion from ice scraping) used in previous attempts to model winter growth (Hoffman and Lascara 2000). Introduction of a diel feeding time budget in the model, based on behavioral patterns observed in larval krill, resulted in reasonable growth rates without assumptions about detrital feeding or reduction of larval krill metabolism.

Model results indicate that many conservative combinations of water column chl *a* (range 0 to 1 $\mu g\ l^{-1}$), sea ice chl *a* (range 0 to 15 $\mu g\ l^{-1}$), and C:chl *a* ratio (range 10 to 100) are suitable for krill during winter. Older larval krill survived and/or grew at the same C:chl *a* ratios as sub-adult krill but generally required higher concentrations of chl *a*. Younger arval krill generally required higher concentrations of chl *a* and did not survive unless C:chl *a* ratios were 40 or higher. Sub-adult krill were able to survive and grow over the lowest chl *a* concentrations for a given C:chl *a* ratio.

Changes in the timing of formation and retreat, and latitudinal extent of sea ice will impact SIMCO biomass and productivity. With our results we can begin to

speculate how krill winter growth might change with regional warming in the Antarctic. For example, if sea ice were restricted to the deep southern latitudes, SIMCO production may be limited by periods of total darkness and krill feeding at the sea ice surface may be reduced. Both of these scenarios would impact larval krill growth and survival by limiting food availability. This model did not include time-varying food concentration and food quality. Linking more sophisticated physiological growth models to dynamic models that predict ice formation and SIMCO primary productivity would allow prediction of the impact of future changes in annual sea ice production on winter survival of krill.

REFERENCES

Anderson T.R., Hessen, D.O., Elser, J.J., Urabe, J. (2005). Metabolic stoichiometry and the fate of excess carbon and nutrients in consumers. Am Nat 165:1-15

Anderson, T., Fœrøvig, J.P., Hessen D.O. (1007). Growth rate versus biomass accumulation: Different roles of food quality and quantity for consumers. Limnol Oceanogr 52(5): 2128-2134

Astheimer H, Krause H, Rakusa-Suszczewski S (1985) Modeling individual growth of the Antarctic krill *Euphausia superba* Dana. Polar Biol 4:65–73

Atkinson A, Meyer B, Stübing D, Hagen W, Schmidt K, Bathman UV (2002) Feeding and energy budgets of Antarctic krill *Euphausia superba* at the onset of winter-II. Juveniles and adults. Limol Oceanogr 47(4): 953-966

Atkinson A, Shreeve RS, Hirst, AG, Rothery P, Tarling GA, Pond DW, Korb R, Murphy EJ, Watkins JL (2006) Natural growth rates in Antarctic krill (Euphausia superba): II. Predictive models based on food, temperature, body length, sex, and maturity stage. Limnol Oceanogr 51: (973-987)

Brightman RI, Smith WO (1989) Photosynthesis-irradiance relationships of Antarctic phytoplankton during austral winter. Mar Eco Prog Ser 53:143-151

Buchholz, F, Morrls, DJ, Watkins, JL (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

Candy SG, Kawaguchi S (2006) Modelling growth of Antarctic krill. II. Novel approach to describing the growth trajectory. Mar Ecol Prog Ser 306:17–30

Clarke A, Morris DJ (1983) Towards an energy budget for krill: the physiology and biochemistry of *Euphausia superba* Dana. Polar Biol 2:69–86

Clarke A, Quetin LB, Ross RM (1988) Laboratory and field estimates of the rate of faecal pellet production by Antarctic krill, *Euphausia superba*. Mar Biol 98: 557-563

Corner, EDS, Head RN, Kilvington CC, Marshall SM (1974) On the nutrition and metabolism of zooplankton. IX. Studies relating to the nutrition of overwintering *Calanus*. J Mar Miol Ass UK 54-319-331

Daly K (1990) Overwintering development, growth, and feeding of larval *Euphausia superba* in the Antarctic marginal ice zone. Limnol Oceanog 35(7) 1564-1576

Daly KL (2004) Overwintering growth and development of larval *Euphausia superba*: an interannual comparison under varying environmental conditions west of the Antarctic Peninsula. Deep-Sea Res Part II 51 (17-19): 2139-2168

DeMott WR (1988) Discrimination between algae and detritus by freshwater and marine zooplankton. Bull. Mar. Sci. 43: 486–499

Elias MC (1990) Effects of photoperiod, phytoplankton level and temperature on the growth, development and survival of larval *Euphausia superba* (Dana). MA thesis, University of California, Santa Barbara, CA

Fraser FC (1936) On the development and distribution of the young stages of krill (*Euphausia superba*). Discovery Rep 14:1–192

Frazer TK (1996) Stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) of larval krill, *Euphausia superba*, and two of its potential food sources. J Plankton Res 18(8):1413-1426

Frazer TK, Quetin LB, Ross, RM (2002) Energetic demands of larval krill, *Euphausia supeba*, in winter. J Exp Mar Biol Ecol 277: 157-171

Hofmann EE, Lascara CM (2000) Modeling the growth dynamics of Antarctic krill *Euphausia superba.* Mar Ecol Prog Ser 194: 219-213

Huntley ME, Nordhausen W, Lopez MDG (1994) Elemental composition, metabolic activity and growth of Antarctic krill *Euphausia superba* during winter. Mar Ecol Prog Ser 107: 232–240

