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Ammonium excretion by Antarctic krill *Euphausia superba* at South Georgia

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Abstract

Excretion by Antarctic krill *Euphausia superba* (hereafter ''krill'') is measured typically in small containers of filtered seawater for 12–24 h, which may cause a reduction of swimming, feeding, and metabolism. If the maximum published excretion rates are realistic, krill would be a major source of regenerated nitrogen in the South Georgia area because of their high biomass there. Because literature values are variable, depending on season, feeding history and the experimental set-up, our aim was to measure both a mean and an upper value of krill excretion rate at South Georgia. Experiments were on juvenile krill during October–November 1997 and January 1998. Freshly caught animals excreted 1.6–2.8 nmol ammonium mg^{-1} dry mass h^{-1}; within the fivefold range of summer literature values for equivalent-sized krill. Maximum rates were determined on acclimated krill in large containers during alternating 1-d periods with and without food. During the feeding periods in saturating food concentrations, the mean daily ration was ~32% of body carbon d^{-1} and excretion was 210% (October–November) and 280% (January) of the values for freshly caught krill. This equates to a maximum loss of ~2% of body nitrogen d^{-1}. Excretion rates decreased during the 1-d periods without food, and rates during the feeding periods were ~30% higher than in those without food. This suggests that the lack of feeding in traditional experiments leads to roughly 30% underestimates of excretion rate. These results help to set some limits on ammonium production rates of South Georgia krill over regional scales. Our calculations suggest that the role of krill in this varies between habitats to the west of the island (insignificant) and those in the east (significant).

Euphausia superba (hereafter ''krill'') plays an important role in some Antarctic ecosystems (Hopkins 1985; Hopkins et al. 1993). In its energy budget, excretion is a significant loss term of nitrogen, and previous researchers have measured ammonium, as in the majority of crustaceans this is the main excretory product (Båmstedt 1985; Regnault 1987; Miller and Glibert 1998; Conover and Gustavson 1999). Published mass-specific excretion rates of krill vary by over an order of magnitude. While this is in part because of seasonal and regional differences in metabolism (Ikeda and Kirkwood 1989), most of the measurements have been made during summer, suggesting that the variability also reflects methodological inconsistencies (George and Fields 1984; Ikeda and Dixon 1984).

Krill excretion has usually been measured in small, 1–5-liter containers and 12–24-h incubations. These constrained conditions and krill's inability to feed are likely to reduce metabolic and excretion rates, as has been found for the majority of zooplankton species (Corner et al. 1965; Gardner and Paffenhöfer 1982; Miller and Landry 1984; Paffenhöfer and Gardner 1984; Båmstedt and Tande 1985). In situ excretion rates of euphausiids have been suggested to be over fourfold those measured in filtered seawater (Takahashi and Ikeda 1975; George and Fields 1984; Ikeda and Dixon 1984). However, it is uncertain whether the often high excretion rates of freshly caught zooplankton reflect genuine rates or are the result of the stress of capture (Båmstedt and Tande 1985; Huntley and Nordhausen 1995). Given these uncertainties and the wide range of krill excretion rates in the literature, further assessments are needed to quantify this part of their energy budget.

Krill biomass is frequently high around the island of South Georgia (Mackintosh 1973). Since Antarctic phytoplankton show a distinct preference for ammonium (Glibert et al. 1982; Owens et al. 1991), an assessment of krill excretion rates is one step toward understanding the process of nitrogen regeneration around the island (Priddle et al. 1997; Whitehouse et al. in press). Ammonium concentrations typical of South Georgia surface waters are consistent with significant inhibition of nitrate uptake but are sufficient to support only a few days of cell growth (Glibert et al. 1982; Dortch 1990; Flynn 1991; Whitehouse et al. 1999). Nitrogen regeneration has been cited as a potentially prime factor that enables high phytoplankton growth around South Georgia (Owens et al. 1991; Priddle et al. 1997; Whitehouse et al. 1999).

Given the uncertainty over excretion rates of krill, our aim was to compare values for freshly caught krill, acclimated animals that were not feeding, and acclimated animals feeding at maximum rates. Large tanks were used to reduce stress on the animals, which were monitored over periods of several weeks. This approach allowed an appraisal of how seriously the lack of feeding in traditional incubations may suppress excretion rate. Our estimates also allowed us to gauge whether krill could be considered over regional scales as an important source of ammonium at South Georgia.

