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Feeding and energy budgets of Antarctic krill *Euphausia superba* at the onset of winter—II. Juveniles and adults

A. Atkinson[1]
British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Rd, Cambridge CB3 OET, United Kingdom

B. Meyer
Alfred Wegener Institute for Polar and Marine Research, Handelshafen 12, D-27570 Bremerhaven, Germany

D. Stübing and W. Hagen
Marine Zoology, University of Bremen, P.O. Box 330440, D-28334 Bremen, Germany

K. Schmidt
Institute for Baltic Sea Research Warnemünde, Seestrasse 5, D-18119 Rostock, Germany

U. V. Bathmann
Alfred Wegener Institute for Polar and Marine Research, Handelshafen 12, D-27570 Bremerhaven, Germany

Abstract

The overwintering success of *Euphausia superba* is a key factor that dictates population size, but there is uncertainty over how they cope with the scarcity of pelagic food. Both nonfeeding strategies (reduced metabolism, lipid use, or shrinkage in size) and switching to other foods (carnivory, ice algae, or detritus) have been suggested. We examined these alternatives in the southwest Lazarev Sea in autumn (April 1999), when sea ice was forming and phytoplankton was at winter concentrations. Both juveniles and adults had a very high lipid content (36% and 44% of dry mass, respectively) of which >40% was phospholipid. However, their low O : N ratios suggested that these reserves were not being used. Results from gut contents analysis and large volume incubations agreed that juveniles fed mainly on phytoplankton and adults fed on small (<3 mm) copepods. This dietary difference was supported possibly by elevated concentrations of 20 : 1 and 22 : 1 fatty acids in the adults. The feeding methods also confirmed that feeding rates were low compared with those in summer. Even when acclimated to high food concentrations, clearance and ingestion rates were <30% of summer rates. Respiration and ammonium excretion rates of freshly caught krill were 60%–80% of those in summer and declined significantly during 18 d of starvation. These findings suggest both switch feeding and energy conservation strategies, with a trend of reduced and more carnivorous feeding with ontogeny. This points to a ''compromise'' strategy for postlarvae, but there are alternative explanations. First, the krill may have reduced their feeding in an autumn transition to a nonfeeding mode, and, second, some of the population may have maintained a high feeding effort whereas the remainder was not feeding.

The importance of krill (*Euphausia superba*) in the Southern Ocean has implications for food web dynamics (Hopkins 1985), biogeochemistry (von Bodungen et al. 1986), and commercial exploitation (Everson 1992). Sea ice extent and overwintering success are major factors dictating their condition, survival, recruitment, and population size (Ross and Quetin 1991; Loeb et al. 1997; Siegel 2000; Quetin and Ross 2001). However, the mechanisms for overwintering in krill are still poorly known, and this topic is characterized by much speculation, few data, and some controversy.

Much of the krill habitat is ice-covered in winter, and pelagic phytoplankton, a major food source during summer, is in short supply. Suggested survival mechanisms fall into two categories: first, nonfeeding strategies and second, switching to alternative foods. Possible nonfeeding strategies include the use of stored lipids (Hagen et al. 1996, 2001), reduction in the metabolic rate (Kawaguchi et al. 1986; Quetin and Ross 1991; Torres et al. 1994*b*), and shrinkage in size (Ikeda and Dixon 1982; Quetin and Ross 1991). Feeding strategies involve switching to ice biota (Marschall 1988; Stretch et al. 1988; Daly 1990), zooplankton (e.g., Hopkins

[1] Corresponding author (a.atkinson@bas.ac.uk).

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et al. 1993; Huntley et al. 1994), or seabed detritus (Kawaguchi et al. 1986).

All of these overwintering mechanisms have been observed at different times and places, but their relative importance remains unclear. Four factors have probably contributed to this. First, the strategies can differ with ontogeny, with furcilia larvae having a greater need to feed than adults (Quetin et al. 1994, 1996). Second, regional differences may be important; for example, the ice types in the Weddell Sea have been suggested to be a better winter habitat than those west of the Antarctic Peninsula (Quetin et al. 1994). Third, there are severe practical problems of covering all strategies simultaneously; both the species and its icy habitat are hard to study. The fourth factor is that krill seems to have flexible behavior. For example, west of the Antarctic Peninsula, Quetin and Ross (1991) found low metabolic rates of postlarvae, whereas, in another winter, Huntley et al. (1994) found them feeding and excreting at summer rates.

Indeed, behavioral flexibility provides a convenient explanation for all the opposing findings on krill overwintering. However, this is inadequate: a feeding strategy involves enzyme synthesis and energy expenditure for foraging, which may preclude a close-down ''hibernation.'' Switching rapidly and flexibly between such opposing modes seems unlikely. It is still unclear whether starvation and shrinkage or feeding and growing are more typical during the long winter period, but the position along this spectrum has clear implications for population dynamics. Most studies have focused on the Weddell Sea–Antarctic Peninsula, neither of which may be typical of their whole circumpolar range. Better regional coverage is one prerequisite for an appreciation of krill overwintering.

In this study, we sampled krill from the shelf break in the southwest Lazarev Sea in austral autumn. Ice cover was locally extensive and in the process of formation, with water column phytoplankton at relatively low winter concentrations. Therefore, this study allows an appraisal of feeding versus nonfeeding strategies at the onset of winter. It is hard to obtain meaningful rate measurements for this large, active animal, so our rationale was to use multiple methods to examine feeding, to use methods comparable to those used in summer, and to compare furcilia, juveniles, and adults caught from the same place at the same time. Measurements include morphometrics, elemental, proximate, and fatty acid composition, plus rates of feeding, excretion, and respiration, with these being compared between freshly caught krill and those acclimated to a range of feeding and starvation regimes. This article addresses juveniles and adults, whereas its companion, Part I (Meyer et al. this volume) covers furcilia.

Materials and methods

Krill were located by use of an Acoustic Doppler Current Profiler (ADCP) on transects of the RV *Polarstern* across the shelf break north of Neumayer station (southwest Lazarev Sea). The study area was in the region 69°43′–69°70′S and 4°38′–6°44′W (see map in Meyer et al. this volume). Krill swarms were found at night at depths of 50–100 m and were sampled between 14 and 20 April 1999 from the top 150 m with vertical tows of a Bongo net (0.5 m diameter, 350 μm mesh). This net had a 5-liter closed cod end, and the slow tows with this comparatively fine-meshed net-collected krill in excellent physiological condition. The drawback, however, was that too few krill were caught to allow large sample sizes across our whole suite of measurements. The krill were either frozen immediately for gut content and biochemical analysis or were used in a series of experiments on feeding, excretion, and respiration.

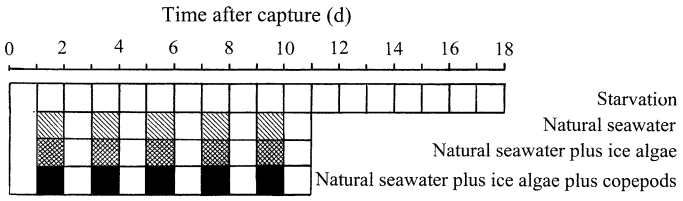

Fig. 1. Schematic representation of the krill experiments in the four feeding regimes. Each box represents a 1-d period in either filtered seawater (open box), natural seawater (single hatch), natural seawater plus ice algae (double hatch), or natural seawater plus ice algae plus copepods (filled box). Each of these four treatments was composed of a single batch of juvenile krill plus a control and a single batch of adults with a control.

Experimental design—There are three main problems in measuring feeding and metabolism of postlarval krill. First, they are stressed by capture, so rates measured on freshly caught animals may not reflect those in the wild. Second, after adequate acclimation, feeding rates obtained can depend partly on the size of their container, which suggests some effect of confinement (Price et al. 1988; Quetin et al. 1994). Third, the feeding rate (and thus respiration and excretion rates) further depends on the food concentrations offered, and these are difficult to relate to those actually located by foraging krill (Price et al. 1988).

To counteract these problems, our experiments were made up of two stages. The first was to measure metabolic rates, gut contents, and biochemical composition of freshly caught krill for comparison with such data from other seasons. The second stage was to acclimate them to various feeding regimes and monitor their feeding and metabolic response. A large suite of measurements (e.g., three methods to examine feeding) was used to reduce possible bias from each method. Because the rates reflect partly the experimental setup, this was standardized with summer studies published elsewhere (Atkinson and Snÿder 1997; Atkinson and Whitehouse 2000), to enable comparison. To follow ontogenetic differences, furcilia, juveniles, and adults were measured concurrently but separately.

