

A comparison of chlorophyll/nutrient dynamics at two survey sites near South Georgia, and the potential role of planktonic nitrogen recycled by land-based predators

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Abstract

There is an apparent mismatch between the high carbon demand of seals and seabirds breeding on the subantarctic island of South Georgia and the overall low primary production measured in the waters that surround the island. However, average phytoplankton production values may not be completely representative, and local systems may exist where primary production is considerably higher. Here, we examine the distribution of phytoplankton and nutrients along with physical oceanographic variables measured during two mesoscale surveys of two sites adjacent to South Georgia (January 1996 and December 1996–January 1997). Chlorophyll *a* concentrations were consistently higher (by up to an order of magnitude during one cruise) at the western end of the island (maximum $>30 \text{ mg m}^{-3}$). Surface phosphate and silicate at times appeared to have been depleted to particularly low levels (<0.8 and $<2 \text{ mmol m}^{-3}$, respectively), whereas nitrate concentrations remained relatively high throughout the two surveys ($\sim 14\text{--}30 \text{ mmol m}^{-3}$). However, ammonium, a crucial reduced nitrogen source for South Georgia phytoplankton, was plentiful and widespread in the upper mixed layer during both surveys (maximum $>3 \text{ mmol m}^{-3}$). An examination of upper mixed layer nutrient dynamics showed an apparent shortfall in phytoplankton use of nitrate-nitrogen compared with silicate and phosphate at the western end of the island, where ammonium-nitrogen use appeared greatest.

The western end of subantarctic island of South Georgia is noted for its large numbers of breeding Antarctic fur seals, *Arctocephalus gazella*, and macaroni penguins, *Eudyptes chrysolophus*, ($\sim 2.6 \times 10^6$ and $\sim 5.4 \times 10^6$ individuals, respectively). As land-breeding endotherms, these animals have high metabolic costs, and they recycle dietary nitrogen rapidly. Furthermore, because they take krill advected into their foraging range and return frequently to their colonies to feed pups and chicks, they concentrate nutrients close to the land. We evaluated the relationship between the preferential use of reduced nitrogen by phytoplankton and its production and concentration by the land-based predators (a minimum of $1 \times 10^7 \text{ mol N d}^{-1}$ in January for the colonies in the study area). We examined the predators' potential for the redistribution of plankton nitrogen in an on-shelf environment where currents were relatively sluggish and encompassed retentive, eddy-like structures, which might have facilitated more stable conditions for phytoplankton growth.

The pelagic ecosystem to the north of South Georgia appears to be more productive than the adjacent areas of the Southwest Atlantic sector of the Southern Ocean. The region was an important whaling ground in the 1920s–1930s and has since supported several major fisheries—apparently indicative of high biological productivity. However, there is a mismatch between the carbon demand of the higher predators and local primary production in the South Georgia area, which appears to be low overall. Whitehouse et al. (1996a) estimated a value of around $30\text{--}40 \text{ g C yr}^{-1}$ on the basis of calculated nutrient drawdown, although they noted that there is considerable spatial variability in phytoplankton biomass and hence presumably production.

The main island and nearby smaller islands (e.g., Willis and Bird Islands) are the locations of large populations of breeding birds and seals, which together consume $\sim 16 \times 10^6$ tonnes fresh mass (16 Mtonne FM) of food annually (Boyd and Croxall 1996). Around half of this food supply

consists of the crustacean Antarctic krill (*Euphausia superba* Dana). Breeding Antarctic fur seals *Arctocephalus gazella* and macaroni penguins *Eudyptes chrysolophus* at the northern end of South Georgia together consume $\sim 6.7 \times 10^3$ tonnes FM of krill per day in early January, when foraging trip duration limits these predators to a zone of ~ 60 km radius (Boyd and Croxall 1996; Boyd pers. comm.). The average extraction of krill is of the order of $0.1 \text{ g C m}^{-2} \text{ d}^{-1}$. If this extraction were to be supported by local primary production, it would require at least $1 \text{ g C m}^{-2} \text{ d}^{-1}$ (Priddle et al. 1998). This value assumes that all krill feed directly on phytoplankton and neglects all other trophic pathways, including the feeding by other warm-blooded predators on larger nekton prey, which may feed in turn on krill. The few measured values for primary production in the South Georgia area are typically $\leq 1 \text{ g C m}^{-2} \text{ d}^{-1}$, and taken with the relatively low annual average value it appears likely that the production of bird and seal predators cannot be supported by the local production system within their foraging range. On this basis, it has been suggested that the South Georgia ecosystem is dependent on the advection of krill zooplankton into the region from the Antarctic Peninsula and the Weddell–Scotia Confluence (Murphy 1995). However, average production values within the area may not be completely representative, and higher predators and their key prey (krill) may have access to local systems where primary production is higher.

Acknowledgments

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In common with high nutrient–low chlorophyll (HNLC) systems in the Southern Ocean, the annual primary production in the South Georgia area is also usually insufficient to utilize completely the macronutrient supply (Whitehouse et al. 1993, 1996a, 1996b; Priddle et al. 1998). Despite typically high concentrations of nitrate, reduced nitrogen appears to be an important nutrient for phytoplankton, with values of f -ratio occasionally <0.2 (Owens et al. 1991). Furthermore, the ammonium concentrations typical of the upper mixed layer waters around South Georgia are consistent with significant inhibition of nitrate utilization (Glibert et al. 1982; Flynn 1991; Semeneh et al. 1998), which would give rise to the observed low f -ratio. As appears to be the case for many parts of the Southern Ocean, the supply of reduced nitrogen sources in the vicinity of South Georgia is probably a key factor in determining phytoplankton production (Priddle et al. 1997).

Microbial remineralization of particulate organic material is a major source of reduced nitrogen in the form of ammonium. This remineralization occurs particularly around the pycnocline, where there is also evidence of preferential remineralization of nitrogen relative to carbon (Priddle et al. 1995). Large zooplankton may also play a significant role in remineralizing phytoplankton nitrogen. This activity may give rise to a diurnal cycle in ammonium concentration where a nighttime concentration increase due to nighttime feeding and excretion is succeeded by a daytime drawdown by phytoplankton (Priddle et al. 1997). A third major source of remineralized nitrogen is excretion by land-based warm-blooded predators. Furthermore, the foraging restraints of land-based animals and their need to regularly return to densely populated breeding colonies may serve to concentrate nitrogen resources.

We examined the small-scale distributions of phytoplankton biomass (as chlorophyll a [Chl a]) and nutrients along with physical oceanography during two mesoscale surveys adjacent to South Georgia. We focused on the major differences in chlorophyll/nutrient dynamics found between two survey sites and examined the potential role of land-based warm-blooded predators in redistributing plankton nitrogen.

Methods

Study site—South Georgia is situated towards the northern limit of the Antarctic Zone (AAZ) in the Antarctic Circumpolar Current (ACC) (Fig. 1). It is influenced by both Polar Frontal Zone (PFZ) waters to the west and north, and the Weddell-Scotia Confluence (WSC), which approaches the eastern end of South Georgia from the south, flows north-west in off-shelf waters to the north of the island before resuming an easterly course (Sievers and Nowlin 1988; Peterson and Whitworth 1989; Trathan et al. 1997). The island is surrounded by a deep, extensive shelf (up to 500 m) that is part of the North Scotia Ridge, which forms the northern limit of the Scotia Sea.

Survey design and water sampling—Oceanographic measurements were made to the north and east of South Georgia 12–28 January 1996 and 23 December 1996–2 January 1997 during cruises JR11 and JR17, respectively, of the RRS

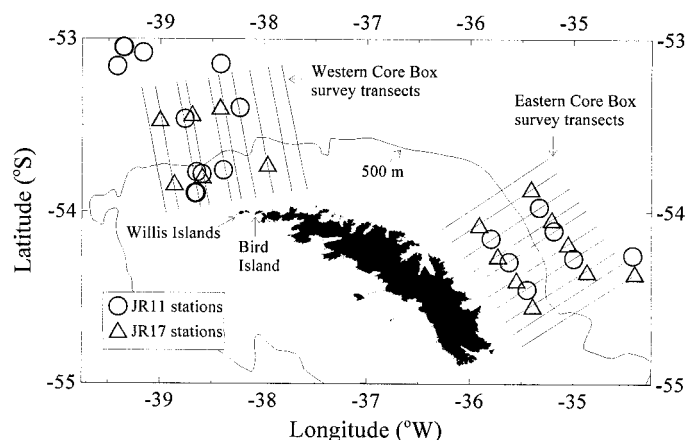


Fig. 1. Western and eastern core box survey station and transect locations at South Georgia, Southern Ocean, during cruises JR11 and JR17. The positions of the Willis and Bird Islands and the 500-m isobath are also indicated.