Ikeda T, Dixon P (1982) Body shrinkage as a possible over-wintering mechanism of the Antarctic krill, *Euphausia superba* (Dana). J Exp Mar Biol Ecol 62(2):143-151

Ikeda T, Bruce B (1986) Metabolic activity and elemental composition of krill and other zooplankton from Prydz Bay, Antarctica, during early summer (November-December). Mar Biol 92:545–555

Ikeda T, Thomas PG (1987) Longevity of the Antarctic krill *(Euphausia superba* Dana) based on a laboratory experiment. Proc N1PR Symp Polar Biol 1: 56-62

Kawaguchi K, Ishikawa S, Matsuda O (1986) The overwintering strategy of Antarctic krill (*Euphausia superba* Dana) under the coastal fast ice off the Ongul Islands in Luetzow-Holm Bay, Antarctica. Proceedings of The Eighth Symposium On Polar Biology, 1985., Mem. Natl. Inst. Polar Res. (Japan) (Spec. Iss.)., (4): 67-85

Kawaguchi S, Candy SG, King R, Naganobu M, Nicol S (2006) Modelling growth of Antarctic krill. I. Growth trends with sex, length, season, and region. Mar Ecol Prog Ser 306:1–15

Kottmeier ST, Sullivan CW (1987) Late winter primary production and bacterial production in sea ice and seawater west of the Antarctica Peninsula. Mar Ecol Prog Ser 36: 287–298

Lizotte MP (2001) The contributions of sea ice algae to Antarctic marine primary production. Am Zool 41:57-73

Makarov R (1980) Larval Development of the Antarctic Euphausiids. BIOMASS Handbook no. 3:6-13

Marin V, Huntley ME, Frost BW (1986) Measuring feeding rates of pelagic hebivores: analysis of experimental design and methods. Mar Biol 93:49-58

Mauchline J (1980) Measurement of body length of *Euphausia superba* Dana: BIOMASS Handbook no. 4:4-9

Meyer B, Atkinson A, Stübing D, Hagen W, Oettl B and Bathman UV (2002a) Feeding and energy budgets of Antarctic krill *Euphausia superba* at the onset of winter-I. Furcilia III larvae. Limnol. and Oceanogr. 47(4): 943-952

Meyer B, Saborowski R, Atkinson A, Buchholz F, Bathmann U (2002b) Seasonal differences in citrate synthase and digestive enzyme activity in larval and postlarval Antarctic krill, *Euphausia superba*. Mar Biol 141, 855-862

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

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

Moloney CL, Field JG (1989) General allometric equations for rates of nutrient uptake, ingestion, and respiration in plankton organisms. Limnol. Oceanogr. 34:1290–1299

Ostapenya AP (1975) Detritus and its role in the aquatic ecosystems. Gidrobiologuichesky Zhumal 11 (1):120-121 (in russian)

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

Pavlovskaya TV, Pechen-Finenko GA (1975) The living and dead organic matter in the nutrition of Pseudocalanus elongatus (Boeck) : the comparative estimation of its role. - Biologuiya morya, 34th issue, 65-70 (in russian)

Pavlyutin AP (1975) The nutritive value of the detritus for the aquatic animals. *In :* The study of the Aquatic Ecosystems : General Foundations, Leningrad, "Nauka" Publishers, 196-113 (in russian).

Pechen-Finenko GA (1987) The nutritive value of the detritus for the marine plankton animals. Production et Relations Trophiques dans les Ecosystèmes marins 2' Coll. Franco- Soviétique. YALTA, 1984 - IFREMER Act. Coll. n°5 - 1987 - : 171-180

Poulet SA (1976) Feeding of *Pseudocalanus minutus* on living and non-living particles. Mar Biol 34 (2):117-125

Quetin LB, Ross RM (1991) Behavioral and physiological characteristics of Antarctica krill, *Euphausia superba.* Am Zool 31: 49-63

Quetin LB, Ross RM (2003) Episodic recruitment in Antarctic krill *Euphausia superba* in the Palmer LTER study region. Mar Ecol Progr Ser 259:185–200

Quetin LB, Ross RM, Frazer TM, Amsler M, Wyatt-Evens C, Oakes SA (2003) Growth of larval Antarctica krill in fall and winter west of the Antarctic Peninsula. Mar Biol, 143 833:843

Quetin LB, Ross RM, Fritsen CH, Vernet M (2007) Ecological responses of Antarctic krill to environmental variability: can we predict the future? Antarct Sci 19: 253–266

Roman MR (1977) Feeding of the copepod *Acartia tonsa* on the diatom *Nitzschia closterium* and brown algae, (*Fucus vesiculosus*) detritus. Mar Biol 42 (2):149-157

Ross RM (1982a) Energetics of *Euphausia pacifica*. 2. Complete carbon and nitrogen budgets at 8 ° and 12 °C throughout the life span. Mar Biol 68:15 - 23

Ross RM, Quetin LB (1986) How productive are Antarctic krill? BioScience 36:264-269

Ross RM, Quetin LB, Newberger T, Oakes SA (2004) Growth and behavior of larval krill (*Euphausia superba*) under ice in late winter 2001 west of the Antarctic Peninsula. Deep Sea Res Part II: 51 (17-19) :2169-2184

Siegel V, Loeb V (1995) Recruitment of antarctic krill *Euphausia superba* and possible causes for its variability. Mar Ecol Progr Ser 123(1-3): 45-56

Spiridonov VA (1995) Spatial and temporal variability in reproductive timing of Antarctic krill (*Euphausia superba* Dana). Polar Biol 15:161-174

Stewart FJ, Fritsen CH (2004) Bacteria–algae relationships in Antarctic Sea ice. Antarct Sci 16(2):143-156

Swadling KM (2006) Krill Migration: Up and down all night. Curr Biol 16 (5) 173-175

Tarling GA, Johnson ML (2006) Satiation gives krill that sinking feeling. Curr Biol 16: 83–84

Table 1. Model results for representiative minimum, median and maximum sized *Euphausia superba*. Model run with latitude, final length, initia carbon mass (CM), final CM, percent change in CM, percent of body carbon ingested per day (%bC d^{-1}), and total percent of body carbon ingested (%bC) for larval and sub-adult krill. Median size krill (med). Negative change in CM in bold.