Figure 1 summarizes the experiments to measure feeding, excretion, and respiration. Excretion and respiration rates were first measured for freshly caught krill, after which they were divided into batches and exposed to one of four regimes for the next 1–2 weeks. These regimes were (1) starvation in filtered seawater, (2) natural seawater, (3) natural seawater plus ice algae, and (4) natural seawater plus ice algae plus copepods. For the three feeding regimes, 24-h periods of feeding were alternated with 24-h periods in fil-

Table 1. Summary of the five sequential feeding experiments on batches of juvenile and adult krill. Values are means for the second, third, fourth and fifth experiments. Grazing rates during the first experiment were lower than in the subsequent four and were thus treated as an acclimation period, the results not being presented.

Treatment	Container	Volume of container (liters)	Mean krill size (mg DM ind^{-1})	Number of krill incubated	Stocking density (mg DM $liter^{-1}$)
NSW	Juveniles	51	54	7	7.4
NSW	Control	6			
NSW	Adults	51	253	4	20
NSW	Control	6			
NSW + IA	Juveniles	52	45	8	6.9
NSW + IA	Control	6			
NSW + IA	Adults	52	257	4	20
NSW + IA	Control	6			
NSW + IA + C	Juveniles	60	50	7	5.8
NSW + IA + C	Control	60			
NSW + IA + C	Adults	60	207	5	17
NSW + IA + C	Control	60			

NSW; natural seawater; IA, ice algae; C, copepods.

tered seawater to monitor excretion and respiration rates (Fig. 1). In the starvation experiment, we changed their filtered seawater every day and measured respiration and excretion over the next 18 d.

Feeding experiments—The feeding experiments are summarized in Table 1, and the food sources are detailed in Table 2. Natural seawater was obtained from a 10-m cast with 30-liter water bottles. These were drained through silicon tubing into eight experimental 60-liter aspirators, homogenizing across them by filling 10 liters at a time from each bottle. Two aspirators were left with natural seawater, whereas ice algae were added in equal quantities to the remaining six. This was obtained by scooping up brown discolored chunks of multiyear ice with the ship's crane, slowly thawing lumps in seawater at 2°C, and sieving out large particles through 100-μm gauze. A copepod food source was added to four of the aspirators with ice algae. These were taken from nighttime 0–150 m hauls from the krill collection area by use of the Bongo net and supplemented with 0–50 m catches

Table 2. Food items enumerated for the three feeding regimes and their mean contribution to available C across experiments 2, 3, 4, and 5 in each regime. The mean lengths of the copepods refer to prosome lengths.

Food group	Group enumerated	Length class (μm)	Mean length	Total C in food source (mg C m^{-3})		
				NSW	NSW+IA	NSW+IA+C
Diatoms	Unidentified small diatom sp.	All sizes	14	0.017	0.085	0.066
	Small centric diatoms	<50	17	0.042	0.078	0.17
	Fragilariopsis spp.	All sizes	23	4.0	9.7	22
	Entomoneis spp.	All sizes	44	0.0016	1.1	0.96
	Nitzschia spp.	All sizes	76	0.33	1.1	1.6
	Large pennate diatoms	>50	88	0.75	2.0	3.1
	Chaetoceros spp.	All sizes	92	0.066	1.0	1.0
	Large centric diatoms	>50	142	NA	NA	0.16
Motile taxa	Small dinoflagellate sp.	All sizes	17	0.24	0.28	0.46
	Dinoflagellates and ciliates	All sizes	22	0.39	1.1	1.4
	Distephanus sp.	All sizes	56	0.13	0.42	1.4
Copepods	Copepod nauplii	All sizes	181	NA	NA	1.4
	Small *Oithona* spp.	<350	423	NA	NA	2.3
	Large *Oithona* spp.	>350	776	NA	NA	4.1
	Very small calanoids	<750	425	NA	NA	1.6
	Small calanoids	750–1,250	962	NA	NA	9.5
	Medium calanoids	1,250–3,000	2,850	NA	NA	54
	Large calanoids	3,000–5,000	4,230	NA	NA	155
Total for available food	**Counted diatom taxa**			**1.8**	**15**	**29**
	Counted motile taxa			**0.67**	**1.8**	**3.3**
	Autotrophs*			**3.9**	**35**	**54**
	Copepods			**0**	**0**	**228**
	Autotrophs plus copepods			**3.9**	**35**	**282**

* Based on Chl *a* assay and converted to C with a C : Chl *a* ratio of 50.
NA, not analyzed; NSW, natural seawater; NSW+IA, natural seawater enriched with ice algae; NSW+IA+C, natural seawater plus ice algae and copepods.

from a hand-hauled Apstein net. These catches were sorted under a microscope to select only the actively swimming copepods with intact setae. *Pareuchaeta* spp. were discarded, because their predation on other copepods could have led to artifacts in the estimates of predation by krill. The copepod food assemblage was mixed gently and decanted equally into four of the aspirators with ice algae.

The controls were set up in the same way as the experimentals, and these were either of the same volume (for the treatment with enriched copepods; see Table 1) or were of 6 liters obtained by decanting mixed experimental water just before the addition of the krill.

At the start of the experiment, two subsamples of 250 ml for microscopic analysis and two of 1 liter for chlorophyll *a* analysis were siphoned from the mixed contents of the incubation water. The 250-ml samples were fixed in 2% acid Lugol's solution, and Chl *a* subsamples were filtered under gentle vacuum onto 25-mm GF/F filters and frozen at −80°C.

Experimental and control containers were incubated in dim light in the cold room (1–2°C) and stirred gently with a plunger every 1–2 h for the experimental duration (mean, 27 h). After the final mixing at the end of the experiment, 250 ml Lugol's subsamples were taken from each container, and the krill were transferred to the next excretion and respiration experiment. Then, for experimental and controls with copepods, the whole of the aspirator contents were filtered onto a 53-μm sieve and preserved in 10% Lugol's solution. After the alternating experiments on feeding and metabolism (Fig. 1), the krill were measured to the nearest 1 mm from the front of the eye to the tip of the telson and frozen.

Analysis of feeding experiments—The protocols for sample enumeration were standardized to those in a summer study (Atkinson and Snÿder 1997), which should be consulted for further details. From the enriched incubations, uneaten copepods were counted under a binocular microscope. These were enumerated in the same size and taxonomic groups as in the Atkinson and Snÿder (1997) study to allow comparison (see Table 2).

Dry masses (DMs) of copepodite stages of the dominant copepods (*Calanus propinquus*, *Metridia gerlachei*, *Calanoides acutus*, and *Ctenocalanus* spp.) were determined directly from the frozen 0–150-m catches of the Bongo net. These were thawed, rinsed, and their prosome lengths measured before being dried at 50°C for >24 h, cooled in a desiccator, and weighed immediately to the nearest microgram. The masses of calanoid copepods in the small size fractions were determined from length-mass regressions constructed from these data. C contents of *Oithona* spp. and copepod nauplii were calculated from their lengths according to the equations in Fransz and Gonzalez (1995, 1997).

Microplankton were enumerated by use of the Utermöhl (1958) technique. Two to three replicate 50-ml aliquots per container were analyzed under an inverted microscope. We selected only the prominent diatoms and motile cells that could be identified consistently (Table 2). However, visual inspection of the settled samples showed that the taxa selected, in particular *Fragilariopsis* spp., were dominant in terms of biolovolume. For each experiment, the dimensions of 30–50 individuals of each category were measured, and their volumes and C concentrations were calculated according to the methods of Eppley et al. (1970) and Putt and Stoecker (1989). Across all experiments and food taxa, the mean reduction due to krill grazing in counted cells was 18%.

The initial Chl *a* values provide independent estimates of available food. These were obtained by use of a Turner 700D fluorometer as described in Meyer et al. (this volume) and have been converted to C under the assumption of a C : Chl *a* ratio of 50. This ratio is in the middle of the range (36–61) for ambient and enriched experiments with the same incubation water (Meyer et al. 2002). The prominent diatoms that were counted comprised ~50% of the total C estimated from the Chl *a* analysis (Table 2).