James Clark Ross. These cruises constitute the first two elements of the British Antarctic Survey's 5-yr Core Programme project, and near-identical sampling regimes were completed during both cruises. Underway surface (~ 6 m) data collected during 4 February 1998 on cruise JR28 are also referred to.

Two box surveys, the western core box (WCB) and the eastern core box (ECB), were conducted to the north of the island, during which on-shelf, shelf-break, and deep off-shelf waters were sampled (Fig. 1). The core boxes consisted of 10 80-km transects perpendicular to the shelf break that were sampled from the northwest to the southeast against the expected flow of water along the South Georgia shelf (Hardy and Gunther 1935). Most water bottle casts were made ~ 20 km from each end of alternate transects.

Temperature and salinity were measured with a Mk IIIB Neil Brown conductivity-temperature-depth (CTD) instrument, and water samples were collected at all stations using a General Oceanics 12-bottle rosette system interfaced to the CTD. Standard sample depths were 6 m (from the ship's nontoxic seawater supply) and 20, 40, 60, 80, 100, 125, 150, and 200 m (from water bottles), and a further four depths were sampled between 200 m and the bottom of the cast. During cruise JR17, the ship's nontoxic seawater supply was monitored continuously for temperature, salinity, Chl a and nutrients. These surface (~ 6 m) data are fully described elsewhere, but contoured plots of the data are presented here because they serve to illustrate the differences between the two core boxes and the on-shelf and off-shelf environments and enhance the spatial coverage of the study. An acoustic doppler current profiler (ADCP) was used to log water velocity continuously. Gridded residual (detided) velocity data were used to derive a stream function that approximates a nondivergent geostrophic velocity field. In such plots, currents flow along contours, and the less distance between contours, the greater the current (Pollard and Regier 1992).

Nutrient chemistry and Chl a analysis—Subsamples from the water bottles and the ship's nontoxic water supply were

filtered through a mixed ester membrane (Whatman WME, pore size 0.45 μm), and the filtrate was analyzed colorimetrically for dissolved nitrate + nitrite ($\text{NO}_3 + \text{NO}_2\text{-N}$), nitrite ($\text{NO}_2\text{-N}$), ammonium ($\text{NH}_4\text{-N}$), silicate ($\text{Si(OH)}_4\text{-Si}$), and phosphate ($\text{PO}_4\text{-P}$) using a Technicon segmented flow analyzer (Whitehouse and Woodley 1987; Whitehouse 1997; Whitehouse and Preston 1997). Nitrite concentrations, which were low throughout this study, have not been deducted from the combined nitrate + nitrite measurements, which hereinafter are referred to as nitrate.

A further water bottle subsample was filtered through a glass fiber filter (Whatman GF/F, nominal retention 0.7 μm), and the particulate material was analyzed for Chl *a* and phaeopigments (Parsons et al. 1984). Filters were extracted in 90% acetone in the dark at approximately 2°C for 24 h. Pigment concentrations were estimated by fluorometry, using a Sequoia Turner model 112 filter fluorometer during cruise JR11 and a custom-built fiber optics unit (with emission and excitation filters comparable to those on the Turner instrument) during cruise JR17. Both instruments were calibrated against commercially prepared Chl *a* standard (Sigma Chemical).

Nitrogen redistribution by higher predators—The role of mammalian and avian predators in releasing nitrogen to the pelagic ecosystem was assessed using calculations of nitrogen turnover and simulations of predator distribution. Simulations were carried out using MathCad Plus 6.0 (MathSoft).

Results

Chl *a* concentrations measured in the ECB were relatively low. However, a clear on-shelf/off-shelf pattern was evident, with concentrations of $\leq 4 \text{ mg m}^{-3}$ along the furthest west on-shelf transects and of generally $< 1 \text{ mg m}^{-3}$ in the off-shelf area (Fig. 2). The highest Chl *a* concentrations were consistently found in the WCB. During cruise JR17, concentrations were mainly $> 5 \text{ mg m}^{-3}$, and the on-shelf section of the westernmost transect passed through a bloom of $> 30 \text{ mg m}^{-3}$. Vertical profiles during both cruises showed that concentrations $> 1 \text{ mg m}^{-3}$ were confined to the top 100 m of the water column.

Upper mixed layer (UML) nitrate concentrations were high throughout all of the core box surveys during both of the cruises. During cruise JR17, particularly high off-shelf concentrations ($> 28 \text{ mmol m}^{-3}$) were evident in the most northern corner of the ECB, whereas on-shelf levels were generally lower during both cruises (Figs. 2, 3). There were no clear distinctions associated with bathymetry in the WCB, where concentrations were lower. Even so, the lowest concentrations were still $\sim 16 \text{ mmol m}^{-3}$ and were found in on-shelf areas in the southwest corner of the survey box and were coincident with exceptionally high Chl *a* levels.

During cruise JR17, surface ammonium concentrations were generally between $\sim 0.1\text{--}1.0 \text{ mmol m}^{-3}$ in the off-shelf areas of ECB and $\sim 0.1\text{--}0.5 \text{ mmol m}^{-3}$ in the WCB. A distinctive plume of high ammonium concentration ($> 2 \text{ mmol m}^{-3}$) coincident with an area of fresher water was evident in the on-shelf areas of the ECB (Fig. 2). During both cruises,

on-shelf surface ammonium concentrations were always higher than those at off-shelf sites (Fig. 3). ECB vertical profiles were relatively uniform during both cruises, whereas in the WCB, surface concentrations tended to be lower and those at the bottom of the UML tended to be higher (maximum of 3.27 mmol m^{-3} in off-shelf waters of the WCB during cruise JR17).

Throughout the surveys, nitrite concentrations were generally low; there was little difference between the two survey areas, and there were no differences associated with bathymetry. Concentrations $> 0.4 \text{ mmol m}^{-3}$ were found in the surface waters of the WCB during cruise JR17 and may have been associated with an eddy; however, the concentration range measured overall was relatively narrow (Fig. 2). The only subsurface maxima (sometimes associated with microbial remineralization and increased ammonium levels) was at the off-shelf sites in the WCB during cruise JR11 (up to 0.45 mmol m^{-3}).

There was a general northwest–southeast gradient evident in UML phosphate measurements during both cruises, with lowest concentrations in the off-shelf waters of the WCB and highest in off-shelf waters of the ECB (Figs. 2, 3). The one notable exception to this trend was found in the on-shelf waters in the southwest corner of the WCB during cruise JR17, where concentrations $< 0.8 \text{ mmol m}^{-3}$ were coincident with exceptionally high Chl *a* levels.

As with phosphate, silicate levels were generally lower in the northwest and highest to the southeast, especially during cruise JR11, with ranges of $\sim 10\text{--}20 \text{ mmol m}^{-3}$ in the WCB and $\sim 20\text{--}40 \text{ mmol m}^{-3}$ in the ECB (Fig. 3). Concentrations were lower and more uniform during cruise JR17, with the notable exceptions of marked decreases at the shelf break of the WCB (to $< 2 \text{ mmol m}^{-3}$) and the southwest corner of the WCB, where concentrations fell to $< 5 \text{ mmol m}^{-3}$, coincident with high Chl *a* concentrations (Fig. 2).