Materials and methods

Experimental design—We wanted to assess how feeding history and measurement method affected excretion rate, and

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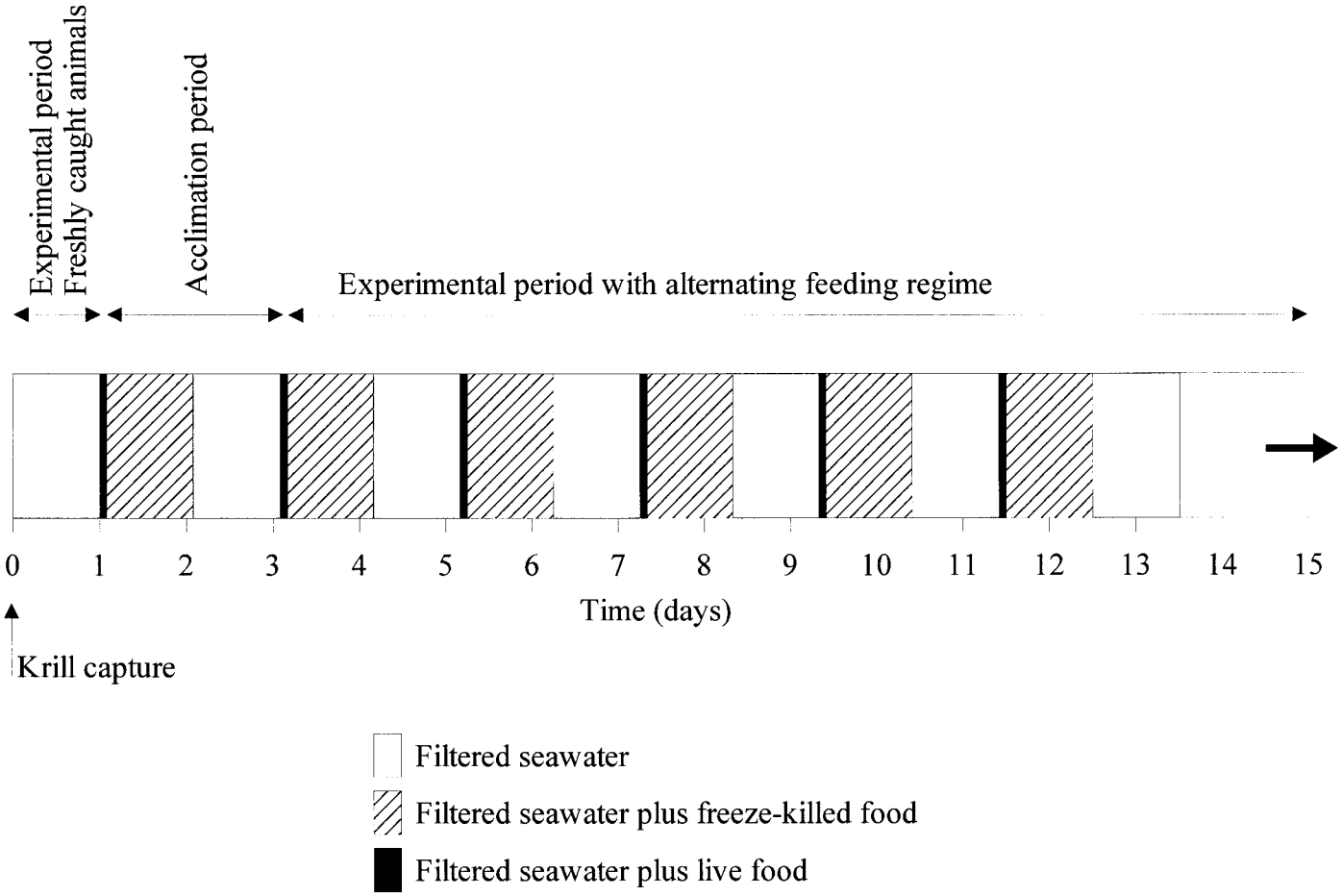

Fig. 1. Schematic representation of krill treatment regimes from capture until the end of the experiments. Experiments were conducted during spring–summer (October–November 1997) and summer (January 1998), each using two containers with krill. Controls containing no krill were subsampled concurrently with the krill containers.

this required that single batches of krill be monitored for several weeks from the time of capture to allow their feeding and excretion to be controlled and measured. Thus, groups of freshly caught animals were placed in filtered seawater for 24 h to measure their excretion (this is the most common method of measuring krill excretion). Then the same individuals were acclimated to laboratory conditions of alternating 1-d periods of feeding in excess food and nonfeeding in filtered seawater (Fig. 1). This alternating regime was maintained for 2 weeks, during which excretion rates were monitored at 2–10-h intervals. With concomitant measurement of feeding rate, this approach allowed us to assess how the excretion rate of krill was affected by the stress of capture versus acclimation to the laboratory and by short-term changes in the feeding rate.

Measuring the excretion rate of a zooplankter that is feeding presents some problems. It can be measured while they are feeding on live, cultured food (Takahashi and Ikeda 1975; Ikeda and Dixon 1984), but this requires knowledge of the time courses of zooplankton excretion, nutrient uptake by the food, and food removal by the grazer (*see Results and Discussion*). We thus used freeze-killed food to ensure that krill was the main organism altering ammonium concentrations in the containers. During the 2-week period, the krill were alternated every day between regimes of filtered seawater and filtered seawater plus freeze-killed food. During the actual experiments, we were unsure at first whether the krill would feed at maximum rates on dead food. Therefore, as a safeguard and to trigger feeding if necessary, we gave the krill live food (of the same type we freeze killed) for 2 h before each transfer to freeze-killed food. No feeding or excretion measurements were made during this interval.