Model Run (latitude)	Final Length (mm)	Initial CM (μg)	Final CM (μg)	Change CM (%)	Daily Carbon Ingested (%bC d^{-1})	Total Carbon Ingested (%bC)
Younger	6.5	73	38	**-47**	12.8	1168
Larvae	11.2 med	73	721	894	7.82	712
64 °S	15.0	73	2099	2792	7.9	719
Older	8.0	351	171	**-51**	1.5	132
Larvae	11.3 med	351	744	112	2.3	212
64 °S	15.0	351	1987	466	3.3	297
Sub-adult	19.0	9175	4313	**-53**	0.16	15
64 °S	24.6 med	9175	9883	7.7	1.1	98
	30.0	9175	18799	105	1.9	171
Younger	6.6	73	40	**-45**	6.8	623
Larvae	11.1 med	73	716	886	5.1	468
66 °S	15.0	73	2073	2757	4.8	439
Older	8.0	351	175	**-50**	1.4	126
Larvae	11.3 med	351	739	111	2.2	203
66 °S	15.0	351	1999	469	3.1	281
Sub-adult	19.0	9175	4347	**-53**	0.17	16
66 °S	24.6 med	9175	9954	8.5	1.1	99
	30.0	9175	18700	104	1.9	171
Younger	6.5	73	37	**-49**	13.7	1249
Larvae	11.1 med	73	874	1103	9.16	834
70 °S	12.0	73	2978	4003	9.2	841
Older	8.0	351	175	**-50**	1.4	122
Larvae	11.2 med	351	740	111	2.5	231
70 °S	15.0	351	1958	457	3.3	296
Sub-adult	19.0	9175	4289	**-53**	0.13	12
70 °S	24.6 med	9175	9942	8.4	1.0	95
	30.0	9175	18654	103	1.8	164

Table 2. Model results for representative minimum, median and maximum *Euphausia superba*. Model run with latitude, initial length, final length, change in wet mass (WM), change in carbon mass (CM), daily growth (mm d^{-1}) and percent growth per intermolt period (% IMP^{-1}) for larval and sub-adult krill. Median size krill (med). SD is standard deviation. Negative values in bold.

Model Run (latitude)	Initial Length (mm)	Final Length (mm)	Average Change WM (mg d^{-1} ± SD)	Average Change CM (µg d^{-1} ± SD)	Average Growth (mm d^{-1} ± SD)	Average Growth (% IMP^{-1} ± SD)
Younger	7.0	6.5	**-0.004 ± 0.006**	**-0.368 ± 0.540**	**-0.005 ± 0.007**	**-2.12 ± 2.36**
Larvae	7.0	11.2 med	0.078 ± 0.084	7.51 ± 8.28	0.047 ± 0.035	17.6 ± 12.9
64 °S	7.0	15.0	0.242 ± 0.315	23.8 ± 31.5	0.092 ± 0.069	30.7 ± 19.6
Older	9.3	8.0	**-0.021 ± 0.006**	**-1.96 ± 0.606**	**-0.015 ± 0.006**	**-5.01 ± 2.35**
Larvae	9.3	11.3 med	0.047 ± 0.018	4.38 ± 1.67	0.022 ± 0.005	6.67 ± 1.67
64 °S	9.3	15.0	0.200 ± 0.116	18.8 ± 11.0	0.063 ± 0.018	17.3 ± 3.31
Sub-adult	24.0	19.0	**-0.548 ± 0.040**	**-50.8 ± 3.78**	**-0.056 ± 0.003**	**-7.49 ± 0.944**
64 °S	24.0	24.6 med	0.112 ± 0.065	10.6 ± 6.29	0.008 ± 0.005	1.02 ± 0.567
	24.0	30.0	1.16 ± 0.465	109 ± 44.7	0.067 ± 0.017	7.79 ± 1.61
Younger	7.0	6.6	**-0.004 ± 0.003**	**-0.363 ± 0.285**	**-0.005 ± 0.004**	**-2.02 ± 1.62**
Larvae	7.0	11.1 med	0.077 ± 0.076	7.40 ± 7.43	0.047 ± 0.032	17.4 ± 11.4
66 °S	7.0	15.0	0.240 ± 0.263	23.1 ± 25.8	0.091 ± 0.055	30.2 ± 14.6
Older	9.3	8.0	**-0.021 ± 0.007**	**-1.93 ± 0.627**	**-0.015 ± 0.005**	**-4.89 ± 1.58**
Larvae	9.3	11.3 med	0.048 ± 0.021	4.47 ± 1.97	0.022 ± 0.007	6.41 ± 2.01
66 °S	9.3	15.0	0.201 ± 0.160	19.2 ± 15.6	0.063 ± 0.029	17.3 ± 6.37
Sub-adult	24.0	19.0	**-52.8 ± 5.41**	**-0.570 ± 0.057**	**-0.055 ± 0.003**	**-7.42 ± 0.899**
66 °S	24.0	24.6 med	0.105 ± 0.025	9.83 ± 2.43	0.007 ± 0.002	0.851 ± 0.219
	24.0	30.0	1.15 ± 0.290	107 ± 27.2	0.067 ± 0.008	7.76 ± 0.557

Table 2 continued.