There was a clear northwest–southeast temperature gradient between the two core boxes during both cruises. It was most marked during cruise JR11, with off-shelf UML waters in the WCB of $> 4.0^\circ\text{C}$, both on-shelf areas between $2\text{--}3^\circ\text{C}$, and off-shelf areas in the ECB $< 2^\circ\text{C}$ (Fig. 3). Although WCB off-shelf waters were a little cooler during cruise JR17, overall the pattern was similar, with a clear division between the cooler off-shelf waters and the on-shelf surface waters of the ECB, where a plume of warmer, fresher water was apparent to the west of the box (Fig. 2).

On-shelf near-surface waters were fresher during all of the core box surveys, presumably because of island runoff (Fig. 2). Of particular note was a plume of fresher water to the west of the ECB, coincident with the warmer high-ammonium water.

Discussion

UML dynamics—Consistent differences were apparent for Chl *a*, nutrient, and temperature values between the UML waters of the ECB and those of the WCB and to a lesser extent between the on-shelf and off-shelf sites. ECB concentrations were generally low and consistent with levels measured further south in the Scotia Sea (Rönnner et al. 1983;

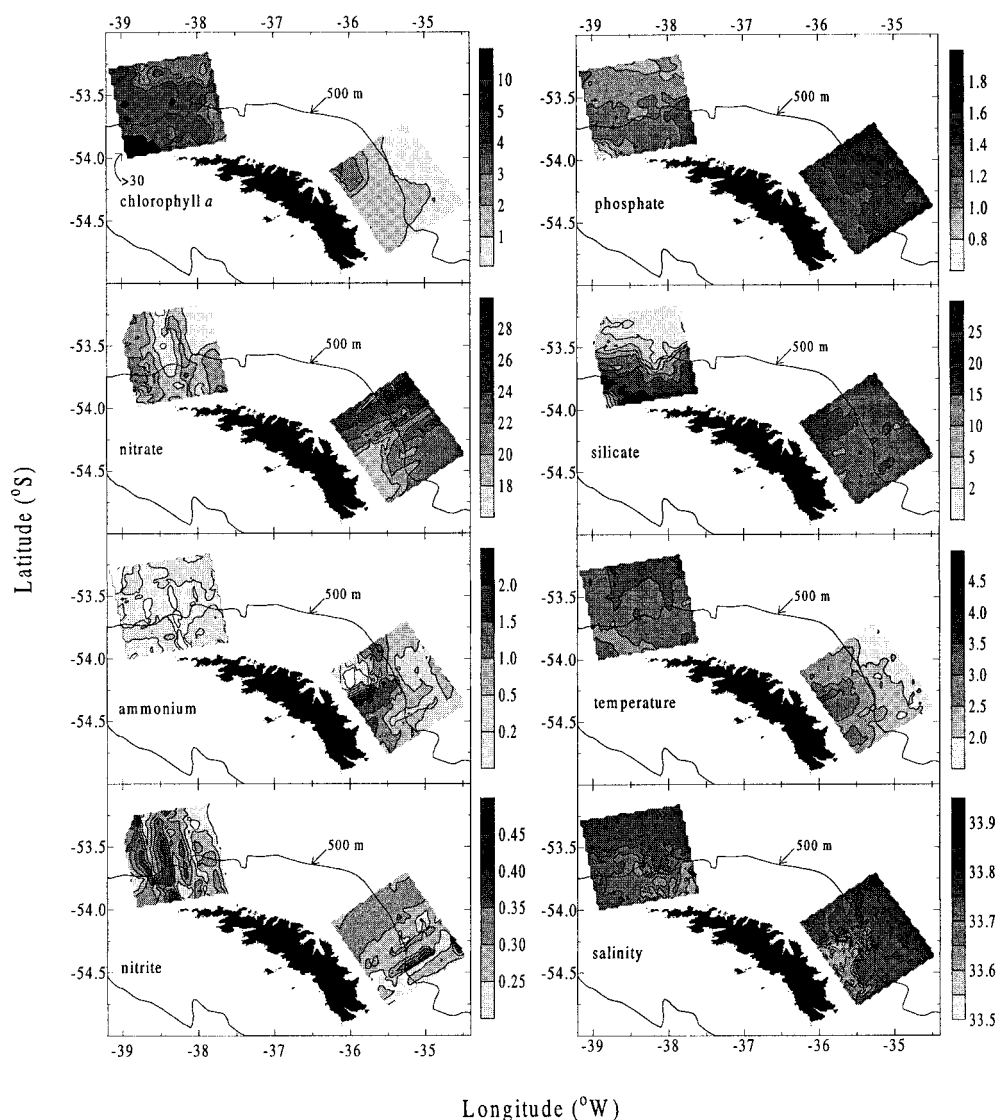


Fig. 2. Chl *a* (mg m^{-3}), nutrient (mmol m^{-3}), temperature ($^{\circ}\text{C}$), and salinity surface (~ 6 m) values collected along the survey transects of the western and eastern core boxes during cruise JR17.

Tréguer and Jacques 1992). Whereas WCB Chl *a* concentrations were far higher, with the exceedingly high levels found during cruise JR17 ($>30 \text{ mg m}^{-3}$) of a magnitude similar to that of previous measurements in neritic areas (e.g., Holm-Hansen and Mitchell 1991). The northwest–southeast temperature gradient was previously documented by Deacon (1977). Although further examination of temperature-dependent phytoplankton growth is beyond the scope of this discussion, throughout the surveyed area Chl *a* values were correlated with temperature, and very few areas with concentrations $>2 \text{ mg m}^{-3}$ occurred in water that was $<2^{\circ}\text{C}$.

The high Chl *a* concentrations of the WCB coincided with considerable deficits of silicate and phosphate, whereas the reduction of UML nitrate concentrations appeared less (average winter concentrations for this area are 26 mmol m^{-3} $\text{Si}(\text{OH})_4\text{-Si}$, 2 mmol m^{-3} $\text{PO}_4\text{-P}$, 23 mmol m^{-3} $\text{NO}_3\text{-N}$; Whitehouse et al. 1996a). We quantified relative nutrient de-

pletion by phytoplankton as the difference between near-surface (0–30 m) and pycnocline (80–100 m) concentrations, presuming that the conditions in the deeper water below the summer UML would be similar to those found before bloom in winter. The horizontal survey surface data were comparable with the CTD near-surface data, there was general agreement in the CTD data collected during the two cruises, and the regional differences in nutrient use were evident (Fig. 4).

Nitrate concentrations at the pycnocline were similar throughout both core boxes at on- and off-shelf sites, ranging from ~ 24 to 28 mmol m^{-3} . However the apparent seasonal depletion of nitrate varied considerably, with the most nitrate removed from the WCB on-shelf sites and diminishing amounts removed from WCB off-shelf sites, ECB on-shelf sites, and ECB off-shelf sites. Phosphate pycnocline concentrations were also similar throughout the surveys, ranging