Experimental details—We ran two excretion experiments aboard RRS *James Clark Ross*, each being of 2 weeks' duration. Both were to the north of South Georgia, the first in austral spring (October–November 1997) and the second in summer (January 1998). Positions of collection of the experimental krill are shown in Fig. 2 in relation to two survey grids that have been monitored annually with acoustics to determine krill biomass (Brierley et al. 1997).

The krill were caught at night with a series of slow (0.5 m s^{-1}) 5-min tows of a neuston net from the foredeck and placed immediately in a 20-liter bucket of surface seawater. Five experiments were done on these freshly caught, undamaged krill, and these were started between 40 min and 4 h

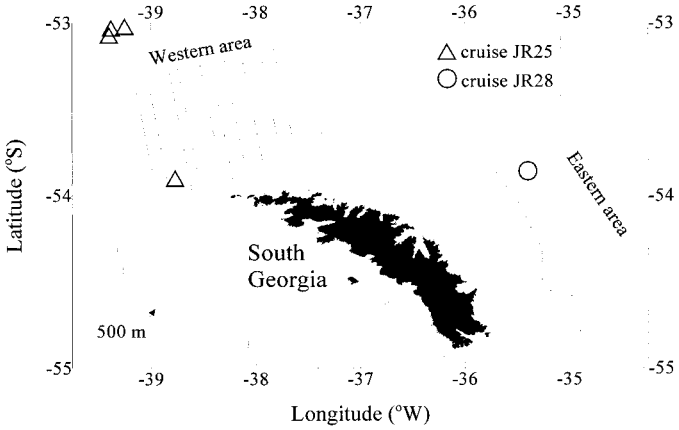

Fig. 2. Study site showing positions of krill capture for the excretion experiments. Parallel lines represent acoustic transects for the eastern area and western area, which have been monitored annually to estimate krill biomass.

(mean, 70 min) after capture. All experiments were in large volumes of seawater, ranging from 11 to 67 liters according to the size of the krill (Table 1). Volumes available to each krill ranged from 2 to 6 liters. After the experiments on the freshly caught krill, subsequent experiments on the same animals were run following a ~2-d acclimation period (Fig. 1). During this time, their behavior changed: they swam freely without bumping into the holding tank's walls, and their feeding rate increased. On each cruise, the time course of acclimated krill was run with two containers of krill and either one (January) or two (October–November) controls of similar volume and food–filtered seawater assemblage but without krill. Experiments with acclimated krill lasted about 14 d, during which they were held at ambient surface water temperature (Table 1). There was only one physical transfer of krill per day, for which a large dip net was used.

The food assemblage differed between cruises. In October–November 1997, we used a 100-μm ring net that had been clogged with diatoms, so the catch comprised mainly large diatoms and small copepods. In January 1998, it comprised copepods, mainly copepodite stages CIV, CV, and CVI of the clausocalaniid *Drepanopus forcipatus.* The food was killed by rapid freezing (−80°C) for ~2 h before adding to the containers. The water for each experiment was prepared fresh beforehand by filtering through a 0.45-μm filter.

To subsample for ammonium analysis, we used a 100-ml syringe fitted with an integral filter unit containing a mixed ester membrane (Whatman WME, pore size 0.45 μm). Three 60-ml subsample replicates were taken at each sampling time from the mixed water in both krill and control containers. These were normally analyzed immediately, but when this was not possible, they were stored for no more than 2 h in the cold, dark conditions of the lab before analysis. Replicate tests confirmed that this minor delay had negligible effects on ammonium concentration. Samples were analyzed colorimetrically for dissolved nutrients using Technicon segmented flow analyzers (Woodward unpubl.). Previous intercalibration tests had shown that the methods used were comparable, with detection limits of 0.01–0.02 mmol m^{-3} and reproducibility (the percentage of significant difference of 10 replicates at ~3.0 mmol m^{-3}) of 0.4–1.0% (Mantoura and Woodward 1983, Whitehouse and Woodley unpubl.).

Each experimental treatment lasted ~24 h, during which three or four subsampling times in addition to the start time were obtained. We only stirred the containers during subsampling. However, because the ingestion rates of krill were very high (*see Results and Discussion*), we were confident that the lack of regular stirring was not hindering their feeding. At the end of each 2-week experiment, the krill were rinsed briefly in fresh water and frozen for dry mass determination. This was done in U.K. by thawing the krill, rinsing briefly in freshwater, drying at 60°C for 48 h, and weighing (to ±0.01 mg) on a Sartorius balance.