Model Run (latitude)	Initial Length (mm)	Final Length (mm)	Average Change WM (mg d^{-1} ± SD)	Average Change CM (μg d^{-1} ± SD)	Average Growth (mm d^{-1} ± SD)	Average Growth (% IMP^{-1} ± SD)
Younger	7.0	6.5	**-0.382 ± 0.309**	**-0.004 ± 0.003**	**-0.005 ± 0.004**	**-2.19 ± 1.30**
Larvae	7.0	11.1 med	0.091 ± 0.117	8.89 ± 11.6	0.054 ± 0.048	20.7 ± 18.4
70 °S	7.0	17.0	0.348 ± 0.587	35.0 ± 60.1	0.111 ± 0.007	37.6 ± 37.4
Older	9.3	8.0	**-0.021 ± 0.008**	**-1.99 ± 0.804**	**-0.015 ± 0.007**	**-4.86 ± 2.89**
Larvae	9.3	11.2 med	0.043 ± 0.048	4.16 ± 4.70	0.021 ± 0.020	6.27 ± 6.67
70 °S	9.3	15.0	0.192 ± 0.175	18.4 ± 17.1	0.063 ± 0.036	17.1 ± 9.18
Sub-adult	24.0	19.0	**-0.573 ± 0.099**	**-53.0 ± 9.42**	**-0.056 ± 0.005**	**-7.55 ± -7.35**
70 °S	24.0	24.6 med	0.093 ± 0.039	8.73 ± 3.78	0.007 ± 0.003	0.839 ± 0.355
	24.0	30.0	1.11 ± 0.998	107 ± 97.6	0.066 ± 0.048	7.68 ± 5.40

Figure 1. Assimilation efficiency (%) for larval krill in winter as a function of available carbon ($\mu g\ l^{-1}$). No significant trend (Spearman's Rank, $r_s = 0.257$, $P = 0.943$, $\alpha = 0.01$).

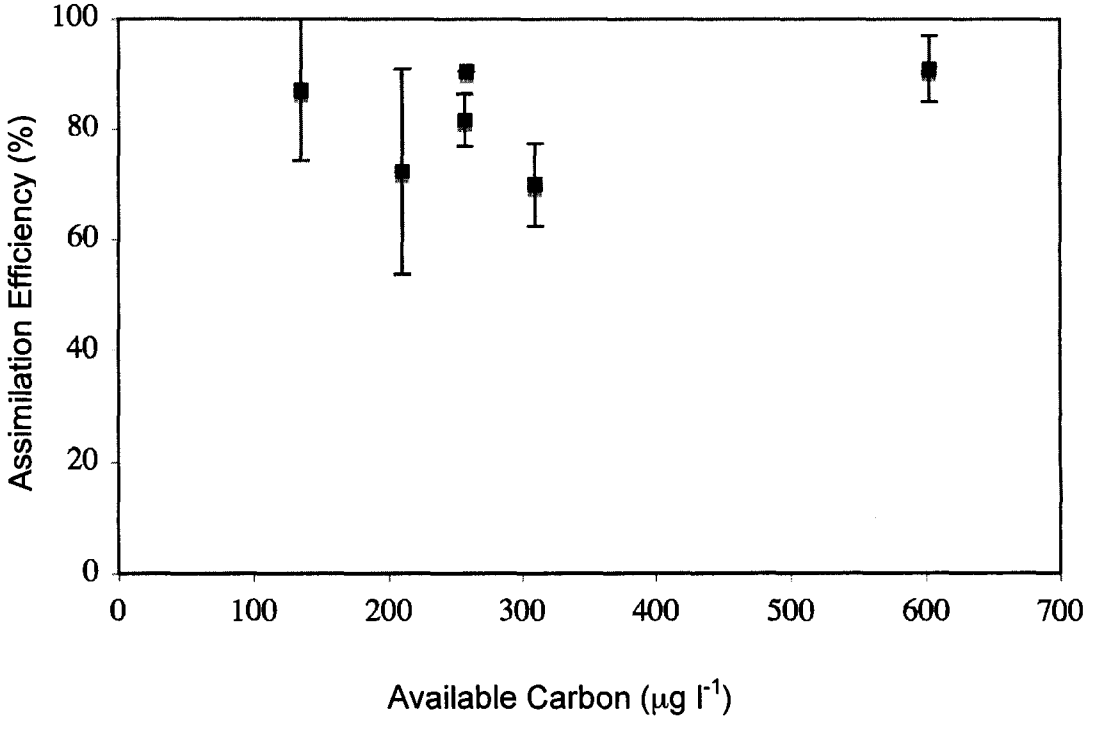

100
80
60
40
20
0
Assimilation Efficiency (%)
0
100
200
300
400
500
600
700
Available Carbon (μg l-1)

Figure 2. Model simulated combinations of chl *a* concentration ($\mu g\ l^{-1}$) in sea ice and water that support winter survival or growth of older larval krill. A) C:chl *a* = 40, latitude 64 °S, B) C:chl *a* = 80, latitude 66 °S, C) C:chl *a* = 40, latitude 66 °S, D) C:chl *a* = 80, latitude 66 °S, E) C:chl *a* = 40, latitude 70 °S and F) C:chl *a* = 80, latitude 70 °S. Color scale represents final sized of krill of 8 to 15 mm after 90-day model simulation.

