

Biogeochemistry of a Southern Ocean plankton ecosystem: Using natural variability in community composition to study the role of metazooplankton in carbon and nitrogen cycles

Julian Priddle,¹ Michael J. Whitehouse, Peter Ward, Rachael S. Shreeve,
Andrew S. Brierley,² Angus Atkinson, Jonathan L. Watkins, Mark A. Brandon,³
and Geoffrey C. Cripps

Biological Sciences Division, British Antarctic Survey, Cambridge, UK

Received 8 May 2000; revised 24 May 2001; accepted 10 September 2001; published 30 April 2003.

[1] The pelagic ecosystem around the island of South Georgia is subject to significant interannual variability, and changes in zooplankton community composition can be used as natural ecosystem experiments to examine biogeochemical cycles. The biomass of the large euphausiid Antarctic krill may range from ca. 2 to 150 g fresh mass (FM) m⁻². When krill biomass is low, copepod biomass may be correspondingly higher and overall zooplankton biomass remains more or less unchanged. Krill are omnivorous, feeding facultatively either as grazers on microplankton or as predators on smaller zooplankton. This leads to complex feedbacks within the plankton. A simple model of the phytoplankton–copepod–krill system is used to simulate two scenarios of zooplankton composition. For the “low krill-high copepod” scenario, the model predicts higher phytoplankton biomass and production, lower mixed layer (ML) ammonium, nitrate and silicate concentrations, and higher detrital carbon production than in the “high krill-low copepod” scenario. Nitrogen cycling provides the most explicit demonstration of the differences between the scenarios. For the “low krill-high copepod” scenario, ML ammonium concentration decreased by 25% over 20 days, but excretion by metazooplankton supplied 30% of phytoplankton nitrogen demand. In the “high krill-low copepod” scenario, ML ammonium only declined by 10% over 20 days, but metazooplankton excretion was much lower, at 10% of phytoplankton N demand. These predictions are compared with data from several surveys covering krill biomass in the range 10–55 g FM m⁻². Phytoplankton chlorophyll biomass is negatively related to krill biomass, and ML nutrients are positively correlated with krill biomass in these data. Both observations and model results suggest that variation in biogeochemical carbon and nitrogen cycles in the South Georgia pelagic ecosystem is determined largely by changes in zooplankton community composition and its impact on phytoplankton dynamics.

INDEX TERMS: 1615 Global Change: Biogeochemical processes (4805); 4207 Oceanography: General: Arctic and Antarctic oceanography; 4215 Oceanography: General: Climate and interannual variability (3309); 4815 Oceanography: Biological and Chemical: Ecosystems, structure and dynamics; 4842 Oceanography: Biological and Chemical: Modeling; *KEYWORDS:* interannual variability, Southern Ocean, pelagic ecosystem, biogeochemistry, phytoplankton, grazing control

Citation: Priddle, J., M. J. Whitehouse, P. Ward, R. S. Shreeve, A. S. Brierley, A. Atkinson, J. L. Watkins, M. A. Brandon, and G. C. Cripps, Biogeochemistry of a Southern Ocean plankton ecosystem: Using natural variability in community composition to study the role of metazooplankton in carbon and nitrogen cycles, *J. Geophys. Res.*, 108(C4), 8082, doi:10.1029/2000JC000425, 2003.

¹Now at Science Training and Education Partnership (STEP), Barrington, UK.

²Now at Gatty Marine Laboratory, University of St. Andrews, St. Andrews, Fife, UK.

³Now at Department of Earth Sciences, Open University, Milton Keynes, UK.

1. Introduction

[2] The island of South Georgia is situated in the northern Scotia Sea, in the Antarctic Circumpolar Current, down-current of the Antarctic Peninsula region (Figure 1). The island lies to the north of the seasonal ice zone in all but the most extreme winters. The South Georgia ecosystem is highly productive, in contrast with some of the surrounding areas of the ice-free Southern Ocean [Atkinson *et al.*, 2001]. The island system has been the subject of several biological