Concurrently with nutrient sampling, additional subsamples of 1–3 liters of the mixed water were filtered onto a 50-μm sieve and usually preserved in 4% formaldehyde–seawater for subsequent laboratory determination of krill feeding rate. This involved enumerating the dominant food items, having used a Folsom plankton splitter to obtain countable aliquots. Copepods were counted under a binocular microscope, and diatoms were enumerated using the settling method of Utermöhl (1958). The dominant food item in January 1998 was the small copepod *Drepanopus forcipatus.* At the end two of the experiments, these individuals were frozen for dry mass determination. In U.K., the dry masses of *D. forcipatus* copepodite stages CIV, CV, and adult females were obtained for two replicate batches of ~30 individuals in the same way as for krill dry mass. Estimates of ingestion rate on other zooplankton taxa were based on measurements of their dimensions. Our unpublished conversion factors for South Georgia plankton were then used to construct biovolumes.

Calculation of excretion and feeding—The rate of ammonium production in the interval between successive subsampling times was calculated from the equation

$$E = [(K_{t2} - c_{t2}) - (K_{t1} - c_{t1})]V/M(t_2 - t_1),$$

Table 1. Summary of experimental conditions using acclimated krill. Experiments with freshly caught krill were under the same conditions as for acclimated krill incubated in filtered seawater.

Cruise	Dry mass of krill (mg)	Mean initial ammonium concn. (μM)	Incubation temperature (°C)	No. controls per experimental bucket	Volume of krill tanks (liters)	No. experiments in filtered seawater	No. experiments with excess food	Food source for acclimated krill
Oct–Nov 1997	17–48	0.62	0	2	11 and 24	6	8	Diatoms and copepods
Jan 1998	55–73	1.78	2	1	40 and 67	6	8	Copepods

where t_1 is time 1, t_2 time 2, E the rate of ammonium production (μmol mg^{-1} grazer dry mass h^{-1}), K_{t1} the concentration of ammonium in krill container at time t_1, K_{t2} the concentration of ammonium in krill container at time t_2, c_{t1} the concentration of ammonium in control at time t_1, c_{t2} the concentration of ammonium in control at time t_2, V the volume of krill container, and M the dry mass of krill.

Volumes were reduced by the repeated subsampling, so volume–concentration adjustments were applied to the calculations of excretion and feeding rates. During the January cruise, ammonium contamination in the laboratory's water supply interfered with the analysis. Baseline measurements were elevated resulting in a lack of sensitivity. Although we have compensated for the background ammonium signals, the lack of sensitivity made evaluation of change over a time scale of hours difficult. Therefore, for the January cruise, we present here only the overall 24-h average excretion rates.

Krill fed readily on both freeze-killed algae and copepods, producing numerous fecal pellets. However, feeding rates were monitored to check that we were indeed measuring excretion at near maximum daily rations. Statistically significant changes in concentration of food items in the control containers were not detected, so clearance rates F (ml mg^{-1} dry mass h^{-1}) on individual food items during the experiment were calculated from Frost's (1972) equation, which we modified to the following:

$$F = \ln(k_{t1}/k_{t2})V/M(t_2 - t_1),$$

where k_{t1} and k_{t2} are the concentrations of prey items in the krill container at times t_1 and t_2, respectively.

Ingestion rates, I, of the counted food items were calculated as

$$I = Fk_{\text{mean}},$$

where k_{mean} is the mean concentration of the food item in the krill container. Total rations (i.e., the percentage of body carbon ingested per day) were calculated by summing the ingestion rates of individual food items and by assuming that carbon contents of both krill and copepods were 45% of their dry mass (Schnack 1985; Ikeda and Kirkwood 1989; Huntley and Nordhausen 1995). Carbon contents of diatom taxa were calculated from Eppley et al. (1970).

Results and Discussion

Problems of measuring excretion by feeding zooplankton—Although zooplankton excretion generally increases with feeding activity, methodological problems mean that most measurements are made with animals in filtered seawater. Measuring excretion by a feeding zooplankter requires knowledge of the kinetics of both nutrient uptake by the food and food removal by the grazer (Miller and Landry 1984). One approach to this has been to use live-cultured algae spiked with excess nutrients to ensure that nutrient uptake rate by algae is independent of cell density (Lehman 1980). Excretion rate is then calculated from time course measurements of ammonium buildup, feeding and algal uptake of ammonium. Although an elegant method, it requires measuring the kinetics of two other processes occurring simultaneously with excretion. To avoid this problem, heat-killed algae have been used as food (Vanderploeg et al. 1986), but against this Conover et al. (1988) cautioned that feeding and excretion rates on killed algae may not be the same as those on live algae.

Our approach, using freeze-killed food, can only be justified if krill were indeed feeding readily. Estimated carbon rations averaged 32% of body carbon d^{-1} (range, 21–43%). This is the highest value measured for postlarval krill (*see Table 6* in Pakhomov et al. 1997*a*). It also corresponds well to values for warmer water euphausiids (Ross 1982; Stuart 1986) and is in line with their potentially high rates of growth (Quetin et al. 1994).

Another methodological factor is sloppy feeding. Breakage and partial ingestion of large or chain forming diatoms can cause them to release ammonium, leading to overestimates of excretion (Miller and Landry 1984; Glibert et al. 1992). However, the krill were large relative to their food, and microscopic examination of uneaten diatoms and copepods in grazed and control containers showed very few damaged cells. This is supported by experiments with live cells at high concentrations (Price et al. 1988; Atkinson and Snÿder 1997), from which we conclude that sloppy feeding was not a problem.