Feeding rate calculations—Clearance rates on each food group in Table 2 were calculated as

$$F = \ln(C_c/C_k) \times V/(m_k \times t)$$

where F is the clearance rate in ml (mg krill DM)$^{-1}$ h^{-1}, C_c is the final concentration in the control, C_k is the final concentration in the carboy grazed by krill, V is the experimental volume (ml), m_k is the krill DM (mg), and t is the experimental duration (h). This equation allows for changes in prey abundance unrelated to krill grazing (Båmstedt et al. 2000). These were in any case minor, because the total concentrations of counted food items at the end of the control runs were within 8% of initial values. Ingestion rates of the various food categories were calculated as the product of the clearance rate of that category and its C concentration in the final control.

Excretion and respiration experiments—These were run in seawater filtered through 0.45-μm mesh and equilibrated to cold room temperature. The six glass flasks for the krill were 12 liters, and six control flasks without krill were 6 liters. Each batch of krill from a feeding aspirator (*see Table 1*) was used together in a single flask, which thus allowed us to keep track of the feeding and metabolic history of each batch. The krill were rinsed and added to the flasks, which were then topped-up and sealed with Parafilm. Subsampling was done by rapidly inserting a glass tube and siphoning the mixed contents of the flasks into bottles, flushing them to purge air. For both the oxygen and ammonium determinations, three replicate subsamples of 20 ml were used.

Oxygen concentrations were measured after immediate fixing for Winkler titrations, as described in Meyer et al. (this volume), by use of a 716 DMS Titrino (METROHM). The decrease in oxygen concentration in all experiments was <20%. Ammonium excretion rates were measured colorimetrically by use of a Technicon Autoanalyzer II (Bran and Lübbe, Norderstedt, Germany). Four standards at the beginning of each run and two at the end were used, and the analytical precision of replicates was ~0.05 μmol.

Metabolic rate calculations—Excretion rates were calculated by use of the general formula in Atkinson and White-

house (2000). Respiration rates were calculated by use of the formula

$$R = (O_c - O_k)\ V/(m_k \times t)$$

where R is the respiration rate in μl O_2 (mg krill DM)$^{-1}$ h^{-1}, O_c is the O_2 concentration in the control flask at the end of the experiment (μl O_2 liter^{-1}), O_k is the corresponding value in the experimental flask, V is the volume before subsampling (liters), and t is the experimental duration (h).

Unfortunately, heavy use of the cold room meant that we were unable to maintain its temperatures at that of the sea, and incubation temperatures were in the range 1–2°C. This is within the normal winter limits of this species, because it is a characteristic temperature of the warm deep layer. However, we have corrected our results to −1°C, a midrange ambient value, by use of a Q_{10} value of 2.5 (Ikeda 1985). This effectively multiplies our measured rates by a factor of 0.75.

Morphometric, elemental, and biochemical analysis—Lengths of fresh krill were measured before they were frozen individually at −80°C. Their DMs were obtained by thawing, rinsing briefly in deionsed water, drying (at 60°C for 48 h), cooling in a dessicator, and weighing on a Mettler UM3 microbalance. All biochemical analyses were on freeze-dried individual krill that had been homogenized to a powder over ice. C and N contents were analyzed in a Carlo Erba Elemental analyzer against an acetanilide standard. Carbohydrate and protein were measured by placing single krill in 5% trichloroacetic acid in an ice bath, homogenizing with a Branson Sonifer B15 cell disrupter, and centrifuging (at 5,000 × *g*) for 10 min. The supernatant was used for carbohydrate analysis and the pellet for protein (*see* Meyer et al. this volume).

Total lipid was measured gravimetrically by extracting whole krill in a 2:1 mixture of dichloromethane and methanol, as described by Hagen (2000). To analyze the component fatty acids (FAs) in the total lipids, they were hydrolyzed and converted to fatty acid methyl ester (FAME) derivatives in methanol that contained 3% concentrated sulphuric acid at 80°C for 4 h (Meyer et al. this volume). FAMEs were then extracted with hexane, analyzed in a gas chromatograph (HP 6890A), and identified by comparing retention times with those obtained from standard mixtures.

Gut-content analysis—Frozen krill were thawed, measured, and dissected to remove their stomachs and guts. These were rinsed and placed separately in counting chambers. Fullness was scored from 0 (empty) to 10 (full) The whole samples were examined for crustacean fragments under an inverted microscope (×64), and copepod mandibles were measured and counted. Numbers of crustacean fragments were scored as 0 (none), 1 (between 1 and 10), or 2 (>10). *Fragilariopsis* spp. was the dominant identifiable diatom, so whole frustules of these were counted at ×160.

Results

Environment—Krill were found over the shelf break in open water between floes of first-year and multiyear ice. The upper mixed layer varied between 40 and 220 m in depth, with salinities of 33.9–34.6 and temperatures of −1.8–0°C (Strass et al. 2000). This area was characterized by very low water column phytoplankton biomass, with five water-bottle profiles showing Chl *a* concentrations in the upper mixed layer ranging from 0.06 to 0.09 mg Chl *a* m^{-3}. The potential food source from sea ice is hard to assess in such an environment, but we saw ice algae as brown discolorations in many of the large, perforated blocks of multiyear ice.

Table 3. Mesozooplankton community composition, as indicated by three 0–150-m tows with a 350-μm Bongo net.

Species, stage	Abundance (number of individuals m^{-3}) Mean	Range
Calanus propinquus		
CI	0.53	0.4–0.8
CII	2.1	2.0–2.2
CIII	11	7.9–16
CIV	8.1	5.6–11
CV	4.2	2.1–7.2
CVI female	0.07	0–0.2
Metridia gerlachei		
CIV	0.83	0–1.6
CV	8.3	6.4–10
CVI female	4.9	0.4–14
Calanoides acutus:		
CIV	1.0	0.5–1.2
Paraeucheta antarctica		
CIV	0.16	0–0.4
CV	0.09	0–0.28
Ctenocalanus spp.:		
CIV–CVI	10	5.7–14
Oithona spp.:		
CIV–CVI	2.5	1–5.3
Euphausia superba:		
Furcilia	9	1.9–15
Ostracoda:		
All stages	0.50	0–1.1
Amphipoda:		
All stages	0.09	0–0.40
Total for copepods:		
All stages	**54**	**40–62**
Total for metazooplankton:		
All stages	**64**	**48–78**

The mesozooplankton assemblage was sparse (Table 3) and was dominated numerically (84%) by copepods. The biomass-dominant zooplankters (*C. propinquus, M. gerlachei,* and *E. superba* furcilia) were retained by the 350-μm net but not the smallest species. The mean biomass of mesozooplankton was 1.37 g DM m^{-2}, within the normal range of values for the East-Wind Drift and the Weddell Sea (e.g., Hopkins and Torres 1989). This biomass was dominated by copepods (60%) and stage III furcilia of *E. superba* (24%).

Distribution and condition of krill—Our direct observations of the underside of the ice were from two daytime observations, each of ~2 h, with a video camera. No furcilia or postlarvae were seen, and none were seen on the under-

Table 4. Biochemical composition of freshly caught juvenile and adult krill.

Measurement	Juvenile krill (n = 34)			Adult krill (n = 21)		
	Mean	Standard deviation	Range	Mean	Standard deviation	Range
Dry mass, DM (mg)	54	20	23–96	249	49	179–384
Carbon content (% of DM)	51	1.3	41–54	54	1.5	46–57
Nitrogen content (% of DM)	8.6	0.59	7.0	7.9	0.48	7.1–8.8
C : N ratio	6.0	0.48	4.3–6.9	6.9	0.59	5.4–8.3
Lipid (% of DM)	36	5.2	26–44	44	8.1	30–58
Protein (% of DM)	35	4.3	28–45	32	1.9	24–38

n, number of krill analyzed. Carbohydrate values were <1% of DM and so not presented.

side of ice floes turned over by the ship. The only krill detected were swarms at 50–100 m depth, located during nighttime ADCP transects across the shelf break. The ADCP transducer was at 8 m depth, so swarms above this would not have been seen.

The postlarval krill were composed of two distinct size groups, 28–38 and 48–58 mm, hereafter termed juveniles and adults. Freshly caught animals had pale yellowish-green hepatopancreases, and food was seen in the guts of some of them.