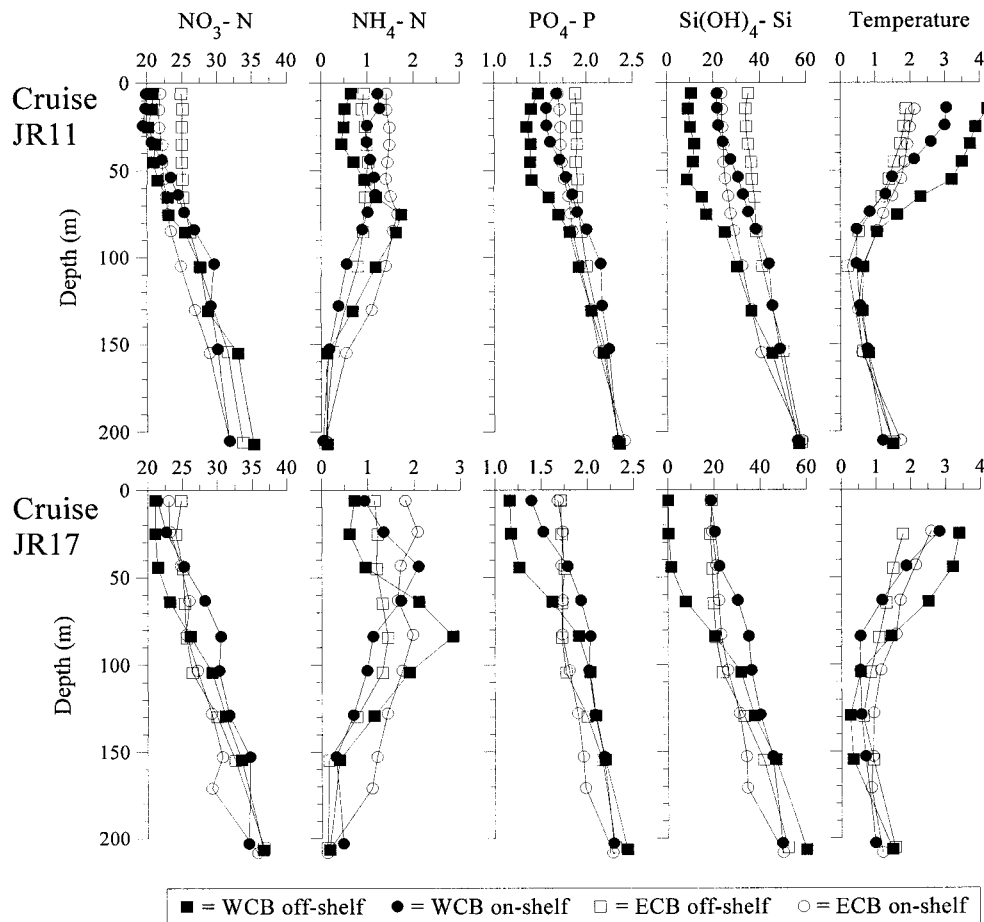


Fig. 3. Mean nutrient (mmol m^{-3}) and temperature ($^{\circ}\text{C}$) vertical profiles from the western core box (WCB) and the eastern core box (ECB) at off-shelf and on-shelf sites during cruises JR11 and JR17.

from ~ 1.8 to 2.0 mmol m^{-3} . As with nitrate, there was a gradient of apparent phytoplankton utilization, except that the depletion at the WCB off-shelf sites was similar to, if not greater than, that at the WCB on-shelf sites. Silicate pycnocline concentrations were far more variable, with particularly high levels at on-shelf sites in the WCB. However, the west-to-east pattern of depletion was similar to that for phosphate. Ammonium pycnocline levels were also variable, with high concentrations at the WCB off-shelf sites and the ECB on-shelf sites. Again, the gradient of apparent nutrient depletion is similar to the phosphate trend (i.e., the reverse of the trend shown by nitrate in the WCB).

Ammonium concentrations typical of the surface waters around South Georgia were consistent with significant inhibition of nitrate utilization (Glibert et al. 1982; Flynn 1991; Semeneh et al. 1998). To further investigate regional nutrient use, we scaled apparent nutrient removal to carbon uptake according to the Redfield ratio and previously published Si:C uptake data (Priddle et al. 1995). We compared the difference in nitrate, phosphate, and silicate deficits with apparent ammonium deficits at the on- and off-shelf sites in the WCB and ECB (Fig. 5). There was little apparent difference between silicate and phosphate deficits associated

with ammonium use. Silicate deficits were generally a little higher than phosphate, possibly because of greater remineralization of phosphate in the UML. However, nitrate-nitrogen deficits were frequently less than those of phosphate and of silicate in the WCB, especially at the off-shelf sites. Furthermore, this apparent nitrate-nitrogen underutilization occurred at sites where ammonium-nitrogen utilization was greatest. This nitrate-nitrogen underutilization can be further demonstrated by comparing surface nutrient measurements made at the southwest corner of the WCB during cruise JR17, the location of the highest Chl *a* levels ($>30 \text{ mg m}^{-3}$), with the nearest pycnocline measurements (Fig. 5). This site shows nutrient deficit characteristics similar to those of WCB off-shelf sites, again with a shortfall of nitrate-nitrogen utilization and a large ammonium-nitrogen deficit. We conclude from these observations that ammonium abundance may be the key factor facilitating high phytoplankton growth.

Ammonium sources—Although the two study sites were barely 90 km apart at their nearest point, the data indicate significant differences in their chlorophyll/nutrient dynamics and the amount of phytoplankton biomass they support.

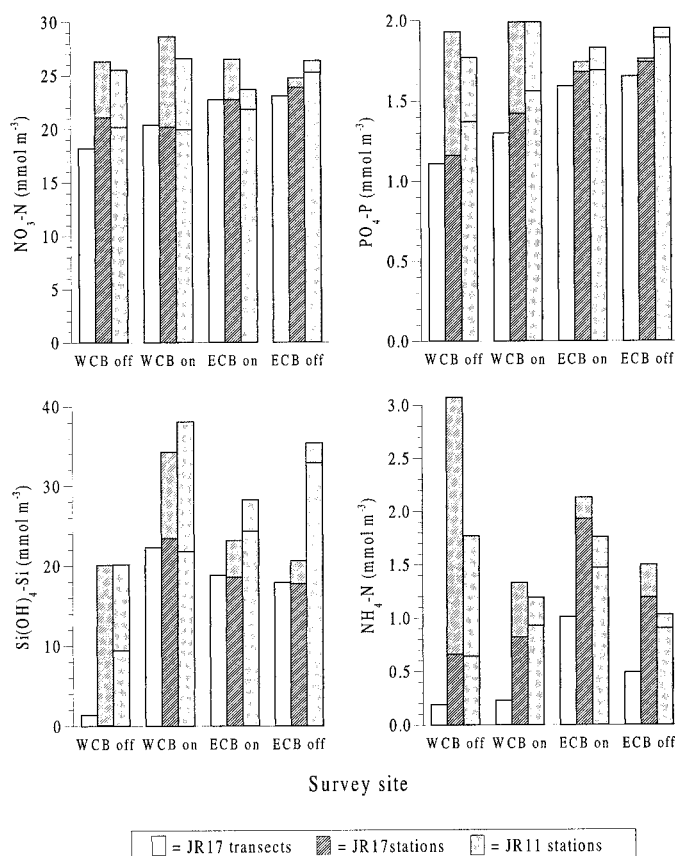


Fig. 4. A comparison of average surface (6 m), near-surface (0–30 m), and pycnocline (80–100 m) nutrient values in the western core box (WCB) and eastern core box (ECB) at off-shelf and on-shelf sites measured along the cruise JR17 transects, at cruise JR17 stations, and at cruise JR11 stations. The lower section of the column represents near-surface values and the entire column represents those at the pycnocline.

Whereas Chl *a* levels were generally $>5 \text{ mg m}^{-3}$ in the WCB and at times $>30 \text{ mg m}^{-3}$, ECB concentrations were generally $<2 \text{ mg m}^{-3}$. Nutrient deficits were greater in the WCB, implying higher phytoplankton growth rates rather than an accumulation of biogenic material. Also ammonium-nitrogen, a crucial nitrogen source for South Georgia phytoplankton, appeared to play a more important role in the WCB.

The remineralization of particulate organic material and phytoplankton nitrogen by microbes and large zooplankton are doubtless major sources of reduced nitrogen to both the WCB and the ECB. However, nitrogen remineralization by land-based endotherms is decidedly skewed towards the northwestern end of the island. Land-breeding higher predators at South Georgia harvest large amounts of food, have high metabolic costs that result in rapid recycling of dietary nitrogen, and have the potential to redistribute large amounts of nitrogen within the island's pelagic ecosystem. Of the 16 Mtonnes annual food requirement of the higher predators of South Georgia, over 43% is taken by just two species, the Antarctic fur seal and the macaroni penguin (Croxall et al. 1984, 1985; Boyd and Croxall 1996; Boyd pers. comm.; Prince pers. comm). These two major predators are concentrated at the northwestern end of the island, where $>87\%$ of the fur seal breeding population and $>90\%$ of that of the macaroni penguins are located within 25 km of Bird Island (Boyd 1993, 1996; Prince and Poncet 1996). Their diet consists primarily of Antarctic krill advected into their foraging range, and they frequently return to their colonies to feed pups and chicks and so concentrate nutrients close to the land. This concentration effect was much in evidence in February 1998 during a water sampling transect between Bird Island and the Willis Islands, both major breeding sites for Antarctic fur seals and macaroni penguins (Fig. 6). There were relatively high ammonium concentrations of $\sim 1\text{--}1.5 \text{ mmol m}^{-3}$ over the eastern part of the transect and then levels peaked at $\sim 2.5 \text{ mmol m}^{-3}$ in the vicinity of the is-

