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# Close coupling between ammonium uptake by phytoplankton and excretion by Antarctic krill, *Euphausia superba*

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ABSTRACT

In this study we examined the hypothesis that, under conditions of replete macronutrients and iron in the Southern Ocean, phytoplankton abundance and specific N uptake rates are influenced strongly by the processes of grazing and $NH_4$ regeneration. $NH_4$ and $NO_3$ uptake rates by marine phytoplankton were measured to the northeast and northwest of the island of South Georgia during January–February 1998. Mean specific uptake rate for $NO_3$ ($\nu NO_3$) was 0.0026 $h^{-1}$ (range 0.0013–0.0065 $h^{-1}$) and for $NH_4$ ($\nu NH_4$) was 0.0097 $h^{-1}$ (0.0014–0.0376 $h^{-1}$). $\nu NH_4$ was related positively with $NH_4$ availability, which ranged from 0.1 to 1.5 mmol $m^{-3}$ within the upper mixed layer. Ambient $NH_4$ concentrations and $\nu NH_4$ were both positively related to local krill biomass values, computed from mean values along acoustic transect segments within 2 km of the uptake measurement stations. These biomass values ranged from ~1 g krill fresh mass $m^{-2}$ in the northwest to >4 kg krill wet mass $m^{-2}$ in the northeast. In contrast to the variability found with $NH_4$ concentrations and uptake rates, $\nu NO_3$ was more uniform across the sampling sites. Under these conditions, increasing $NH_4$ concentration appeared to represent an additional N resource. However, high $\nu NH_4$ tended to be found for stations with lower phytoplankton standing stocks, across a total range of 0.24–20 mg chlorophyll *a* $m^{-3}$. These patterns suggest a coupling between phytoplankton biomass, $\nu NH_4$ and krill in this region of variable but high krill biomass. Locally high concentrations of krill in parts of the study area appeared to have two opposing effects. On the one hand they could graze down phytoplankton stocks, but on the other hand, their $NH_4$ excretion supported enhanced uptake rates by the remaining, ungrazed cells.

## 1. Introduction

The two main sources of N for primary producers are nitrate, $NO_3$ and ammonium, $NH_4$ (Koike et al., 1986; Flynn et al., 1997). These two sources differ in their "value" to phytoplankton, with assimilation of $NH_4$ generally preferred on energetic grounds (Dortch, 1990). However, a direct interaction between the two uptake systems has also been found (Dortch, 1990; Flynn et al., 1997), with high $NH_4$ concentrations having an inhibitory effect on $NO_3$ uptake. Where $NO_3$ is in short supply or cannot be utilised efficiently, $NH_4$ can become the dominant N source. Under these circumstances, values of the *f*-ratio (the share of total N-uptake contributed by $NO_3$) will decrease rapidly as $NH_4$ concentrations increase towards saturating values (Olson, 1980; Glibert et al., 1982; Owens et al., 1991).

In the Southern Ocean $NO_3$ stocks are plentiful (Sarmiento et al., 2004), with typical winter surface values of 25–30 mmol $m^{-3}$ (e.g. Whitehouse et al., 1996). However, efficient $NO_3$ utilisation by phytoplankton is controlled by the availability of iron, Fe (Franck et al., 2003) and is generally confined to areas of mixing where sub-surface Fe stocks are made available at the surface (De Baar and de Jong, 2001; Boyd et al., 2007; Meskhidze et al., 2007). $NO_3$ remains underutilised in large parts of the Southern Ocean where reduced forms of N such as $NH_4$ are more readily utilised. Uptake of these reduced forms of N can fuel C export, so use of $NO_3$ uptake as a measure of export production cannot be applied here (Sambrotto et al., 1993; Priddle et al., 1995, 1998). This is due to decoupling of C and N cycles, whereby recycling of N within the water column is more efficient than that of C. While $NH_4$ is thus important in modulating primary production levels its concentrations are highly variable, both in space and in time. Therefore we need to understand the processes dictating both the supply and demand for $NH_4$ and $NO_3$.