Morphometrics and body composition—The regression of DM (mg) on length (mm) was

$$\log_{10}(\text{DM, mg}) = 3.25 \log_{10}(\text{length, mm}) - 3.18$$

$$(n = 31 \text{ krill}, r^2 = 0.978)$$

Lipid reserves were very large, reaching 58% of DM (Table 4). These C-rich stores meant that C comprised >50% of DM, as reflected in C : N ratios >6. Triacylglycerols (TAGs) and phospholipids dominated the lipids, with minor contributions from the others (Table 5). TAG is recognized as an energy store for krill, but phospholipids are considered to be primarily structural membrane lipids. However, the quantities of these in both juveniles and adults are in excess of those required for structural purposes, which supports suggestions that polar lipids are an unusual energy store in *E. superba* (e.g., Hagen et al. 1996, 2001).

FA composition—The FA compositions of the experimental krill were similar to the freshly caught specimens and so are not presented here. The latter contained saturated fatty acid (SFAs) and polyunsaturated fatty acids (PUFAs) in similar amounts (Table 6). Three indices have been suggested to reflect the degree of carnivory in krill. These are the content of 20 : 1 and 22 : 1 FAs, the 18 : 1(n-9)/18 : 1(n-7) ratio (Falk-Petersen et al. 2000; Virtue et al. 2000), and the PUFA : SFA ratio (Cripps and Atkinson 2000). The latter two were similar for adults and juveniles (Table 6), whereas the former was greater for adults, which suggests more reliance on carnivory.

Table 5. Lipid class composition (% by mass) of four freshly caught juvenile krill and four freshly caught adults.

Lipid class	Juveniles mean % (SD)	Adults mean % (SD)
Triacylglycerol	54 (1.6)	51 (2.5)
Phospholipid	42 (1.5)	44 (2.6)
Sterol	3.3 (0.53)	4.4 (0.20)
Sterolester	1.2 (0.45)	0.65 (0.12)
Free fatty acid	0.02 (0.01)	0.04 (0.03)

SD, standard deviation.

Gut contents—Although only 12 krill were available for analysis, the adults and juveniles differed clearly in diet (Table 7, Fig. 2) Juveniles had fuller stomachs and guts and contained more phytoplankton than the adults, which contained crustacean fragments. The sizes of the copepod mandibles, m (mm), were used to estimate their prosome lengths, l, from Båmstedt et al. (2000):

$$l = 0.0431 + 0.0112m$$

This equation is for north Atlantic copepods, and individual species differ, so results are presented in broad size categories to show the general picture (Fig. 3). The sample size is small, but the results support those from the feeding incubations (see next section), which suggests that adult krill ate mainly the small copepods (<3 mm).

In situ ingestion rates—The numbers of *Fragilariopsis* spp. in the guts of juvenile krill could not be used to calculate ingestion because most were fragmented and not countable. However, for adults we used the paired mandible method (Båmstedt et al. 2000) to estimate ingestion rates of copepods. Not all of its component measurements were made in this study, which forced some assumptions; nevertheless, this is an independent check on whether feeding rates at our site were indeed low.

In this method, each matched pair of mandibles represents the ingestion of one copepod. Prosome lengths of these were calculated from mandible width (previous section) and then to C by use of regressions constructed from this study site. Literature values of gut passage times of freshly caught postlarvae, albeit from spring and summer (Clarke et al. 1988; Perissinotto and Pakhomov 1996; Atkinson and Snÿder 1997; Daly 1998 and references therein) yielded a value of ~4 h, which we used herein. The final assumption was that feeding rates at the time of capture are representative of daily rates. Daily C rations based on these assumptions were low (mean 0.3%) and variable (range 0–1.0%). Our last two as-

Table 6. Fatty acid composition of freshly caught *Euphausia superba.* Values are percentages by mass of total fatty acids in storage plus structural lipids. Data are for 10 juveniles (mean DM 51 mg) and 8 adults (mean DM 262 mg). Summary data in bold type are for fatty acid characteristics that have been used in previous studies as an index of carnivory (see Results section).

	Juvenile krill		Adult krill	
Fatty acids	Mean	Range	Mean	Range
14 : 0	11.9	11.1–13.5	12.5	10.5–13.7
15 : 0	0.5	0.3–0.6	0.4	0.2–0.6
16 : 0	19.3	17.5–21.4	18.2	15.4–20.4
16 : 1(n-7)	6.6	1.4–8.2	8.1	5.5–10.5
16 : 1(n-5)	1.0	0.3–5.5	0.4	0.2–0.5
16 : 2(n-7)	1.7	1.5–1.8	1.5	1.2–1.7
16 : 3(n-4)	0.4	0.2–0.4	0.3	0.2–0.4
16 : 4(n-1)	0.7	0.4-1.0	0.6	0.3–0.7
17 : 0	0.1	0.05–0.2	0.1	0.05–0.2
18 : 0	1.7	1.0–1.9	1.4	0.7–1.7
18 : 1(n-9)	11.7	9.9–16.1	12.8	9.3–15.8
18 : 1(n-7)	6.5	5.9–7.1	7.1	6.0–8.0
18 : 2(n-6)	2.6	2.04–2.94	2.3	1.7–2.6
18 : 3(n-3)	0.7	0.69–0.8	0.7	0.6–0.7
18 : 4(n-3)	2.3	1.9–2.78	2.2	1.4–2.9
20 : 1(n-9)	1.1	0.8–1.7	1.4	1.2–1.8
20 : 1(n-7)	0.4	0.2–1.8	0.4	0.3–0.4
20 : 4(n-6)	0.7	0.5–0.8	0.7	0.5–1.0
20 : 4(n-3)	0.6	0.4–0.8	0.6	0.4–0.8
20 : 5(n-3)	15.2	13.0–16.3	15.3	12.5–16.0
22 : 1(n-13)	0.2	0.02–0.3	0.08	0.01–0.2
22 : 1(n-11)	0.7	0.6–1.2	1.0	0.7–1.2
22 : 1(n-9)	0.1	0.07–0.2	0.2	0.1–0.2
22 : 4(n-3)	0.4	0.3–0.5	0.4	0.3–0.5
22 : 5(n-3)	0.5	0.3–0.9	0.5	0.3–0.7
22 : 6(n-3)	8.2	5.6–9.9	9.1	6.3–10.7
Unknown	3.4	1.5–4.7	2.2	1.2–3.7
Total lipid (% of DM)	37	35–48	44	30–60
Total PUFA (% of fatty acids)	33.9	27.4–37.6	33.1	27.8–40.2
Total SFA (% of fatty acids)	34.4	30.9–36.9	33.2	28.9–36.9
Sum of 20 : 1 and 22 : 1 (% of total FA)	**1.8**	**1.4–2.9**	**2.4**	**1.9–3.0**
18 : 1 (n-9)/18 : 1(n-7) ratio	**1.81**	**1.6–2.6**	**1.8**	**1.37–2.6**
PUFA/SFA ratio	**0.99**	**0.77–1.1**	**1.0**	**0.78–1.3**

sumptions were probably generous, so the in situ ingestion rate of the adult krill was probably low.

Experiments: clearance rates—Compared with juveniles, the mass-specific clearance rates of adults were low, and they fed more carnivorously (Figs. 4, 5). Adult clearance rates on algae and protozoans were negligible, and the only consistently positive rates were on copepods. In contrast, the juveniles had similar clearance rates on algae, protozoans, and copepods.

The same methods have been used in a summer study at South Georgia (Atkinson and Snÿder 1997), enabling a valid comparison of juvenile feeding behavior (Figs. 4, 5). In the summer, postbloom study, they cleared motile foods (protozoans, ciliates, and copepods) faster than diatoms, even when autotrophs dominated available C. In the present study, however, raptorial feeding was seen only in adults. Juveniles fed at similar rates across the whole size range (Fig. 4), even though copepods made up ~80% of C in the enriched food (Table 2). Also, clearance rates on motile cells were similar to those on diatoms of similar size.

There are two possibilities for artifacts in these interpretations. The first is that krill excretion caused higher growth rates of autotrophs in the grazed containers than in the controls, leading to an underestimation of their clearance rates. However, Fig. 4 shows adult clearance rates consistently around zero for all autotrophs except *Fragilariopsis* spp., which were consistently negative. The use of median clearance rates to summarize these data (Fig. 5) is therefore robust.