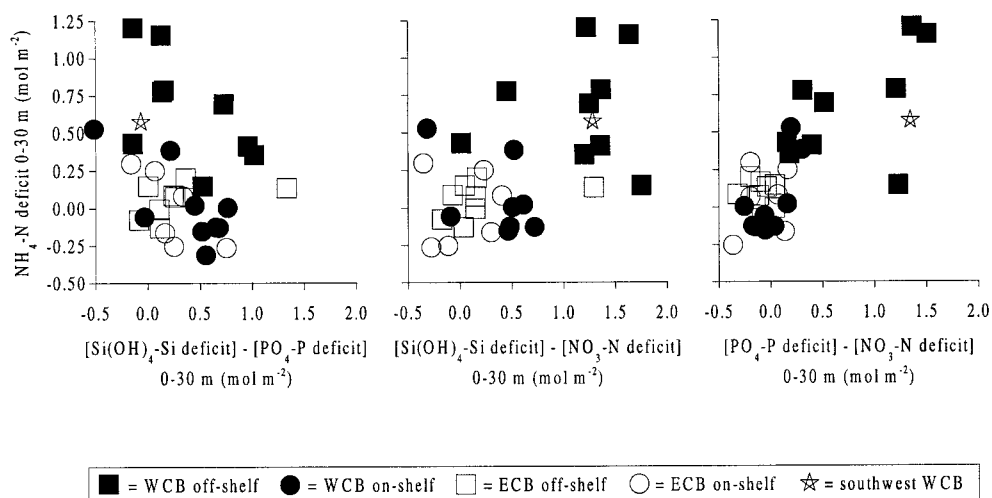


Fig. 5. A comparison of near-surface (0–30 m) $\text{Si(OH)}_4\text{-Si}$, $\text{PO}_4\text{-P}$, and $\text{NO}_3\text{-N}$ deficits and their association with $\text{NH}_4\text{-N}$ deficits in the western core box (WCB) and the eastern core box (ECB) at off-shelf and on-shelf sites and an indication of southwest WCB deficits. Concentrations are scaled to carbon uptake (Redfield ratio and C:Si; Priddle 1995).

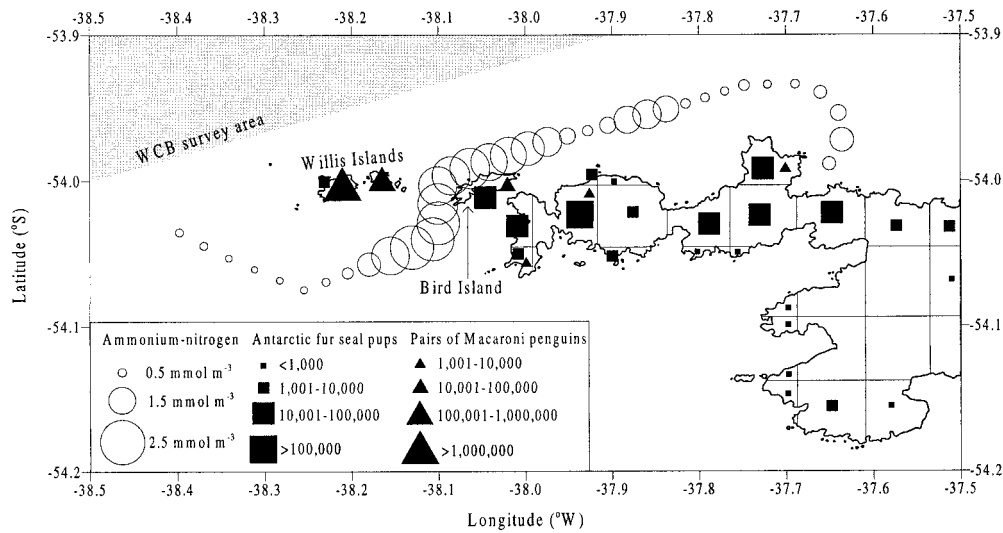


Fig. 6. Surface (6 m) $\text{NH}_4\text{-N}$ concentrations measured at the western end of South Georgia during 4 February 1998, and an indication of the regional population density (per 5 km square) of Antarctic fur seal pups and breeding macaroni penguin pairs (Boyd 1996; Prince and Poncet 1996).

lands, before a rapid decrease to $<0.5 \text{ mmol m}^{-3}$ to the west. We investigated the magnitude of the reduced nitrogen made available during early January (the period during the breeding season that is equivalent to our shipboard surveys) by Antarctic fur seals and macaroni penguins for phytoplankton

Table 1. Parameter values used to model nitrogen excretion by the breeding populations of Antarctic fur seals and macaroni penguins at the western end of South Georgia, Southern Ocean (within 25 km of Bird Island), during January.

a. Factors for conversion of prey uptake (polar euphausiids*) to nitrogen excretion		
Fresh-mass (FM) to dry-mass conversion	0.235	(range, 0.17–0.34)
Nitrogen proportion of dry mass	0.096	(range, 0.073–0.11)
b. Predator breeding population and feeding parameters†		
	Antarctic fur seal	Macaroni penguin
Total no. adult females	5.2×10^5	2.7×10^6
No. adult females at sea per day	3.4×10^5	2.7×10^6
No. young	5.2×10^5	1.3×10^6
Excretion rate of young, as proportion of adult	0.5	0.1
Excreting population on land, as adult equivalents	4.4×10^5	0.13×10^6
Daily ration per feeding adult (kg FM d^{-1})	12	1
Daily krill uptake by population, as fresh mass (g FM d^{-1})	4×10^9	2.7×10^9
Daily krill uptake by population, as nitrogen (mol N d^{-1})	6.5×10^6	4.4×10^6
Foraging range (km)	85	40

* Sidhu et al. 1970; Bykov 1975; Ikeda 1988; Ikeda and Skjoldal 1989.

† Williams and Croxall 1991; Boyd 1993, 1996; Boyd and Croxall 1996; Prince and Poncet 1996.

growth in the waters around the western end of the island in the vicinity of the WCB.

Nitrogen recycled by land-based predators—The breeding populations of female Antarctic fur seals, female macaroni penguins, and their young present within 25 km of Bird Island during early January have a total krill consumption of $\sim 6.7 \times 10^3$ tonnes FM d^{-1} (Table 1). Assuming that $\sim 80\%$ of the predators' dietary intake is catabolized (Humphries 1979; Priddle et al. 1998), so that this proportion of the dietary nitrogen intake is eventually excreted, the breeding colonies at Bird Island and nearby excrete $\sim 1 \times 10^7$ mol N d^{-1} during this period. In early January, adult male fur seals are fasting on land or will have dispersed away from the breeding colonies; therefore, their contribution to the area's nitrogen flux is uncertain and thus was disregarded for this exercise. Similarly, we also disregarded adult male macaroni penguins, who fast during this period while they guard the chick.

To model the dispersion of the nitrogen excreted by the female predators and their young, we need to know where the excretion is deposited. We assumed constant excretion rates by the seals and penguins, whether on land or in the sea. In early January, breeding female fur seals spend $\sim 33\%$ of their time feeding their pups on shore and the rest of their time foraging at sea, whereas female macaroni penguins spend the majority of their time at sea. For animals at sea, we assumed that nitrogen loading through excretion was related directly to the density of animal numbers. The limited data available on the distribution of South Georgia predators at sea are based on observations from ships (e.g., Hunt et al. 1992; Veit et al. 1993) and from satellite telemetry (Boyd pers. comm.); therefore, we have modelled their distribution on the basis of a simple inverse relationship between density and distance from the island. Thus, Bird Island was considered a circular mass 1 km diameter (in fact, it is approximately 5×0.5 km), and predators were assumed to forage

over a 270° sector away from the South Georgia mainland. We assumed that predators leave the island in straight trajectories and can be found with equal probability along these trajectories at any distance r up to the theoretical average foraging range R_F . Predator density D_r at any distance from the island is found by

$$D_r = \frac{P_0}{r^2} \cdot \frac{4}{3}$$

where the factor $4/3$ is included to compensate for the 270° sector over which the predator foraging is modelled. P_0 is the notional predator population at the island's coast ($r = 1$) and is calculated by integrating the expression for the number of animals versus distance from the island out to R_F and then setting this integral equal to the total population of predators at sea. Initially, P_0 is set to a notional value of 1, so that the integral yields a value of the population given by

$$\text{Population}^* = \int_{r=1}^{R_F} \frac{1}{r^2} \cdot \frac{4}{3} 2\pi r dr$$

The expression $2\pi r dr$ derives from the area of an annulus distance r from the coast and of small but finite width δr . The value of P_0 is then obtained by dividing this notional population into the known population of animals at sea.