A potential problem was that ammonium tended to increase slightly in the controls (mean increase across all experiments was 0.15 mmol m^{-3}, SD 0.066). If krill were eating a significant fraction of the particles producing ammonium, their excretion would have been underestimated. But concentrations increased both in controls with filtered seawater and with added freeze-killed food (although this tended to be more pronounced in the latter), so ammonium did not come just from the food source. The experiments were at saturating food concentrations so the high ratios came from the removal of a fairly small fraction (mean 28%) of food. Also, the ammonium increase in krill containers averaged sixfold that in the controls. This combination of conditions, as a worst-case scenario (i.e., if the food particles were the sole cause of the ammonium buildup) would lead to an average 4% underestimate of krill excretion.

Excretion in relation to feeding—Figure 3 summarizes the excretion rates for the two cruises under the various treatments. The krill used in October–November were mainly smaller than in January (Table 1), and mass specific rates were higher. Both cruises, however, followed a similar pattern (Fig. 3). Comparing measurements made in filtered seawater, excretion rates for acclimated krill were 3.3–4.2 nmol ammonium mg^{-1} dry mass h^{-1}; significantly higher than values of 1.6–2.8 nmol ammonium mg^{-1} dry mass h^{-1} obtained just after capture (t-test, $P < 0.05$). For acclimated krill, rates measured during feeding were significantly higher than those in filtered seawater (t-test, $P < 0.05$). For a 60-mg dry mass krill, the maximum daily excretion equates to a daily loss of 1.9% of their nitrogen content, assuming that nitrogen content is 10% of dry mass (Ikeda and Bruce 1986; Ishii et al. 1987; Ikeda and Kirkwood 1989; Huntley and Nordhausen 1995).

For the acclimated krill, Fig. 4 summarizes the rate of excretion in relation to the time since the start of each feeding–nonfeeding treatment. Excretion rate tended to decline

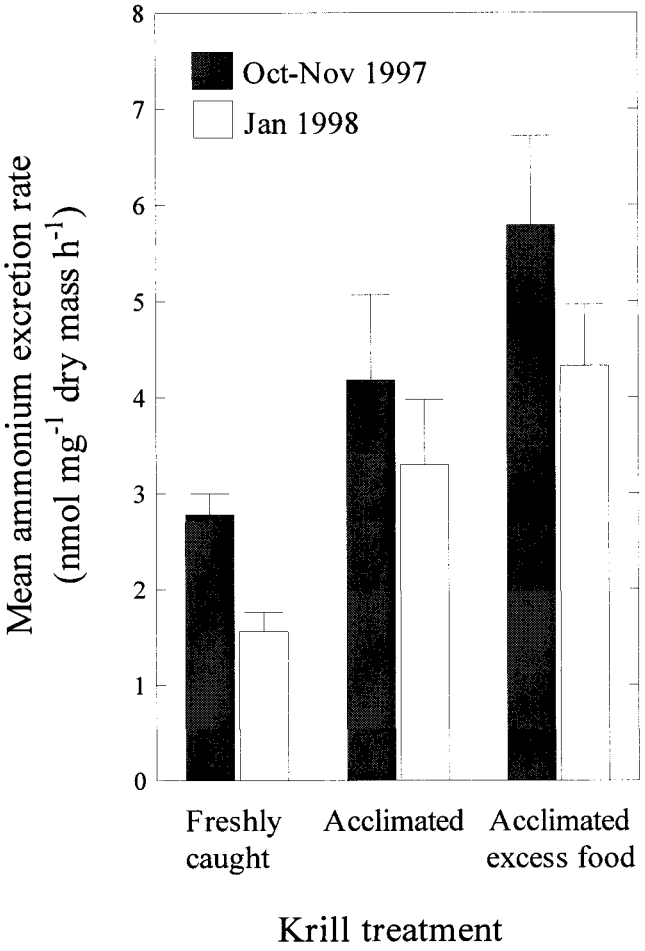

Fig. 3. *Euphausia superba.* Mean ammonium excretion rates of freshly caught krill compared with 24-h average values for acclimated krill without food and with excess food.

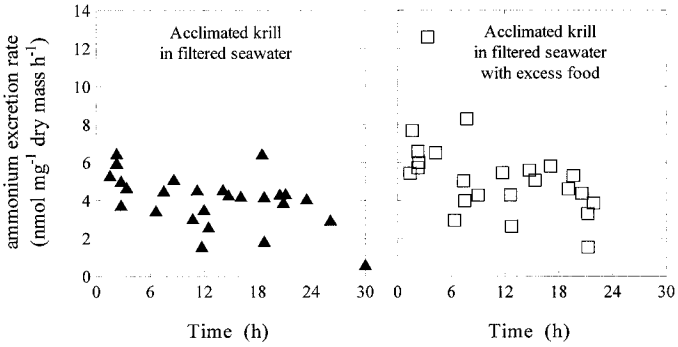

Fig. 4. *Euphausia superba.* Mass-specific rate of ammonium excretion of acclimated krill during October–November 1997, in relation to elapsed time since the start of the treatment. Data are shown for all six incubations in filtered seawater and all eight incubations with excess food. Each point represents an excretion rate measurement, plotted for the midtime of the measurement interval.

during the experiments, whether the krill were feeding or not. However, the decline was only slight, with the mean rate in filtered seawater in the second half of the incubation period being 24% less than in the first half.