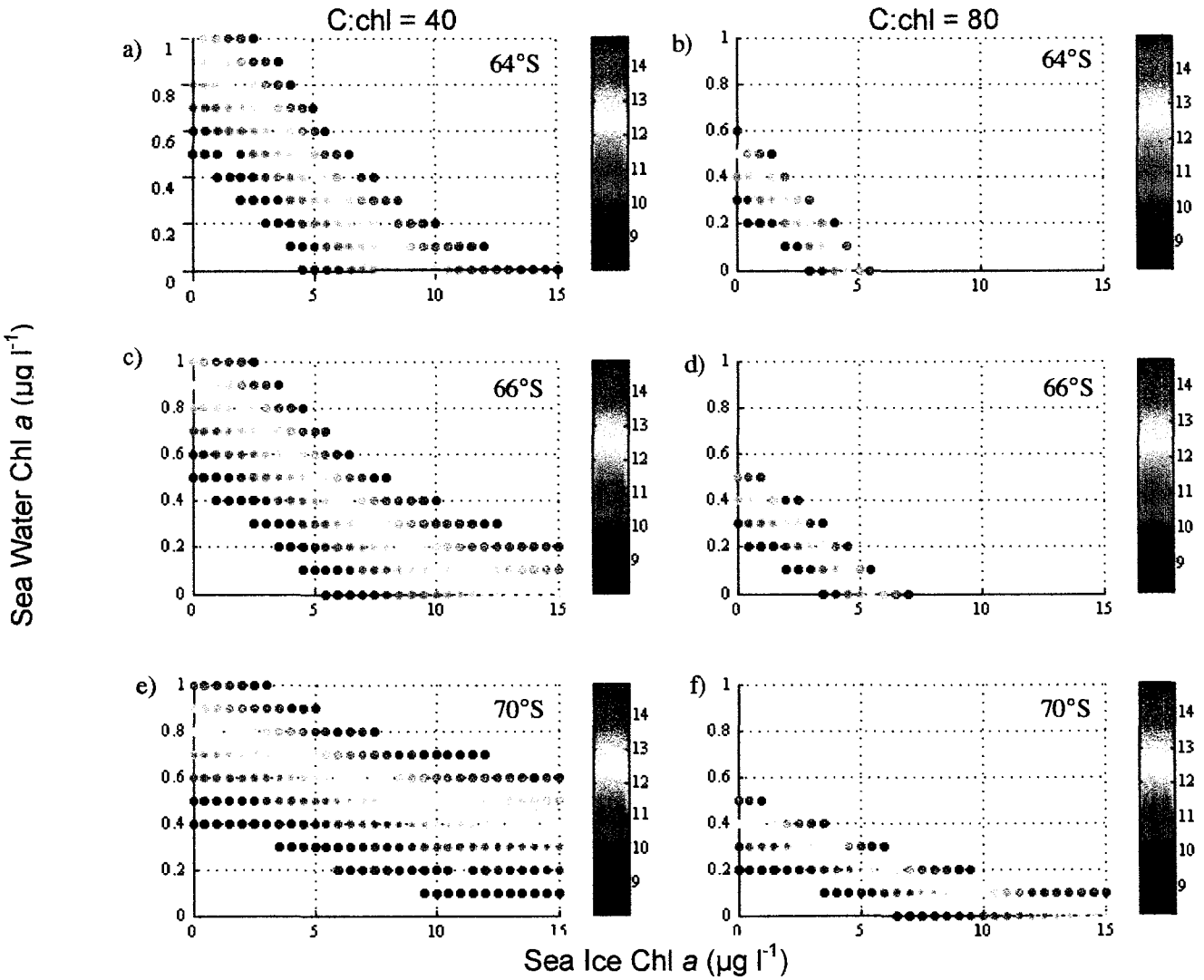

C:chl = 40
C:chl = 80
a)
b)
c)
d)
e)
f)
64°S
66°S
70°S
Sea Water Chl a (µg l-1)
Sea Ice Chl a (µg l-1)

Figure 3. Model simulated combinations of chl *a* concentration ($\mu g\ l^{-1}$) in sea ice and water that support winter survival or growth of younger larval krill. A) C:chl *a* = 40, latitude 64 °s, B) C:chl *a* = 80, latitude 64 °S, C) C:chl *a* = 40, latitude 66 °S, D) C:chl *a* = 80, latitude 66 °S and E) C:chl *a* = 80, latitude 70 °S. Color scale represents final sized krill of 6.5 to 12 or 15 mm after 90-day model simulation.