The second possible artifact is for ''food chain effects'' to occur in mixed prey assemblages. If krill ingested the higher trophic levels (e.g., copepods) that were feeding on diatoms, then the measured clearance rates of krill on the latter would be artificially low. However, for the copepod-enriched incubations, a paired *t* test showed no significant change in the counted taxa within the controls ($P < 0.05$), which suggests that the copepods had little grazing effect at the con-

Table 7. Analysis of stomach and gut contents of krill, arranged in order of increasing body length. See Materials and Methods: gut content analysis section for explanation of indices. Dashes indicate that data are not available.

	Analysis of stomach contents				Analysis of gut contents		
Krill size, mm	Fullness index (0–10)	No. whole frustules of *Fragilariopsis* spp. per stomach	No. crustacean fragments (score 0, 1, 2)	No. mandibles	No. whole frustules of *Fragilariopsis* spp. per gut	No. crustacean fragments (score 0, 1, 2)	No. mandibles
Juvenile, 28	5	1,678	0	0	433	0	0
Juvenile, 30	7	3,114	1	0	241	0	0
Juvenile, 30	5	986	1	0	234	1	0
Juvenile, 31	5	1,125	0	0	65	0	0
Juvenile, 32	3	35	2	0	0	0	0
Juvenile, 33	6	6,005	0	0	433	0	0
Juvenile mean	**5.2**	**2,157**	**0.67**	**0**	**234**	**0.17**	**0**
Adult, 43	3	69	2	2	0	0	0
Adult, 47	2	440	2	1	—	—	—
Adult, 48	2	880	1	0	—	—	—
Adult, 50	3	346	2	3	17	2	1
Adult, 56	3	1,371	2	5	104	1	0
Adult, 57	2	0	2	1	0	0	0
Adult mean	**2.5**	**518**	**1.8**	**2.0**	**30**	**0.75**	**0.25**

centrations used. Thus, any food chain artifacts are small compared with krill grazing, and the contrasts in Fig. 5 are too large to be explainable by container artifacts.

Experiments: ingestion rates and functional response—Even after a week of acclimation to high food concentrations (~300 μg C liter^{-1}), juvenile rations were <1% of body C d^{-1} (Fig. 6). On the basis of the regressions in Fig. 6, this autumn ration at 300 μg C liter^{-1} is only 17% of that in the comparable South Georgia study, which used the same methods and container sizes but at summer temperatures of 2°C.

Respiration rates—Mean respiration rates of freshly caught krill were 18 (juveniles, mean DM 44 mg) and 39 (adults, mean DM 148 mg) μl O_2 ind h $^{-1}$. On the basis of a compilation of equivalent summer data (Rakusa-Suszczewski and Opalinski 1978; Segawa et al. 1979; Ikeda and Hing-Fay 1981; Kils 1981; Ikeda and Mitchell 1982; Ikeda 1984; Ikeda and Bruce 1986; Ishii et al. 1987 in fig. 7 of Quetin et al. 1994), our autumn values for −1°C are 60% (adults) and 77% (juveniles) of summer rates. Starved krill had much lower respiration rates than when freshly caught, and they continued to decline during the experiment (Fig. 7).

Gains and losses of C due to feeding and respiration are

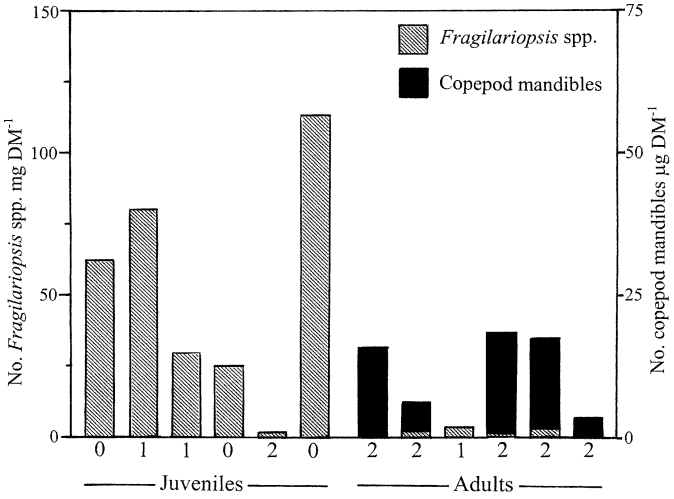

Fig. 2. *E. superba.* Gut contents of the six adults and six juveniles. Hatched bars, left axis: numbers of whole frustules of *Fragilariopsis* spp. mg^{-1} Krill DM. Solid bars, right axis: numbers of copepod mandibles μg^{-1} krill DM. The numbers below the bar for each krill denote the scores (0, 1, or 2) for the number of crustacean fragments found in the stomach (*see Table 7*).

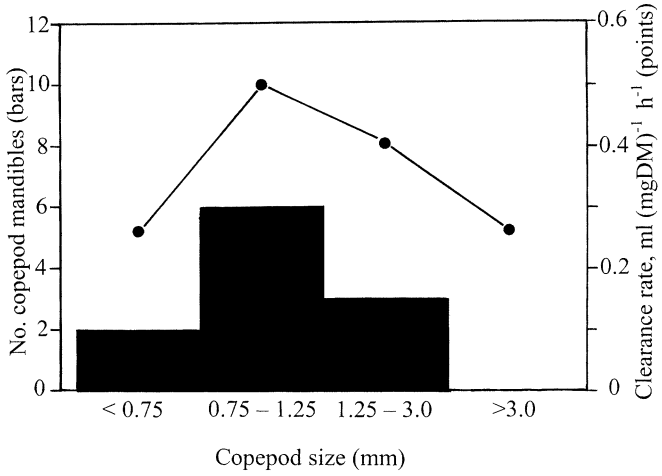

Fig. 3. Adult *E. superba.* Size spectrum of copepods in the diets of adults. Left axis and bars: frequency distribution of prosome lengths of copepods in krill guts as based on mandible widths. Right axis and points: mass specific clearance rates on the same size categories as based on the incubations (*see Fig. 4*).

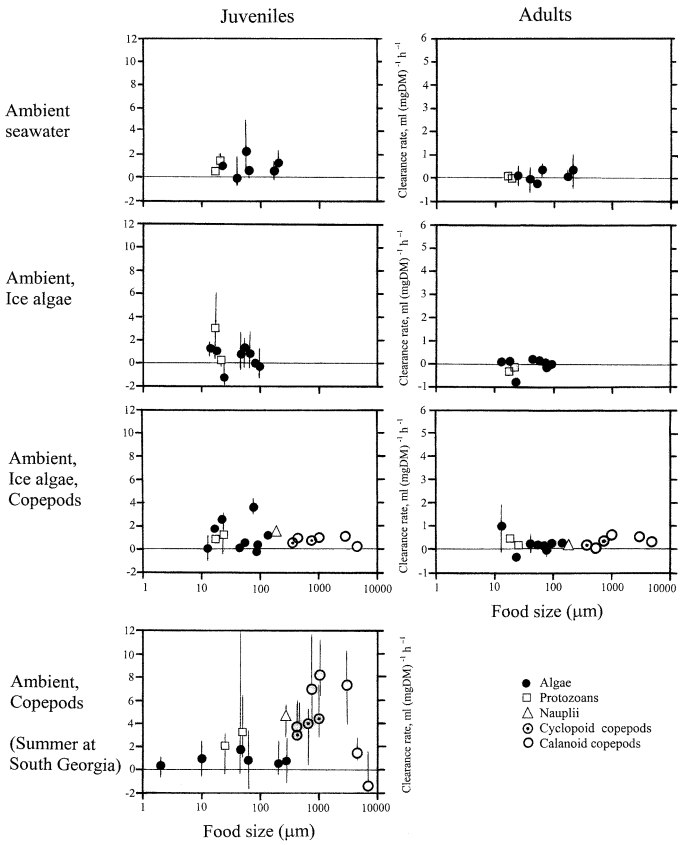

Fig. 4. *E. superba.* Mean and range of mass-specific clearance rates on the various prey categories in relation to prey length. Results are presented in relation to median and interquartile ranges from a comparable summer study at South Georgia.