Krill excretion rates have been measured typically over 24-h periods in small, ~1–5-liter containers of filtered seawater. This is artificial for a large, active euphausiid, so our aim was to gauge how much excretion rates are enhanced when krill are acclimated and feeding at maximum rates. Our use of large-volume tanks and our exposure of the krill to high food concentrations were designed to promote swimming, feeding, and excretion. The alternating food–no food regime was maintained for 2 weeks to enable acclimation to this regime. Zooplankton tend to eat faster after short-term starvation (Mackas and Burns 1986; Kremer and Kremer 1988), and pulsed feeding on a day-to-day frequency may not be unnatural for krill (Price et al. 1988). Excretion was measured for the 24-h period ~2 h after they were allowed to feed, when it would likely have been at its highest daily rate.

Ikeda and Dixon (1984) compared excretion rates of krill feeding on six types of food and in filtered seawater, having acclimated them to these regimes. Their incubation volumes were 2 liters, and rations at maximum food concentration averaged ~5% body C d^{-1}. By comparing krill feeding on diatoms with a daily ration of 5% with those acclimated to filtered seawater, Ikeda and Dixon (1984) calculated that feeding krill excreted 4.5 times more ammonium than those acclimated and maintained in filtered seawater. Because their setup differed from the traditional one where feeding krill are switched to filtered seawater, it is not possible to gauge from their results how seriously excretion is underestimated by traditional methods. Our results for acclimated krill allow some assessment of this. Excretion rates during the feeding periods were ~30% higher than those in filtered seawater (Fig. 3), and the mean rate over the 24-h filtered seawater incubations was 24% less than that at the start. This suggests that traditional 24-h incubations without food result in roughly a 30% underestimate of the excretion rate before the experiment.

Our results are compared with all available literature data for spring and summer in Fig. 5. These values were obtained across a temperature range of −1.7 to 2°C, so all values, including ours, have been adjusted to 0°C using a Q_{10} of 1.92 (Ikeda 1985). Excretion rates for freshly caught krill at South Georgia are within the fivefold range of literature values for animals of equivalent size (Fig. 5a). For acclimated krill switched to filtered seawater (Fig. 5b), literature values are very scattered, but our results are 150–200% of those for freshly caught krill (Fig. 3). For acclimated krill whose excretion was measured during feeding (Fig. 5c), a regression line of only our own data has been drawn. This lies above the results of Ikeda and Dixon (1984) for larger krill ingesting 5% of body C d^{-1}. This may reflect the much higher ration and possibly greater swimming activity of the krill in our large containers.

Therefore, the maximum excretion rate sustainable over a 24-h period is only two- to threefold that of our freshly caught krill. Excretion can be faster for the first few hours of transfer of a starved krill to food (Fig. 4), but these high rates were not sustained over 24 h. The fact that excretion during the intervening 24-h periods in filtered seawater averaged 60–70% of that during the feeding period, and that rates in the second half of the starvation period were 76%