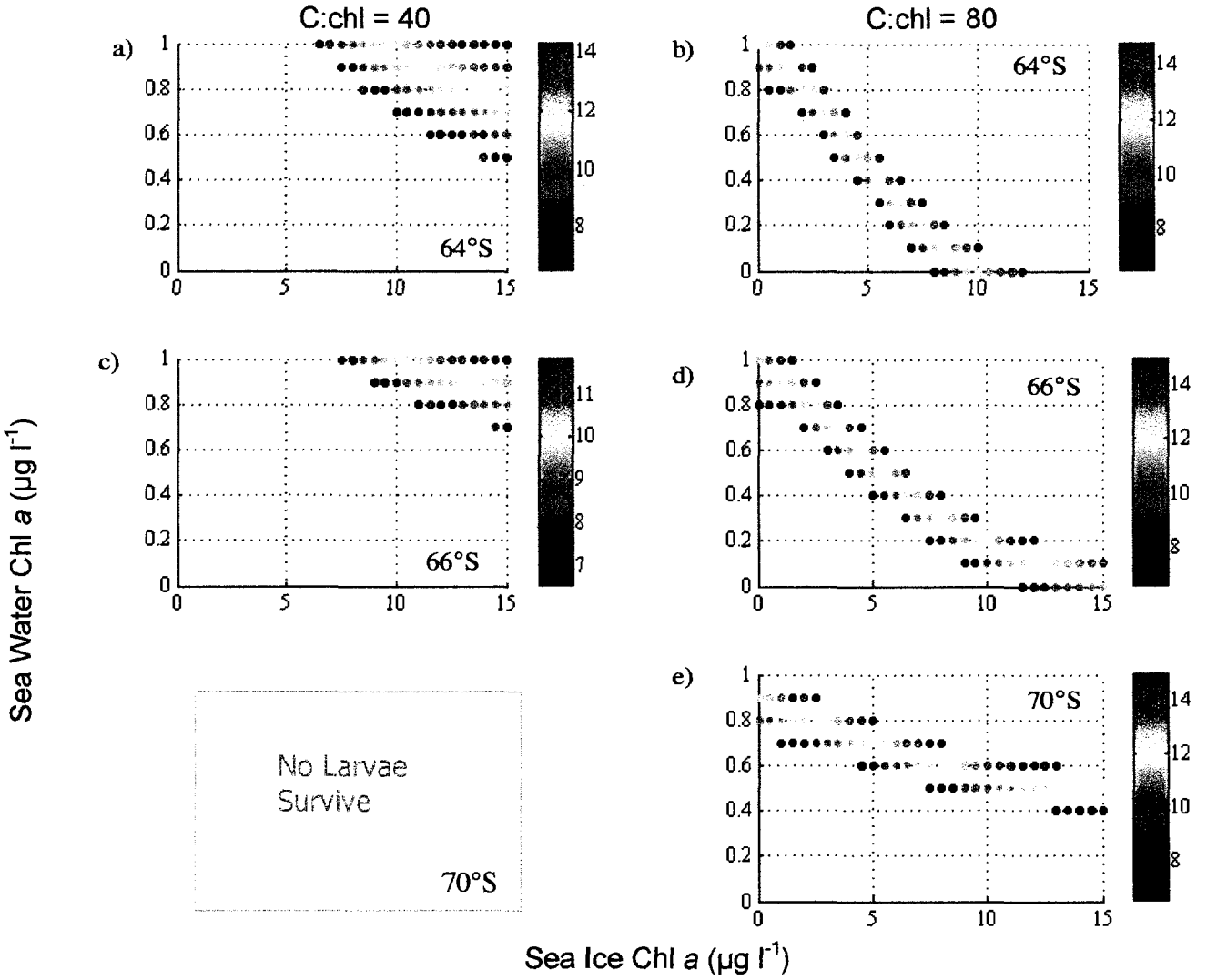

C:chl = 40
C:chl = 80
a)
b)
c)
d)
e)
64°S
64°S
66°S
66°S
70°S
No Larvae
Survive
70°S
Sea Water Chl a (µg l-1)
Sea Ice Chl a (µg l-1)

Figure 4. Model simulated combinations of chl *a* concentration ($\mu g\ l^{-1}$) in sea ice and water that support winter survival or growth of sub-adult krill. A) C:chl *a* = 40, latitude 64 °S, B) C:chl *a* = 80, latitude 64 °S, C) C:chl *a* = 40, latitude 66 °S, D) C:chl a = 80, latitude 66 °S, E) C:chl a = 40, latitude 70 °S and F) C:chl a = 80, latitude 70 °S. Color scale represents final sized krill of 19 to 30 mm after 90-day model simulation.