It is problematic to estimate the extent of the influence of runoff from the island. We have little knowledge of the dispersal of the water derived from the island nor do we know the timescale on which excreted nitrogen will be altered biochemically or removed from the nitrogen pool by microbial growth. We have set a notional limit of 10 km for the influence of excreted nitrogen in runoff. This distance scale is of the same order as the Rossby radius at the latitude of South Georgia (Mann and Lazier 1991).

Our simulation used approximate mean foraging ranges for the two species: 85 km for fur seals and 40 km for the macaroni penguins (Boyd pers. comm.). For both species, densities of animals at sea decrease sharply relatively close to the island, at around 10 individuals km^{-2} and 100 individuals km^{-2} for seals and penguins, respectively, at 20 km from the island. Fur seals produce a total nitrogen loading of $\sim 130 \text{ mmol m}^{-2} \text{ d}^{-1}$ close to the island, of which $\sim 95 \text{ mmol m}^{-2} \text{ d}^{-1}$ derives from females and pups on land (Fig. 7). The nitrogen loading at 20 km from the island is about $0.7 \text{ mmol m}^{-2} \text{ d}^{-1}$, of which $0.2 \text{ mmol m}^{-2} \text{ d}^{-1}$ derives from animals in the water. The loading decreases gradually as distance from the island increases, and the share of direct input from animals in the sea increases as influence from the island runoff is reduced. In the same simulation, penguins produce a loading of $\sim 70 \text{ mmol m}^{-2} \text{ d}^{-1}$ close to the island, but nearly all of this is attributable to animals in the sea because the contribution to runoff by chicks is minimal and that by fasting males is zero. At 20 km distance, the loading is around $0.4 \text{ mmol m}^{-2} \text{ d}^{-1}$. Overall, the nitrogen loadings for both species at 1 and 20 km distance from the island are ~ 205 and $1.0 \text{ mmol m}^{-2} \text{ d}^{-1}$, respectively, with around equal

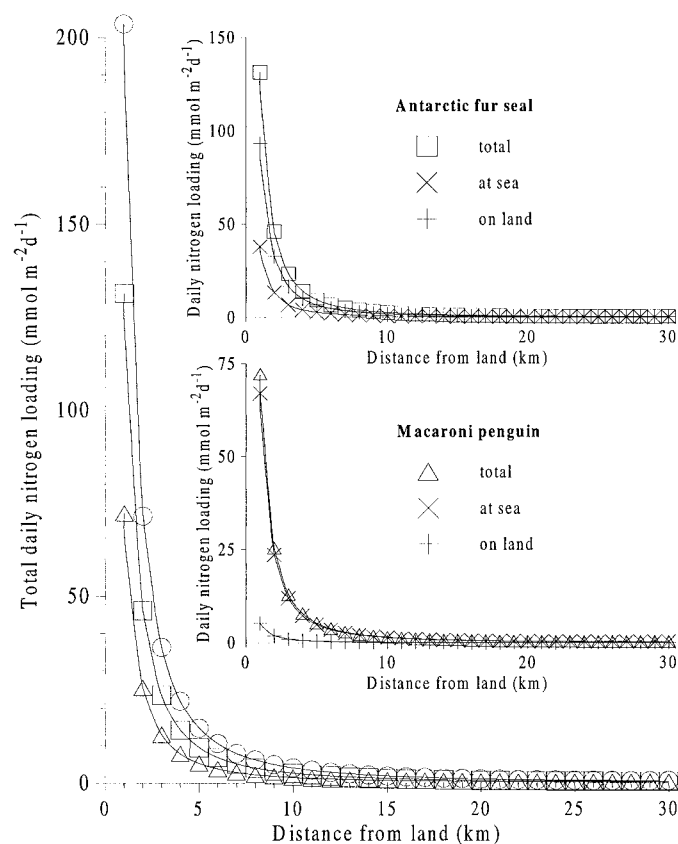


Fig. 7. The predicted daily nitrogen loading due to excretion by Antarctic fur seals (squares) and macaroni penguins (triangles) in the surface waters near their breeding colonies during early January. Total concentrations (circles) are also shown. The calculations are based on foraging ranges of 85 km for the fur seals and 40 km for the penguins. *Insets*: The predicted daily nitrogen loading due to fur seals and penguins partitioned into excretion at sea and on land.

shares from runoff and at-sea animals close to shore and increasing dominance by at-sea animals as distance increases. This change with distance is shown by the respective contributions of the two predators, with fur seals dominating the input close to the island but penguins producing an increasingly important share of the loading at 20 km. Beyond 20 km, loadings fall off gradually.

We also simulated the effects of both predator species feeding close to the island. For this simulation, we selected a maximum foraging range of 30 km, which is the approximate distance from Bird Island to the northern shelf break. This simulation produced relatively small changes to the pattern observed for the mean foraging ranges, suggesting that the simulation is relatively robust with respect to the distance the animals travel to feed. For the 30-km foraging range, nitrogen loading close to the island increased to $\sim 145 \text{ mmol m}^{-2} \text{ d}^{-1}$ for fur seals and $\sim 75 \text{ mmol m}^{-2} \text{ d}^{-1}$ for penguins, both values reflecting the increased density of animal numbers at sea. The total loadings at 1 km and 20 km in this simulation were ~ 220 and $\sim 1.2 \text{ mmol m}^{-2} \text{ d}^{-1}$, respectively, both only slight increases over the values derived for the mean foraging ranges.

The results of the simulation suggest that land-based pred-

ators (i.e., those feeding young) are extremely effective at bringing a large amount of zooplankton nitrogen (1×10^7 mol d^{-1}) from an extensive area, about 3×10^4 km², and releasing most of it by excretion into a smaller region, perhaps 75 km² or 2.5% of the area from which it was abstracted. Overall contributions from runoff derived from animals on land and from at-sea excretion are roughly equal for the total input from the two predators considered here in the critical zone within 20 km of the island. However, because of differences in breeding biology, fur seals contribute more to runoff and penguins contribute more to direct input to the water. Foraging distance is relatively unimportant. For the most part, these modelled foraging distributions (evenly through 270°) compare favorably with the limited observations for the macaroni penguin, but some fur seal observations suggest a level of aggregation that was not encompassed in this model.

At the subantarctic Marion Island in the Indian Ocean, Burger et al. (1978) estimated that 3 million birds (98% penguins) deposited 3.3×10^4 tonnes of fresh guano on the island annually and that 53% of the total was produced during December–February. About 97% of the guano was voided on the coastal lowlands, which ultimately drain to the sea, where Ismail (1990) recorded exceedingly high concentrations of reduced nitrogen within 2–3 km from land (>16 mmol m^{-3} ammonium, >2.8 mmol m^{-3} urea).

We considered only two dominant krill-feeding predators. There are many other land-breeding predators (including a proportion of the breeding male fur seals) in the Bird Island area that also provide a nitrogen contribution to the seas close to the island. Thus, our estimate of nitrogen loading, although high compared with concentrations normally observed in the South Georgia region, should be viewed as realistic if not an underestimate.