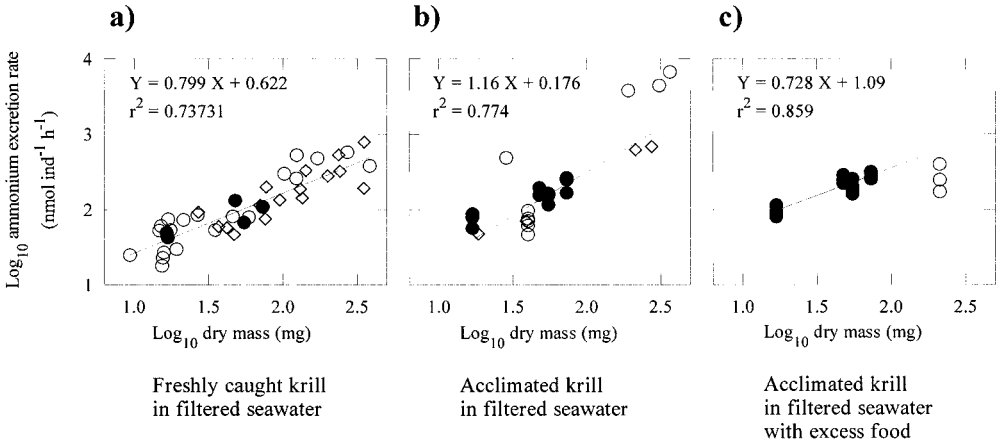

Fig. 5. *Euphausia superba.* Comparison of literature values of ammonium excretion rate (open symbols) with those in this study (solid symbols). Diamonds represent means of replicate determinations, and circles are single determinations. The calculated regression lines are weighted toward the former in proportion to the number of replicates. Excretion rates are adjusted to a temperature of 0°C (*see Results and Discussion*). (a) Excretion in filtered seawater, measured within 24 h of capture. Regression is for all data. Literature data are Biggs (1982), Ikeda and Mitchell (1982), Segawa et al. (1982), Hirche (1983), Ikeda and Bruce (1986), Ikeda and Kirkwood (1989). (b) Excretion in filtered seawater for krill acclimated to feeding (usually on excess food) in the laboratory. Regression is for all data, including the high values by George and Fields (1984). Literature data are Ikeda and Hing-Fay (1981), George and Fields (1984), and Ishii et al. (1987). (c) Excretion for acclimated krill while they were feeding at high rates. Regression is for the current study only, but note position of literature data (Ikeda and Dixon 1984) compared with the extension of our regression line.

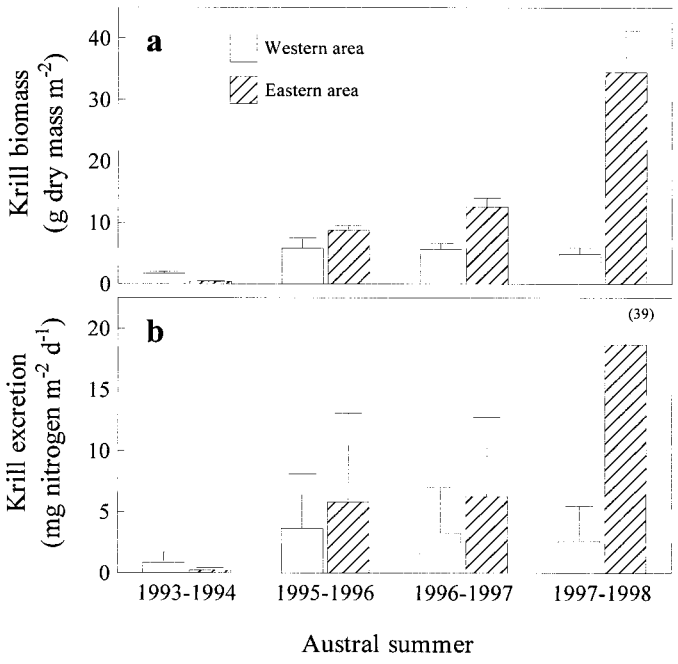

Fig. 6. *Euphausia superba*. (a) Mean biomass in the Western and Eastern survey areas during December–January of 4 yr. The 1994–1995 year was anomalously poor for krill. Bars represent one standard deviation. (b) Total nitrogen excretion by krill, based on ammonium excretion rates of freshly caught krill (regression in Fig. 5a) and mean krill biomass (Fig. 5a). Bars represent values based on mean biomass and maximum excretion rate (regression in Fig. 4c).

of those in the first half, suggest that excretion increases within just a few hours of feeding. Starvation for 24 h and then exposure to food may have induced a burst of very rapid feeding and a pulse of excretion. The time scale of this (a few hours) corresponds to the gut passage time of the krill (Clarke et al. 1988; Pond et al. 1994; Perissinotto and Pakhomov 1996; Atkinson and Snÿder 1997). For a variety of animals, excretion has been found to increase after a meal, often after the rise in respiration rate (i.e., the specific dynamic action) associated with processing food. However, the extent to which these rates increase and their relative timing vary greatly between species (e.g., Chapelle et al. 1994; Boyce and Clarke 1997).

Potential contribution of krill to ammonium regeneration—The main regenerators of ammonium are generally considered to be protists, with metazooplankton having modifying effects through selective grazing (e.g., Glibert et al. 1992; Miller and Glibert 1998). However, the South Georgia system supports an exceptionally high metazooplankton biomass, often at least half of which is krill (Ward et al. 1995; Pakhomov et al. 1997b; Atkinson et al. 1999). Because of contrasting suggestions over the large-scale importance of ammonium regeneration by krill (Olson 1980; Owens et al. 1991; Huntley and Nordhausen 1995; Priddle et al. 1997), this topic warrants further appraisal. We have therefore made some simple calculations using our mean and maximum values to set some limits to estimates of their ammonium production rate (Fig. 6).

Interannual krill biomass data are available for two 80-by-80–km acoustic survey grids to the north of South Geor-

Table 2. Ammonium excretion by krill compared with that estimated to be taken up by algae. *See* Fig. 1 for locations of eastern and western monitoring areas. Primary production values were compiled from December to February data only. Percentage contributions of krill excretion to estimated ammonium uptake are based on mean krill biomass, the mean excretion rate for freshly caught krill, and median primary production rate, and values are expressed as a range based on the range of mean biomass values across the three ''normal'' krill years (*see text and Fig. 6a*).