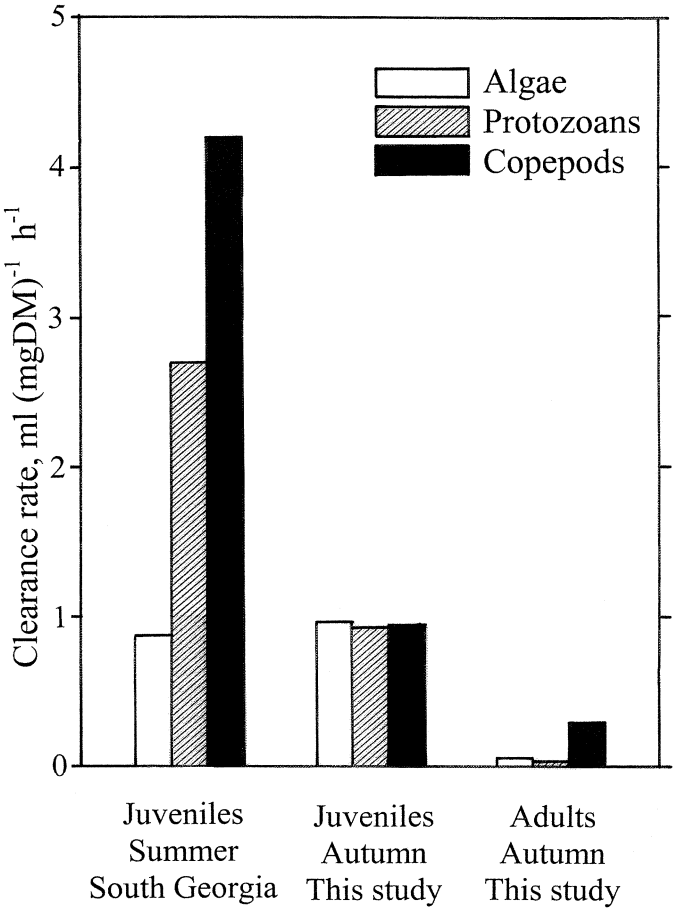

Fig. 5. *E. superba.* Median clearance rates of juveniles and adults on algae, protozoans, and copepods, calculated across all feeding regimes. The food category ''algae'' is composed of mainly diatom taxa, ''protozoans'' here includes the counted ciliate and dinoflagellate taxa, which have been assumed for simplicity as mainly heterotrophic, and ''copepods'' are composed of nauplii and copepod size groups (Table 2) up to a prosome length of 5 mm.

compared in Fig. 8. Respiration rates are expressed as daily C losses by use of a respiratory quotient of 0.97 (Ikeda and Kirkwood 1989). These values are plotted against food availability in the preceding feeding periods. For freshly caught krill, in situ food concentration is plotted as the mean copepod and autotroph biomass from the net samples and water bottle profiles. This is almost certainly an underestimate of the mean, because krill can forage on patches. Indeed, the C gains and losses from freshly caught krill are relatively high compared with those in acclimated krill, being similar to those at the highest food concentrations. At lower values of food availability, respiration rates declined to 0.18% body C d^{-1}, which was observed at the end of the 18-d starvation. Respiratory C losses exceeded the gains from ingestion at all food concentrations measured, and this was also true for freshly caught krill. This discrepancy is particularly marked at low food concentrations.

Excretion rates—Mean ammonium excretion rates of freshly caught adult krill of mean DM 148 mg were 183 nmol NH_4^+ ind^{-1} h^{-1}. This is 81% of that predicted from a regression of summer data at 0°C (fig. 5a in Atkinson and Whitehouse 2000, compiling data of Biggs 1982; Ikeda and Mitchell 1982; Segawa et al. 1982; Hirche 1983; Ikeda and Bruce 1986; Ikeda and Kirkwood 1989). Another comparison with summer data is possible for krill acclimated to feeding in the lab at high food concentrations (the regression in fig. 5b of Atkinson and Whitehouse 2000). Our values for the krill in the treatment with added copepods are only 33% of the corresponding summer values.

In common with the respiratory losses of C, daily losses of NH_4^+ ind^{-1}-N increased with feeding rate (Fig. 9). Also in common was the fact that the daily N loss of freshly caught krill was at a rate nearer that found in the copepod-enriched incubations than that of starving krill.

O : N ratios—Ikeda et al. (2000) calculated that O : N ratios lower than ~21 indicate the dominance of proteins as a metabolic substrate, and values greater than this meant the dominance of lipids. The highest ratios we found were in krill either starving or subjected to low food concentrations (Table 8), which suggests that they were relying on body lipids more than those in situ or at higher food concentrations.

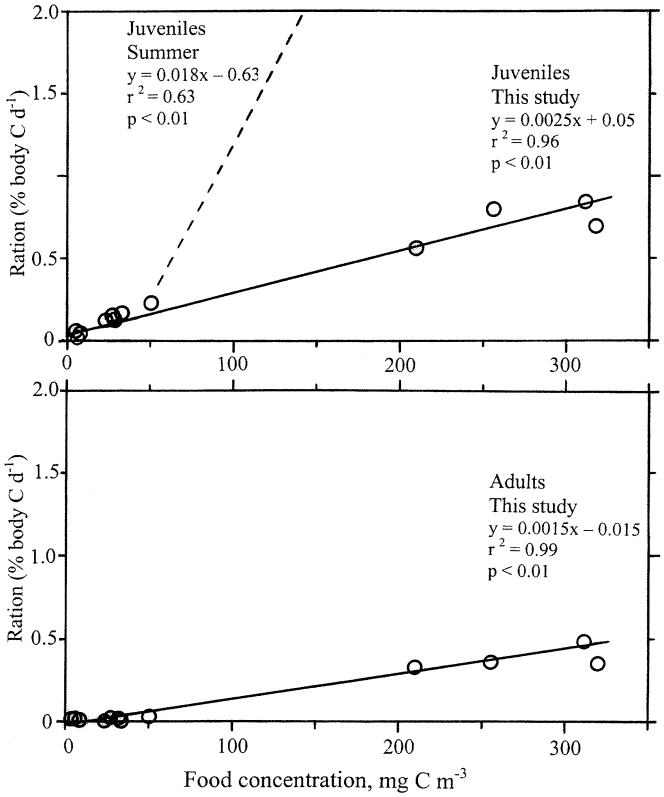

Fig. 6. *E. superba.* Daily C ration as a function of food availability. Data points represent individual experiments for the three feeding regimes. Functional responses are approximated by simple, least-squares linear regressions, because the data were insufficient to define the shape of a functional response curve. The broken regression line describes the functional response for juveniles from Atkinson and Snÿder (1997) on the basis of 43 data points (food concentration 25–1,164 mg C m^{-3}, ration up to 36% body C d^{-1}).

Discussion

In this April study, phytoplankton biomass was at winter levels and there was partial ice cover, so krill had to cope with low phytoplankton concentrations at the onset of winter. Despite having lipid reserves among the highest recorded, their low O : N ratios suggested that they had not resorted to burning these reserves. Feeding rates were lower than those in summer; concomitantly, respiration and excretion rates were lower. Adults had switched to feeding on copepods, but clearance rates could not increase quickly to take advantage of abundant food. Our results thus suggest that both switch feeding and energy conservation mechanisms were being adopted. Below, we outline the evidence for each and examine some of the tradeoffs involved in such a ''compromise'' strategy.

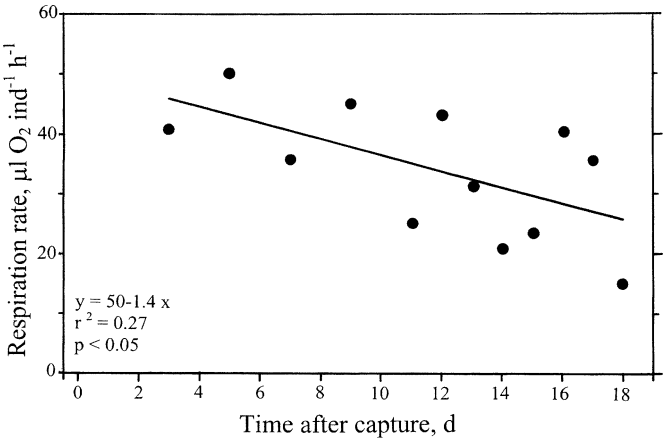

Fig. 7. Adult *E. superba.* Time course of respiration rates of starving krill (mean DM 194 mg) maintained in daily changes of filtered seawater.