Additional hydrological observations—Little information is available on how nitrogen from land-based animals is actually dispersed around South Georgia, either by horizontal advection or by vertical mixing. Mixed layer depths in this region in midsummer are approximately 50–70 m, so that a loading of 50 mmol m^{-2} will be required to produce an average of 1 mmol m^{-3} increase in concentration. However, vertical mixing is unlikely to cause homogeneous dispersal over the UML within the lifetime of the nitrogen input; thus, the predator-related nitrogen loading will be high in near-surface water. Horizontal advective and retentive mechanisms are likely to be important in the way in which this nitrogen input will be returned to the pelagic ecosystem. Studies at the Prince Edward Island group, Indian Ocean, have shown that freshwater runoff retained by an eddy field between Marion and Prince Edward Islands may represent a significant input of buoyancy into the UML and increase water column stability (Ismail 1990; Perissinotto and Duncombe Rae 1990). Therefore, the runoff, containing high concentrations of reduced nitrogen forms, may be of major importance to the formation of phytoplankton blooms in the island group.

Current vectors in the fine-resolution antarctic model (FRAM Group 1991) from the depth range 185–245 m indicate that water leaves the shelf at the western end of South

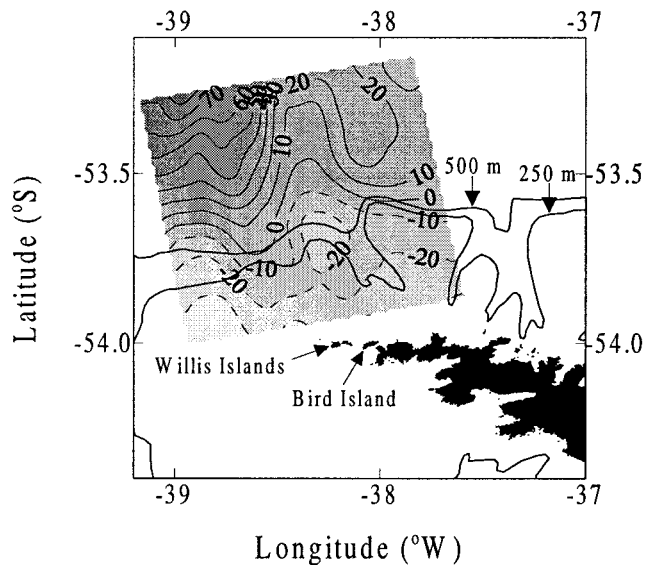


Fig. 8. Nondivergent horizontal stream functions ($100 \times m^2 s^{-1}$) calculated from acoustic doppler current profiler measurements for the western core box during cruise JR17. The dashed contour lines and negative values represent a general west–east flow.

Georgia in a north–northwesterly direction. The model also shows a front between the eastward flowing ACC and water flowing west to the northwest of Willis and Bird Islands. During cruise JR17, ADCP measurements showed an anticyclonic eddy in the WCB centered ~ 30 km north of the Willis Islands (Fig. 8). A feature such as this would presumably provide a retentive and stable mechanism for phytoplankton growth. Furthermore, in the on-shelf waters and particularly in the area to the southwest of the WCB where the highest Chl *a* concentrations were measured, currents were flowing relatively sluggishly from west to east compared with the rapidly flowing east–west currents in the off-shelf waters. Both the eddy and the relatively slow currents passing through the foraging ranges of the land-based predators increase the potential loading of predator-recycled nitrogen into the UML waters, thereby increasing the availability of reduced nitrogen for phytoplankton growth.

Temperature may also play an important role in the promotion of phytoplankton growth in the subantarctic waters around South Georgia. Indeed, the UML water temperatures were higher in the WCB than in the ECB. However, in the past the warmer waters northwest of South Georgia have been regarded as the least phytoplankton productive. During the Discovery investigations, major phytoplankton growth was recorded in the colder waters influenced by the WSC north, east, and south of the island. During the 1930s circumisland spring surveys (November 1930), by far the greatest phytoplankton abundance was found in the colder waters south and east of the island, and the waters around Bird and Willis Islands were particularly sparse in phytoplankton (Hart 1934). In the previous summer (January–February 1930), conditions were “abnormally” warm, and the greatest phytoplankton abundance was found in the coolest waters to the east. On-shelf waters were particularly lacking in phytoplankton growth other than “a moderately rich patch round

Bird Island." Fur seals had been virtually hunted to extinction on the island during this period prior to the phenomenal increase in the population between the late 1930s and the present day (Matthews 1929; Bonner 1968). However, this period would have coincided with the height of the macaroni penguin breeding season, when krill consumption (and presumably nitrogen recycling) would have been at its greatest (Boyd and Croxall 1996).

Conclusion—Exceedingly high concentrations of Chl *a* were discovered north and west of South Georgia. These measurements suggest that the pelagic environments at either end of the island are very different. Whereas Chl *a* and nutrient concentrations at the eastern end of the island were similar to those found in HNLC areas of the Scotia Sea to the south, the western end of the island was capable of supporting extensive high levels of phytoplankton production more typical of neritic areas. Furthermore, this region of high Chl *a* concentrations was not confined to the on-shelf areas but extended northwest from the island for at least 110 km into deep oceanic waters.

Differences in nitrate-nitrogen and ammonium-nitrogen deficits suggest an important role for reduced nitrogen sources at the western end of the island, where a plentiful stock of ammonium was evident. The potential for elevated phytoplankton growth promoted by high nutrient runoff from penguin rookeries on subantarctic islands has been observed previously at the Prince Edward Island group (Perissinotto and Duncombe Rae 1990). Further south, Biggs et al. (1985) speculated that a charge of ammonium into the water column underlying the retreating sea ice may stimulate or accelerate the extensive development of phytoplankton blooms. Our dispersion model of nitrogen regenerated by fur seals and penguins breeding at the northwestern tip of South Georgia shows that the concentration of nutrients provided by these animals would be sufficient to fuel the observed phytoplankton blooms. Eddies and sluggish on-shelf currents measured in the area would further facilitate conditions in which increased phytoplankton growth could take place.