Region	Reference	Time of year	Method	Primary production values (mg C $m^{-2}d^{-1}$)	Median for region (range)	Estimated contribution of krill excretion to algal ammonium uptake (%)
Eastern area	Owens et al. (1991)	Dec–Feb	^{15}N	1,200	450	3–4
				1,200	(69–1,200)	
	Pakhomov et al. (1997)	Feb–March	^{14}C	150		
				69		
	Savidge et al. (unpubl. data)	Jan	^{14}C	450		
				700		
				250		
Western area	Owens et al. (1991)	Dec–Feb	^{15}N	2,120	1,200	16–50
				742	(323–8,900)	
				536		
				464		
	Atkinson et al. (1996)	Jan	O_2 budget	8,900		
	Pakhomov et al. (1997)	Feb–March	^{14}C	371		
				323		
				1,660		
				444		
	Savidge et al. (unpubl. data)	Jan	^{14}C	1,900		
				1,450		
				2,750		
				1,000		
				1,400		

gia (Fig. 2; *see* Brierley et al. 1997 and Brierley et al. in press for further details). Krill biomass varied both between years and between regions, so data from four available summers were used, and the two monitoring grids were analyzed separately. The eastern area covers the shelf and oceanic water immediately northeast of the island (Fig. 2) and is characterized by high krill biomass (Fig. 6a) and modest primary production (Table 2, Whitehouse et al. 1999). The western area, covering shelf and ocean immediately northwest of the island, has lower krill biomass (Fig. 6a) but high primary production. Krill biomass estimates are based on parallel daytime transects with a dual-frequency (38–120 kHz) echosounder and echointegrator (see Brierley et al. 1997). Length frequency data of krill came from nighttime target verification net hauls along the transects. Krill biomass is presented as wet mass in Brierley et al. (in press), so this was converted to dry mass using the equations in Morris et al. (1988). Their age structure differed between years (Brierley et al. pers. comm.), so excretion rate was based on the size for each year. Mean and maximum estimates of ammonium produced by these krill (Fig. 6b) were based on the regressions for freshly caught krill (Fig. 5a) and for those feeding at near maximum rates, respectively.

To gauge whether or not krill should be considered seriously as regenerators of ammonium, we have compared our best estimates of their ammonium excretion (Fig. 6b) with those of ammonium uptake by phytoplankton (Table 2). Summer primary production values vary widely, but values in the western area tend to be higher than those in the eastern area (Table 2). From these median values, ammonium uptake was calculated using a Redfield C : N ratio of 100 : 15 and an *f* ratio (i.e., nitrate uptake as a fraction of ammonium plus nitrate uptake) of 0.46 (Owens et al. 1991). This mean *f* ratio, determined for South Georgia in summer, is consistent with other values for the Southern Ocean (Olson 1980; Glibert et al. 1982; Probyn and Painting 1985; Koike et al. 1986; Smith and Nelson 1990).

The percentage contributions of krill excretion to ammonium uptake (Table 2) reflect our best estimates using mean or median values. While the variability in all the variables involved would lead to high local variation, there are several possibilities for systematic error. Factors increasing the calculated importance of krill include our conservative use of excretion rates obtained in filtered seawater. The percentages could therefore be multiplied by ~1.5 to allow for the decrease in excretion such incubations cause (*see Results and Discussion*). Second, krill biomass was monitored by a transducer 7 m below the surface, so animals excreting within the topmost 7 m would not be accounted for. A factor potentially reducing the calculated importance of krill is the fact that although krill were found mainly in the top 100-m layer, animals excreting below the upper mixed layer would not resupply the most productive upper layers on a daily time scale. Nitrogen uptake is also a dynamic, complex process (Flynn et al. 1997), and differences in nutrient preference would also affect the calculated values in Table 2.

These budgets are based on ammonium, but urea is another potential nitrogen source that was not assessed. However, at low temperatures and high (>1 mmol m^{-3}) ammonium concentrations typical of our study area, phytoplankton appear to prefer ammonium to urea (Kristiansen 1983; Wheeler and Kokkinakis 1990; Bury et al. 1995).

Notwithstanding these caveats, our calculations suggest a large regional difference in the importance of krill in ammonium regeneration. In the western area (moderate krill biomass, high primary production), krill appear to contribute little, but they could be important in the eastern area, with high krill and lower primary production. It is well known that krill swarms could be important localized sources of regenerated nitrogen (Hirche 1983; Johnson et al. 1984; Huntley and Nordhausen 1995). So far, however, suggestions about their importance over wider scales have been contradictory, largely because of uncertainties over their natural rates of excretion (Olson 1980; Huntley and Nordhausen 1995; Priddle et al. 1997). Our data suggest that traditional methods do not lead to such severe underestimates of in situ excretion rates as would be predicted from earlier studies. Even using conservative values of krill excretion, however, our simple calculations suggest that to the northeast of South Georgia where krill are abundant, this species might regenerate a significant amount of ammonium over a regional scale.

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