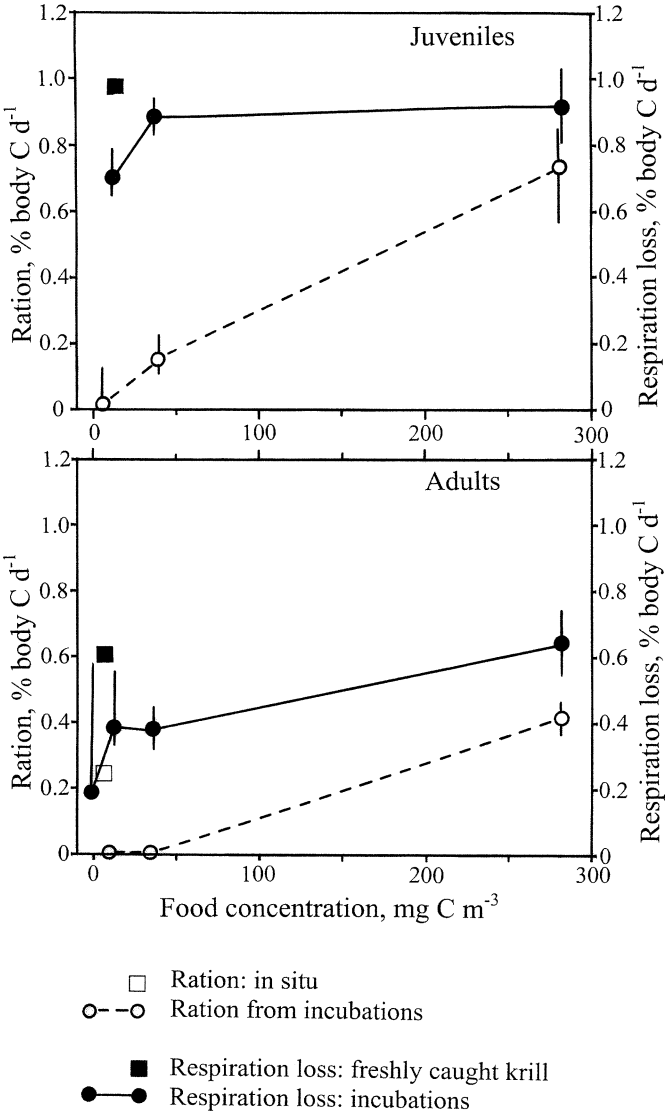

Fig. 8. *E. superba.* Left axis: daily C ration from ingestion. Right axis: daily percentage of body C losses from respiration of freshly caught krill, after 18 d starvation and in the three food regimens. The points represent a mean across experiments, with bars denoting the range. Food concentrations are the means of the four experimental periods (*see Table 2*), with a value of zero for the starved animals.

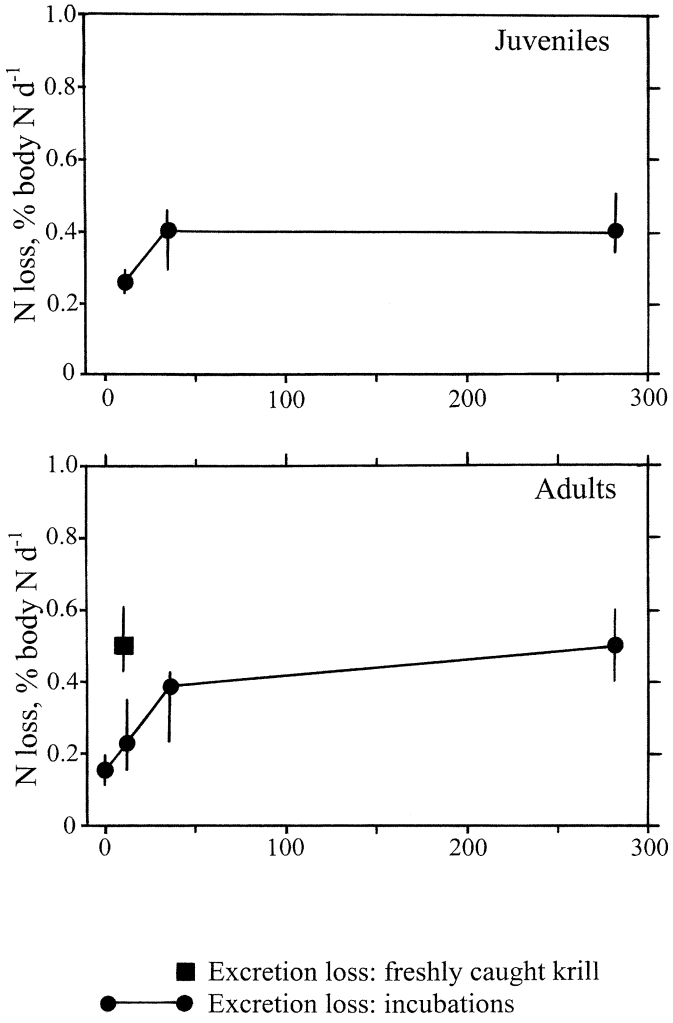

Fig. 9. *E. superba.* Excretion rates of freshly caught and starving krill and those in the three food regimens. The open circle represents freshly caught krill. The points represent a mean across the experiments with bars denoting the range. Food concentrations are the means of the four experimental periods (*see Table 2*), with a value of zero for the starved animals.

Feeding—Because quantifying feeding in krill is difficult yet critical in elucidating overwintering mechanisms, we used three approaches—namely, FA biomarkers, gut content analyses, and incubations. One of the three FA indices in Table 6 suggests that the adults were more carnivorous than juveniles, but low levels of 20:1 and 22:1 FAs imply less carnivory than in the northern krill, *Meganyctiphanes norvegica* (*see* Virtue et al. 2000). However, without measuring the signatures of food and pathways of biosynthesis, the degree of carnivory at the time of lipid deposition is uncertain (Falk-Petersen et al. 2000; Virtue et al. 2000; Hagen et al. 2001). Future ''calibration'' experiments will be needed to place measurements such as those in Tables 5 and 6 into a trophic context.

Gut content analysis is more direct but also has problems, such as feeding occurring in the net. However, the presence of crustaceans in the hind guts as well as in the stomachs suggests that they had not been eaten recently. Furthermore, the juveniles contained diatoms that were not retained by the 350-μm mesh net, whereas adults contained copepods too small to be caught in abundance. These points are hard to explain in terms of net feeding and imply that adults were more carnivorous than juveniles.

Table 8. Atomic O:N ratios of juvenile and adult krill, both freshly caught and in the various food regimes. Dashes indicate no data. Data are ratios of mean values of experiments 2, 3, 4, and 5, plus mean values for freshly caught krill and at the end of 18 d of starvation.

Treatment	Juveniles	Adults
Freshly caught	—	10
Starved	—	23
Natural seawater	22	15
Natural seawater plus ice algae	16	8
Natural seawater, ice algae; plus copepods	17	11

Incubations provide insights into feeding behavior but could suffer from container artifacts. Against the notion that krill just eat anything and everything in captivity, the juveniles fed differently from those in a comparable study (Atkinson and Snÿder 1997). In the present study, they had similar clearance rates across most of the food spectrum, which suggests a ''filtration'' type of behavior. During the summer, postbloom study at South Georgia, juveniles cleared motile food, especially small copepods, most rapidly. Only the adults fed like this in the present study, and this contrast supports the gut content analysis, pointing to a different feeding behavior.

The analyses of gut contents and the incubations provide insights into the spectrum of food available to krill. Feeding rates on copepods >3 mm were low in this study (Figs. 3, 4) and in that by Atkinson and Snÿder (1997). Because most of the winter copepod biomass is in these large, lipid-rich species, many of which are at depth, total biomass values may overplay the importance of this alternative food source. The availability of suitable size copepods varies regionally as well, which perhaps explains why the juveniles were less carnivorous than those at South Georgia. There, the mean copepod biomass was higher (26 mg DM m^{-3}; Atkinson et al. 1999) than in the seasonal ice zone of this study (4.3 mg DM m^{-3}). Microplankton biomass was low in the South Georgia study, and, because ice was not present, an alternative was copepods. In our study, the very limited observations did not reveal krill feeding under sea ice, but it is possible that they did so and fed across a wide size spectrum.