References

- BIGGS, D. C., A. F. AMOS, AND O. HOLM-HANSEN. 1985. Oceanographic studies of epi-pelagic ammonium distributions: The Ross Sea NH_4^+ flux experiment, p. 93–103. *In* W. R. Siegfried, P. R. Condy, and R. M. Laws [eds.], Antarctic nutrient cycles and food webs. Springer.
- BONNER, W. N. 1968. The fur seal of South Georgia. *Br. Antarct. Surv. Sci. Rep.* **56**: 1–81.
- BOYD, I. L. 1993. Pup production and distribution of breeding Antarctic fur seals (*Arctocephalus gazella*) at South Georgia. *Antarct. Sci.* **5**: 17–24.
- . 1996. South Georgia distribution of breeding Antarctic fur seals *Arctocephalus gazella*, map 3.2. *In* P. N. Trathan, F. H. J. Daunt, and E. J. Murphy [eds.], South Georgia: An ecological atlas. British Antarctic Survey.
- , AND J. P. CROXALL. 1996. Preliminary estimates of krill consumption by Antarctic fur seals and macaroni penguins at South Georgia. Document WG-EMM-96/96. CCAMLR.
- BURGER, A. E., H. J. LINDEBOOM, AND A. J. WILLIAMS. 1978. The mineral and energy contributions of guano of selected species of birds to the Marion Island terrestrial ecosystem. *S. Afr. J. Antarct. Res.* **8**: 59–70.
- BYKOV, V. P. 1975. Biological value of Antarctic krill and possibility of their utilization for human consumption. *Oceanol. Int. Conf.* **75**: 361–363.
- CROXALL, J. P., P. A. PRINCE, I. HUNTER, S. J. MCINNES, AND P. G. COPESTAKE. 1984. The seabirds of the Antarctic Peninsula, islands of the Scotia Sea and Antarctic Continent between 80°W and 20°W: Their status and conservation, p. 637–666. *In* J. P. Croxall, P. G. H. Evans, and R. W. Schreiber [eds.], Status and conservation of the world's seabirds. ICBP Tech. Publ. 2. International Council for Bird Preservation.
- , ———, AND C. RICKETS. 1985. Relationships between prey life cycles and the extent, nature and timing of seal and seabird predation in the Scotia Sea, p. 516–533. *In* W. R. Siegfried, P. R. Condy, and R. M. Laws [eds.], Antarctic nutrient cycles and food webs. Springer.
- DEACON, G. E. R. 1977. Seasonal and annual variations in water temperature and salinity near South Georgia 1925–1937. *Inst. Oceanogr. Sci. Rep.* **49**.
- FLYNN, K. J. 1991. Algal carbon–nitrogen metabolism: A biogeochemical basis for modelling the interactions between nitrate and ammonium uptake. *J. Plankton Res.* **13**: 373–387.
- FRAM GROUP. 1991. An eddy-resolving model of the Southern Ocean. *Eos. Trans. Am. Geophys. Union* **72**: 169–175.
- GLIBERT, P. M., D. C. BIGGS, AND J. J. MCCARTHY. 1982. Utilization of ammonium and nitrate during austral summer in the Scotia Sea. *Deep-Sea Res.* **29**: 837–850.
- HARDY, A. C., AND E. R. GUNTHER. 1935. The plankton of the South Georgia whaling grounds and adjacent waters, 1926–1927. *Discovery Rep.* **11**: 1–456.
- HART, T. J. 1934. On the phytoplankton of the south-west Atlantic and the Bellingshausen Sea, 1929–31. *Discovery Rep.* **8**: 1–268.
- HOLM-HANSEN, O., AND B. G. MITCHELL. 1991. Spatial and temporal distribution of phytoplankton and primary production in the western Bransfield Strait region. *Deep-Sea Res.* **38**: 961–980.
- HUMPHRIES, W. F. 1979. Production and respiration in animal populations. *J. Anim. Ecol.* **48**: 427–453.
- HUNT, G. L., JR., D. HEINEMANN, AND I. EVERSON. 1992. Distributions and predator–prey interactions of macaroni penguins, Antarctic fur seals, and Antarctic krill near Bird Island, South Georgia. *Mar. Ecol. Prog. Ser.* **86**: 15–30.
- IKEDA, T. 1988. Metabolism and chemical composition of crustaceans from the Antarctic mesopelagic zone. *Deep-Sea Res.* **35**: 1991–2002.
- , AND H. R. SKJOLDAL. 1989. Metabolism and elemental composition of zooplankton from the Barents Sea during early Arctic summer. *Mar. Biol.* **100**: 173–183.
- ISMAIL, H. E. 1990. Surface nutrients in the vicinity of the Prince Edward Islands during April/May 1989. *S. Afr. J. Antarct. Res.* **20**: 33–36.
- MANN, K. H., AND J. R. N. LAZIER. 1991. Dynamics of marine ecosystems. Blackwell.
- MATTHEWS, L. H. 1929. The natural history of the elephant seal with notes on other seals found at South Georgia. *Discovery Rep.* **1**: 235–255.
- MURPHY, E. J. 1995. Spatial structures of the Southern Ocean ecosystem: Predator–prey linkages in Southern Ocean food webs. *J. Anim. Ecol.* **64**: 333–347.
- OWENS, N. J. P., J. PRIDDLE, AND M. J. WHITEHOUSE. 1991. Variations in phytoplankton nitrogen assimilation around South Georgia and in Bransfield Strait (Southern Ocean). *Mar. Chem.* **35**: 287–304.
- PARSONS, T. R., Y. MAITA, AND C. M. LALLI. 1984. A manual of

- chemical and biological methods for seawater analysis. Pergamon.
- PERISSINOTTO, R., AND C. M. DUNCOMBE RAE. 1990. Occurrence of anticyclonic eddies on the Prince Edward Plateau (Southern Ocean): Effects on phytoplankton biomass and production. *Deep-Sea Res.* **37**: 777–793.
- PETERSON, R. G., AND T. WHITWORTH III. 1989. The Subantarctic and Polar Fronts in relation to deep water masses through the southwestern Atlantic. *J. Geophys. Res.* **94**: 10817–10838.
- POLLARD, R. T., AND L. A. REGIER. 1992. Vorticity and vertical circulation at an ocean front. *J. Phys. Oceanogr.* **22**: 609–625.
- PRIDDLE, J., I. L. BOYD, M. J. WHITEHOUSE, E. J. MURPHY, AND J. P. CROXALL. 1998. Estimates of Southern Ocean primary production—constraints from predator carbon demand and nutrient drawdown. *J. Mar. Syst.* **17**: 275–288.
- , AND OTHERS. 1995. Nutrient cycling by Antarctic marine microbial plankton. *Mar. Ecol. Prog. Ser.* **116**: 181–198.
- , M. J. WHITEHOUSE, A. ATKINSON, A. S. BRIERLEY, AND E. J. MURPHY. 1997. Diurnal changes in mixed layer ammonium concentrations—interplay between zooplankton and phytoplankton. *J. Plankton Res.* **19**: 1305–1330.
- PRINCE, P. A., AND S. PONCET. 1996. South Georgia distribution of macaroni penguins *Eudyptes chrysolophus*, map 2.5. In P. N. Trathan, F. H. J. Daunt, and E. J. Murphy [eds.], *South Georgia: An ecological atlas*. British Antarctic Survey.
- RÖNNER, U., F. SORENSSON, AND O. HOLM-HANSEN. 1983. Nitrogen assimilation by phytoplankton in the Scotia Sea. *Polar Biol.* **2**: 137–147.
- SEMENEH, M., F. DEHAIRS, M. FIALA, M. ELSKENS, AND L. GOEYENS. 1998. Seasonal variation of phytoplankton community structure and nitrogen uptake in the Indian Sector of the Southern Ocean. *Polar Biol.* **20**: 259–272.
- SIDHU, G. S., W. A. MONTGOMERY, G. L. HOLLOWAY, A. R. JOHNSON, AND D. M. WALKER. 1970. Biochemical composition and nutritive value of krill (*Euphausia superba* Dana). *J. Sci. Food Agric.* **21**: 293–296.
- SIEVERS, H. A., AND W. D. J. NOWLIN. 1988. Upper ocean characteristics in Drake Passage and adjoining areas of the Southern Ocean, 39°W–95°W, p. 57–80. In D. Sahrhage [ed.], *Antarctic Ocean and resources variability*. Springer.
- TRATHAN, P., M. A. BRANDON, AND E. J. MURPHY. 1997. Characterization of the Antarctic Polar Frontal Zone to the north of South Georgia in summer 1994. *J. Geophys. Res.* **102**: 10483–10497.
- TRÉGUER, P., AND G. JACQUES. 1992. Dynamics of nutrients and phytoplankton, and fluxes of carbon, nitrogen and silicon in the Antarctic Ocean. *Polar Biol.* **12**: 149–162.
- VEIT, R. R., E. D. SILVERMAN, AND I. EVERSON. 1993. Aggregation patterns of pelagic predators and their principal prey, Antarctic krill, near South Georgia. *J. Anim. Ecol.* **62**: 551–564.
- WHITEHOUSE, M. J. 1997. Automated seawater nutrient chemistry. British Antarctic Survey.
- , AND M. PRESTON. 1997. A flexible computer-based technique for the analysis of data from a sea-going nutrient autoanalyser. *Anal. Chim. Acta* **345**: 197–202.
- , J. PRIDDLE, AND C. SYMON. 1996a. Seasonal and annual change in seawater temperature, salinity, nutrient and chlorophyll *a* distribution around South Georgia, South Atlantic. *Deep-Sea Res.* **43**: 425–443.
- , ———, P. N. TRATHAN, AND M. A. BRANDON. 1996b. Substantial open-ocean phytoplankton blooms to the north of South Georgia, South Atlantic, during summer 1994. *Mar. Ecol. Prog. Ser.* **140**: 187–197.
- , C. SYMON, AND J. PRIDDLE. 1993. Variations in the distribution of chlorophyll *a* and inorganic nutrients around South Georgia, South Atlantic. *Antarct. Sci.* **5**: 367–376.
- , AND V. R. WOODLEY. 1987. Automated seawater nutrient analysis. British Antarctic Survey.
- WILLIAMS, T. D., AND J. P. CROXALL. 1991. Annual variation in breeding biology of the macaroni penguin, *Eudyptes chrysolophus*, at Bird Island, South Georgia. *J. Zool. Lond.* **223**: 189–202.

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