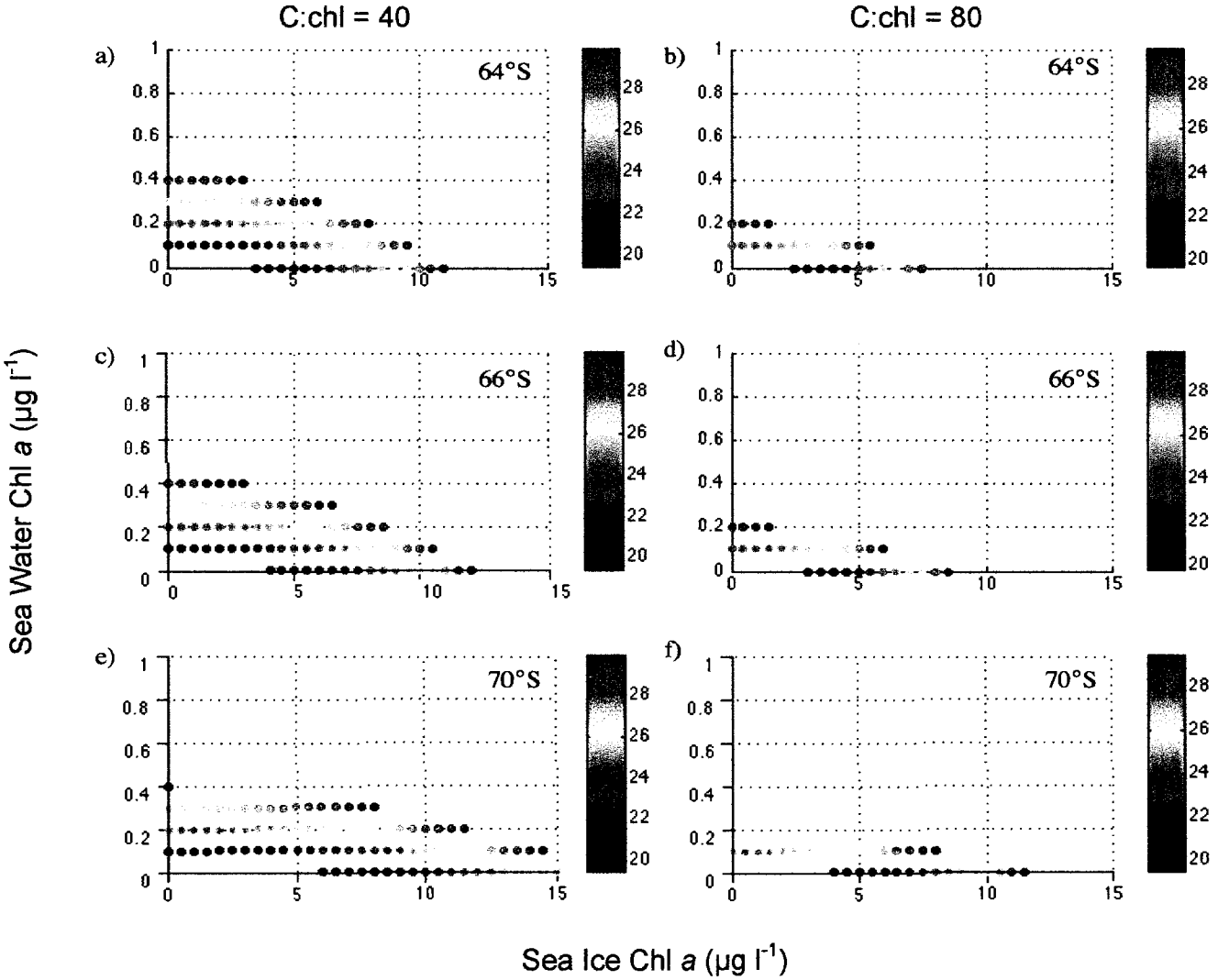

C:chl = 40
C:chl = 80
a)
b)
c)
d)
e)
f)
64°S
66°S
70°S
Sea Water Chl a (µg l-1)
Sea Ice Chl a (µg l-1)

Figure 5. Model simulated combinations of C:chl *a* ratio and chl *a* concentration (μg l^{-1}) in sea ice and water that support winter survival or growth of older larval krill (A-C) and younger larval krill (D-F). A) latitude 64 °S, B) latitude 66 °S, C) latitude 70 °S, D) latitude 64 °S, E) latitude 66 °S, F) latitude 70 °S. Color scale represents final sized krill of 8 to 15 mm and 6.5 to 12 or 15 mm after 90-day model simulation for older larval krill and younger larval krill, respectively.