The main regenerators of $NH_4$ are generally considered to be microheterotrophs (Goeyens et al., 1991; Glibert et al., 1992; Miller and Glibert, 1982). These groups tend to have higher turnover rates and mass-specific processing rates than mesozooplankton or macrozooplankton, and indeed dominate grazing and

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biogeochemical processing in both polar and lower latitude systems (Calbet and Landry, 2004). A possible exception may apply to Antarctic krill (*Euphausia superba*). Due to the high biomass of krill across parts of the Southern Ocean, and its schooling behaviour, this species is also suggested to have a role in nutrient cycling (Smetacek et al., 2004; Tovar-Sanchez et al., 2007; Schmidt et al., in press). However, the direct numerical evidence for this role is surprisingly scant (Olson, 1980; Owens et al., 1991; Huntley and Nordhausen, 1995; Priddle et al., 1997). Some of the observations, for example, are from within localised krill schools (e.g. Johnson et al., 1984) and hardly representative of wider areas.

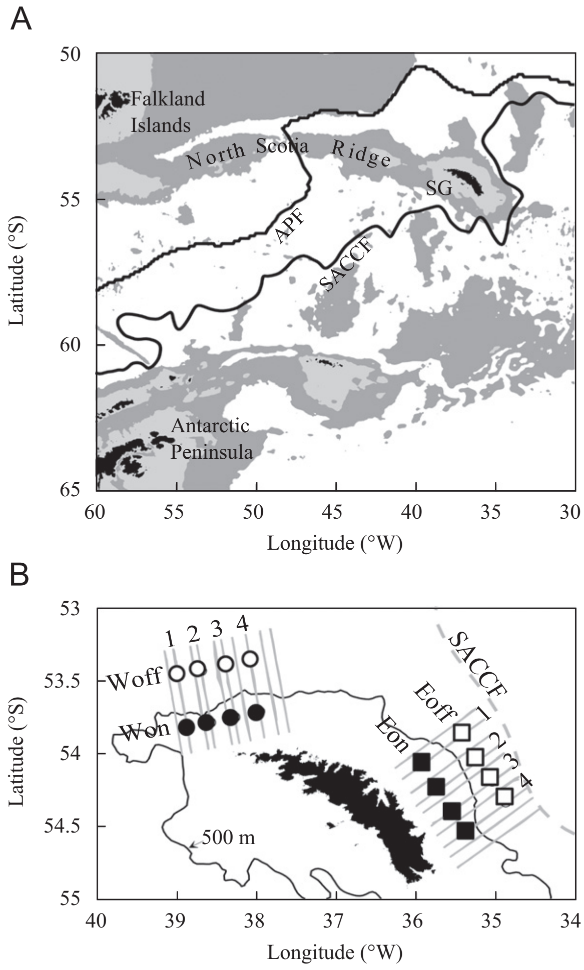

**Fig. 1.** (A) Location of South Georgia (SG) relative to the mean positions of the Antarctic Polar Front (APF; Moore et al., 1999) and the Southern Antarctic Circumpolar Current Front (SACCF; Thorpe et al., 2002). The pale and dark grey shading delineate the 0–500 m and the 500–3000 m depth ranges, respectively. (B) The west and east survey transects and CTD station locations in relation to South Georgia, the 500 m isobath, and the mean position of the SACCF. The western stations are delineated with circles and eastern stations by squares, with off-shelf and on-shelf stations having open and filled symbols, respectively.

In the laboratory it is difficult to follow the complex interplay between the natural phytoplankton assemblage and its grazers that are simultaneously grazing and excreting (Peters and Rigler, 1973; Lehman, 1980). As a different approach we chose South Georgia as a natural system to study *in situ* the links between krill, $NO_3$, $NH_4$ and phytoplankton. The waters just north of the island are replete in Fe in summer (Korb and Whitehouse, 2004; Holeton et al., 2005; Whitehouse et al., 2008, Neilsdottir unpubl. data). However regionally averaged krill concentrations in our study were highly variable, reaching values over 4 kg wet mass $m^{-2}$; truly remarkable values for a single grazer species. This situation, of universally high macronutirent (and probably Fe) concentrations, but extremely variable phytoplankton, $NH_4$ and krill concentrations provide some insights into the interactions between a grazer and its food.

## 2. Methods

### 2.1. Study site and sampling

The island of South Georgia is located on the North Scotia Ridge, towards the northern edge of the Scotia Sea (Fig. 1). The sampling was based on a British Antarctic Survey (BAS) monitoring programme whereby two mesoscale, 80 km × 80 km areas known as the Eastern and Western Core Boxes were sampled aboard RRS *James Clark Ross* (Fig. 1B). While productivity at all trophic levels is enhanced to the north of the island (Atkinson et al., 2001), the survey boxes encompass a wide diversity of food web structure, with generally higher krill biomass and lower phytoplankton stocks in the east (Brierley et al., 1999; Whitehouse et al., 2009).