The incubations and gut content analyses also converge on the conclusion that feeding rates of krill were <25% of their capabilities in summer. They were not feeding slowly simply because food was scarce and temperatures were lower; clearance rates failed to increase even after 5 d in abundant food. However, the rations are probably underestimates: even 60-liter containers might constrain feeding (Quetin et al. 1994). In parallel experiments in similar maximum food concentrations but in 180-liter containers, rations averaged 1.3% of body C d^{-1} (K. Schmidt unpubl. data), which is still well below summer values (e.g., Clarke et al. 1988; Pakhomov et al. 1997; Perissinotto et al. 1997).

Carbon and nitrogen conservation—By autumn, these krill were already relying to some extent on energy conservation strategies, because excretion and respiration rates were 60%–80% of summer values. This percentage reduction is not so great as that observed during midwinter (Kawaguchi et al. 1986; Quetin and Ross 1991; Torres et al. 1994*a*) and may be explained simply by lower feeding rates and lower water temperatures rather than by prolonged starvation or ''dormancy.'' Nevertheless, it is still a significant saving. The only clear evidence for a major physiological change is that clearance rates were low and did not respond to increased food.

The potential for more radical energy conservation measures was already available to the krill. They had large lipid depots and reduced their metabolic losses greatly during the starvation experiment. However, the freshly caught animals had low O:N ratios and high metabolic losses compared with these starved animals, which suggests that they had not yet progressed fully into energy conservation.

A myth still persists that krill do not accumulate large lipid depots. Their stores in this study were very high: 36% of DM for juveniles and 44% of DM for adults. These are at the top end of the seasonal range (Hagen et al. 1996, 2001) and indeed would be respectable for diapausing Antarctic copepods (Hagen and Schnack-Schiel 1996). Coupled to this are the very low metabolic losses of adults after only 18 d of starvation: 0.18% of body C d^{-1} and 0.15% of body N d^{-1}. These losses are similar to those during longer term starvation (Ikeda and Dixon 1982) and translate to only 30% of body C and 25% of body N lost over a 200-d winter. Thus, the adults at least would be able to use body lipids and protein and survive an entire winter without feeding.

Central to these arguments is the actual amount of energy krill expend in the sea compared with that in a respirometer. Our flasks were large (12 liters), to minimize stress, but some problems remain. During summer, when krill have low lipid levels, they need to expend energy merely to avoid sinking. However, during early winter, their large lipid reserves add significant buoyancy (Falk-Petersen et al. 2000). Although the krill swam freely in our respirometers, a buoyancy advantage would be hard to measure. Furthermore, Ritz (2000) suggested that wild, schooling krill have lower swimming costs than nonaggregated individuals—for example, those in respirometers. Because winter may last 6 months, the subtleties of these small gains and losses could dictate the condition of krill emerging the following spring (Hofmann and Lascara 2000).

Feeding and energy conservation: A viable compromise strategy for overwintering?—Torres et al. (1994*b*) classed overwintering strategies of Antarctic zooplankton and micronekton into three types. ''Business as usual'' involves continued feeding and growth, whereas at the other extreme was ''dormancy'' with cessation of feeding and energy conservation. A third strategy, ''compromise,'' involves a mixture of reduced, opportunistic feeding and reduced metabolism (*see also* Hagen 1999). Most studies of postlarval krill have found low or zero feeding rates during winter (e.g., Morris and Priddle 1984; Daly and Macaulay 1991; Quetin and Ross 1991; Hopkins et al. 1993). Our autumn study also suggests a compromise.

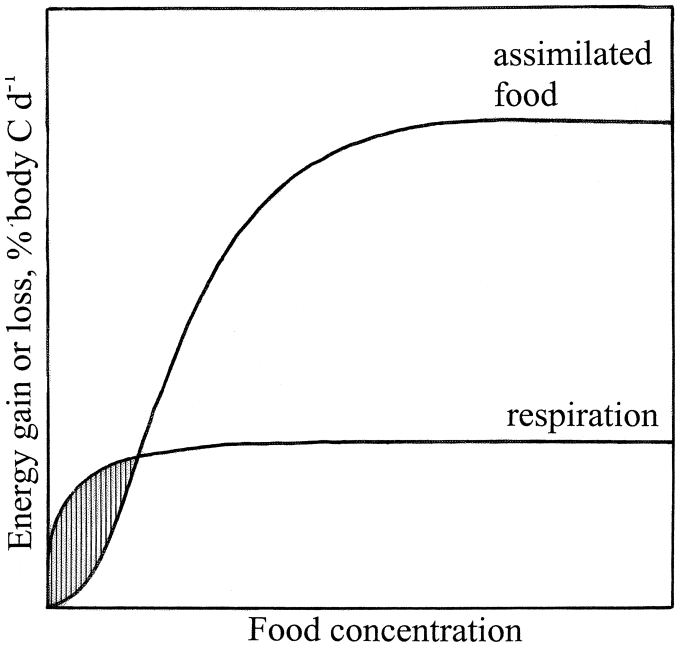

Fig. 10. Schematic representation of the C loss from respiration and gain from assimilated food, expressed in the same units of percentage of body C gained or lost d^{-1}. The horizontal axis represents food concentration. The hatched range of food concentrations represents those in which the animal gained no net energy from feeding.

This strategy sounds plausible: with a reduced metabolism, low food intake might suffice to balance the energy budget. Although this ''bet hedging'' sounds appealing, our results suggest some problems. For it to pay, food intake must cover the costs of feeding and evading predators. At the low food levels of winter, intake increases slowly with food concentration, but metabolic loss increases sharply (Figs. 8, 9). This sharp initial increase may reflect the large difference between nonfeeding and the energy costs of foraging, ingesting, and digesting food. Thus, at low food concentrations, the high basic cost of feeding provides little payback. This tradeoff is shown schematically in Fig. 10. At low winter food concentrations, a low clearance rate might even lead to greater loss of energy than what would result from a nonfeeding strategy. This deficit is probably exaggerated by the constrained conditions in our 60-liter feeding experiments. Nevertheless, if food is indeed scarce during winter, it is hard to see how reduced clearance rates are beneficial.

This point suggests some risk in ''compromise'' overwintering strategies and a paradox: why don't krill simply stop feeding altogether in winter? Possibly, net energy losses are the rule, but feeding is maintained to benefit from brief contacts with dense food patches. This might explain why Huntley et al. (1994) found krill feeding at high rates during midwinter, whereas Quetin and Ross (1991) found very low rates in the same region. Another explanation is that our autumn study was in a transition period, when the krill were

still physiologically active but feeding was slowing to a winter close down. A further alternative is that ''compromise'' is a population-level strategy, not an individual-level one. Our measurements were averages from pooled krill; if only some of them stopped feeding and the remainder had summer clearance rates, the impression would be of a compromise strategy for individuals.

Several authors (Torres et al. 1994*b;* Quetin et al. 1996) have suggested that postlarval krill use a compromise overwintering strategy. Such a strategy now needs to be better defined and characterized. After allowing for temperature differences, are clearance rates similar to those during summer, with the lower metabolic losses resulting simply from lower ingestion rates? Or do they reduce their foraging activity and clearance rate more substantially to achieve energy savings? It is still not clear whether the observed ''flexibility'' of krill is real or is a reflection of the methodologies used. The full implications of the various overwintering strategies will require integrated models of behavior, physiology, growth, predation, and mortality risk.

Ontogenetic differences—In this study and its companion (Meyer et al. this volume), furcilia, juvenile, and adult krill were sampled from the same place at the same time. Insufficient krill were caught to allow large samples sizes across our broad suite of measurements. Alone, these provide circumstantial evidence, but together they demonstrate that furcilia, juveniles, and adults adopt strategies so different that they could almost have been different species.

The furcilia had high feeding and metabolic rates (Meyer et al. this volume), in contrast to the reduced rates for the postlarvae. This supports suggestions that the importance of winter feeding decreases with ontogeny and implies that the furcilia were feeding on ice algae (Daly 1990; Ross and Quetin 1991). But if furcilia could feed at such high rates, why not the postlarvae? Either the under-ice habitat was partitioned to reduce competition or predation risk or simply the adults simply could not enter the narrow ice crevices to feed. Although these general differences between larvae and postlarvae have hitherto been suggested, our study adds to a growing appreciation that the behaviors of juvenile and adult krill are also fundamentally different.

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