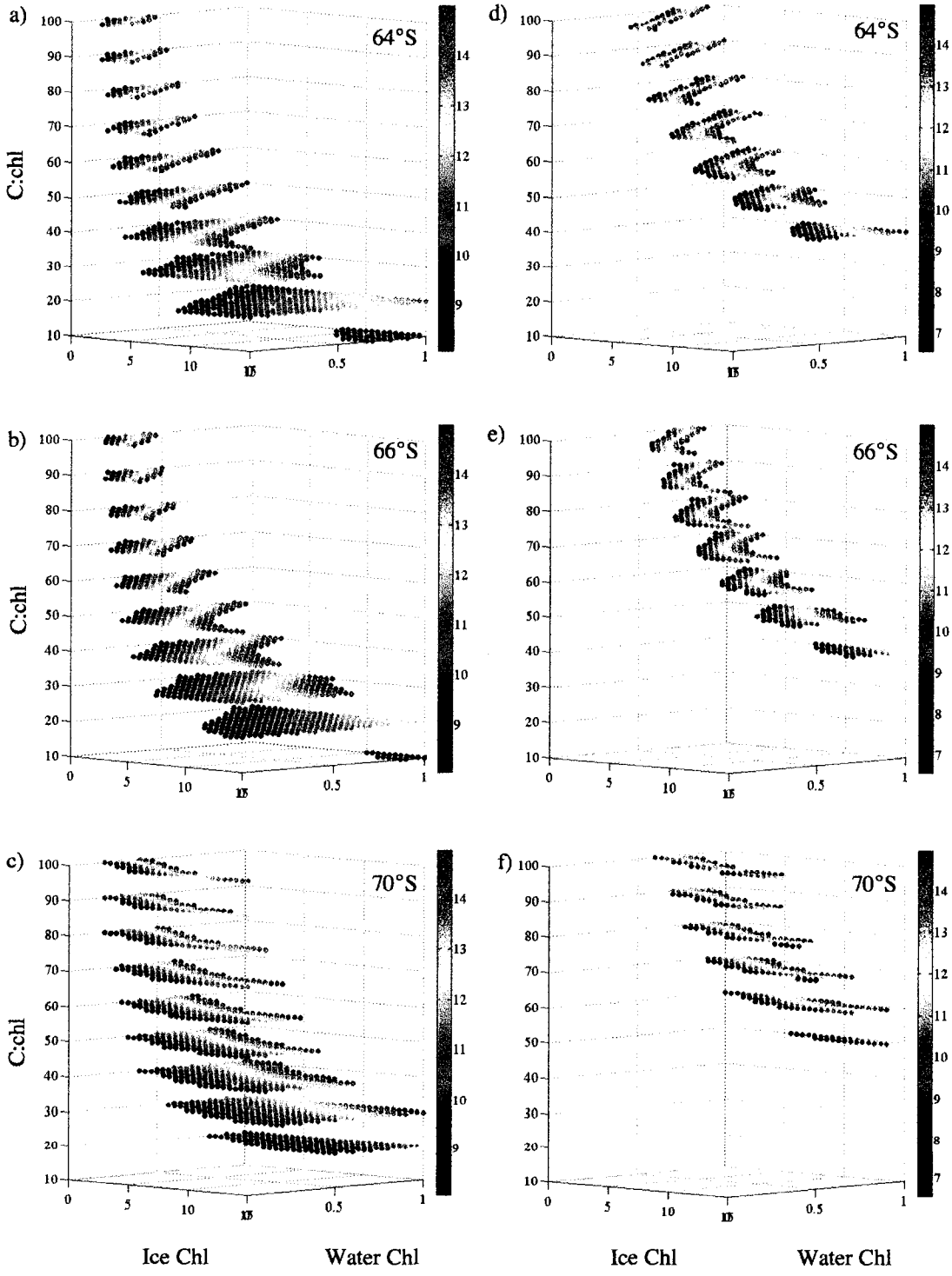
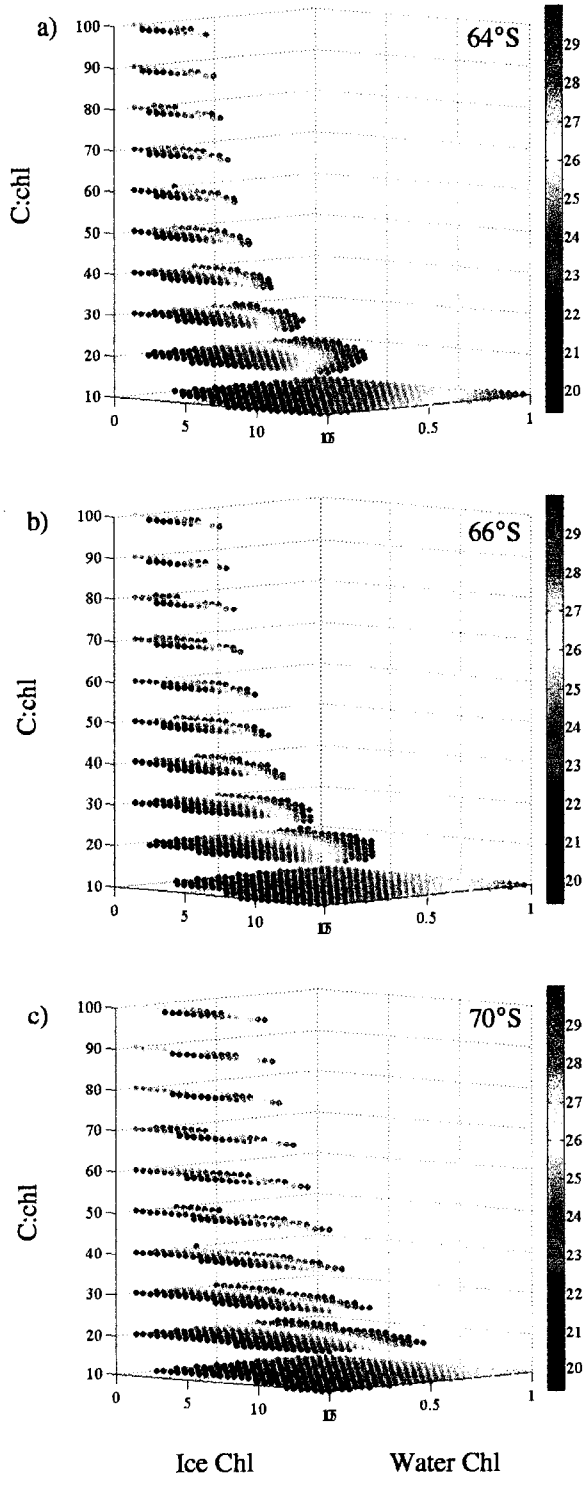

a)
64°S
C:chl
b)
66°S
C:chl
c)
70°S
C:chl
Ice Chl
Water Chl
d)
64°S
e)
66°S
f)
70°S
Ice Chl
Water Chl

Figure 6. Model simulated combinations of C:chl *a* ratio and chl *a* concentration (μg l^{-1}) in sea ice and water that support winter survival or growth of sub-adult krill. A) latitude 64 °S, B) latitude 66 °S, C) latitude 70 °S. Color scale represents final sized krill of 19 to 30 mm after 90-day model simulation.


a)
64°S
C:chl
100
90
80
70
60
50
40
30
20
10
0
5
10
15
0.5
1
29
28
27
26
25
24
23
22
21
20
b)
66°S
C:chl
c)
70°S
C:chl
Ice Chl
Water Chl