Underway acoustic data were collected along transects spaced ~7–10 km apart within each survey grid between 24 January and 3 February 1998 (cruise JR28). Within these grids, 16 CTD casts were made at dawn and dusk within on- and off-shelf waters. These are designated here as along transect lines 1–4 in the sub-regions west on-shelf (Won), west off-shelf (Woff), east on-shelf (Eon), and east off-shelf (Eoff) as shown in Fig. 1B and Table 1.

**Table 1**
Biomass-specific N uptake rates and major station environmental variables along with mean (Std. Dev.) krill biomass within 2 km of the station.

| Station | $\nu NO_3$ ($h^{-1}$) | $\nu NH_4$ ($h^{-1}$) | *f*-ratio | Particulate N (mmol $m^{-3}$) | Chl-*a* (mg $m^{-3}$) | $NO_3$ (mmol $m^{-3}$) | $PO_4$ (mmol $m^{-3}$) | $Si(OH)_4$ (mmol $m^{-3}$) | $NH_4$ (mmol $m^{-3}$) | Krill biomass (g $m^2$ wet mass) |
|---|---|---|---|---|---|---|---|---|---|---|
| Woff1 | 0.00183 | 0.00166 | 0.53 | 0.664 | 2.41 | 14.67 | 1.11 | 23.73 | 0.11 | 5 (4) |
| Woff2 | 0.00221 | 0.00193 | 0.53 | 0.677 | 1.71 | 15.39 | 0.95 | 22.84 | 0.14 | 4 (2) |
| Woff3 | 0.00217 | 0.00564 | 0.28 | 0.692 | 1.19 | 16.91 | 1.00 | 26.08 | 0.85 | 1 (0.4) |
| Woff4 | 0.00142 | 0.00600 | 0.19 | 0.790 | 0.52 | 16.87 | 0.95 | 19.29 | 0.73 | 3 (2) |
| Won1 | 0.00189 | 0.00415 | 0.31 | 0.864 | 5.20 | 13.41 | 1.07 | 14.89 | 0.76 | 27 (10) |
| Won2 | 0.00318 | 0.00373 | 0.46 | 0.745 | 7.66 | 12.43 | 0.80 | 13.22 | 0.85 | 8 (3) |
| Won3 | 0.00650 | 0.00369 | 0.64 | 1.838 | 19.85 | 10.37 | 0.35 | 7.53 | 0.62 | 26 (13) |
| Won4 | 0.00359 | 0.01542 | 0.19 | 0.761 | 5.24 | 15.44 | 0.82 | 15.45 | 0.89 | 10 (13) |
| Eoff1 | 0.00355 | 0.00754 | 0.32 | 0.610 | 0.75 | 19.55 | 1.31 | 30.27 | 0.90 | 398 (554) |
| Eoff2 | 0.00305 | 0.00303 | 0.50 | 0.402 | 0.24 | 15.86 | 1.21 | 25.71 | 1.04 | 131 (140) |
| Eoff3 | 0.00197 | 0.03757 | 0.05 | 0.382 | 0.36 | 17.19 | 1.32 | 24.20 | 1.52 | 224 (241) |
| Eoff4 | 0.00224 | 0.00593 | 0.27 | 0.356 | 0.32 | 16.77 | 1.20 | 23.17 | 1.05 | 249 (146) |
| Eon1 | 0.00324 | 0.01437 | 0.18 | 0.485 | 0.67 | 18.88 | 1.39 | 30.96 | 1.32 | 199 (170) |
| Eon2 | 0.00171 | 0.00310 | 0.36 | 0.659 | 2.76 | 14.68 | 1.27 | 27.71 | 0.24 | 212 (308) |
| Eon3 | 0.00235 | 0.02153 | 0.10 | 0.336 | 0.40 | 17.15 | 1.34 | 26.42 | 1.42 | 4634 (5346) |
| Eon4 | 0.00127 | 0.01944 | 0.06 | 0.467 | 0.71 | 16.44 | 1.26 | 26.15 | 1.42 | 130 (172) |