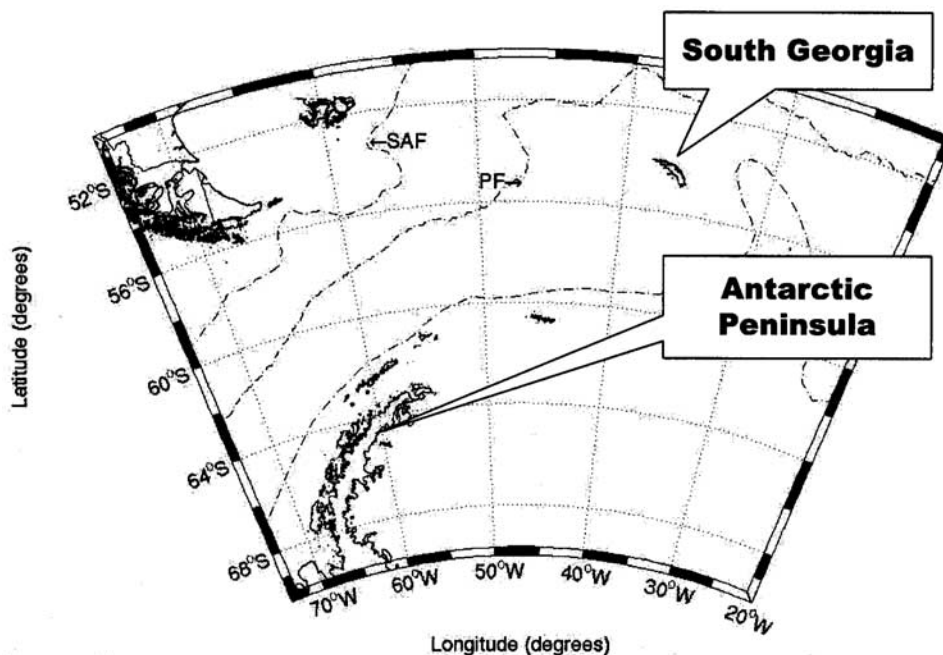


Figure 1. Location of South Georgia in the Scotia Sea (SW Atlantic sector of the Southern Ocean). SAF = Subantarctic Front, PF = Antarctic Polar Front.

oceanographic studies during the 20th century [see *Whitehouse et al.*, 1996]. The British Antarctic Survey (BAS) has recently undertaken a 5 year program of repeat surveys in two mesoscale sampling areas along the north coast of the island.

[3] Shipborne and satellite-derived ocean color measurements show that an extensive phytoplankton bloom develops around the island in November and persists until February or March [Atkinson *et al.*, 2001]. Chlorophyll biomass in dense diatom blooms may exceed 20 mg m^{-3} [Whitehouse *et al.*, 1993]. As with much of the Southern Ocean, it is rare that macronutrient (e.g., N, Si, and P) concentrations become reduced to limiting concentrations during the summer.

[4] Biomass of the metazoan zooplankton (metazooplankton) community around the island is high, both in comparison with most of the Southern Ocean and in a global context. Typical summer metazooplankton biomass is in the range $10\text{--}15 \text{ g dry mass (DM) m}^{-2}$ [Atkinson *et al.*, 1999], approximately $4\text{--}6 \text{ g C m}^{-2}$. Much of the metazooplankton biomass consists of two groups of crustaceans: copepods and euphausiids. Copepods are herbivorous and omnivorous, and range in size from small oithonids ca. 1 mm long to large calanoid species ca. 10 mm. The euphausiids comprise fewer species, of which Antarctic krill, *Euphausia superba*, is not only the main species but may also account for much of the overall metazooplankton biomass. Krill is an atypical zooplankton: it is comparatively large and long lived, has high energetic demands relative to its size [Quetin *et al.*, 1994] and a wide range of diet [Cripps *et al.*, 1999; Cripps and Atkinson, 2000].

[5] Modern acoustic techniques have been used to quantify the variability of krill biomass in the South Georgia pelagic ecosystem [Brierley *et al.*, 1999b]. Krill biomass in two mesoscale survey areas was highly variable, especially

at the eastern end of the island. Maximum mean biomass for single survey areas was $150 \text{ g fresh mass (FM) m}^{-2}$, while the minimum was 2 g FM m^{-2} [Brierley *et al.*, 1999b]. Interannual variability in krill abundance reflects changes in immigration to the local population from upcurrent areas [Brierley *et al.*, 1999a; Reid *et al.*, 1999]. The South Georgia krill population is thought not to be self-sustaining [Marr, 1962; Ward *et al.*, 1990; Watkins *et al.*, 1999]. The demonstrable consequences of periods of low krill abundance for the large populations of dependent predators suggest that these conditions are atypical. However, the exact spatial and temporal scales of these events are unclear, and krill abundance may recover from low values to more normal levels within a single summer season [Reid *et al.*, 1999].

[6] Here, we are concerned with plankton processes, especially those relating to biogeochemical cycles. Variability in nutrient drawdown, phytoplankton biomass and productivity have been documented [Whitehouse *et al.*, 1996]. The nitrogen cycle appears to be especially sensitive to variability. Recycling of nitrogen in the mixed layer (ML) is both rapid and large relative to phytoplankton demand. In some years, changes in the balance between regeneration and uptake may be large enough to cause a diurnal cycle in ML ammonium with an amplitude of $0.2\text{--}0.3 \text{ mmol m}^{-3}$. This diurnal variability appears to be present only in some years, and may be linked to high krill abundance [Priddle *et al.*, 1997].

[7] There are complex interactions within the metazooplankton. There appears to be an inverse relationship between the abundance of krill and that of the other major metazooplankton group, copepods [Atkinson *et al.*, 1999]. This relationship has been established on the basis both of comparison between large-scale surveys in different years, and smaller-scale spatial variability during individual sur-

Table 1. Initial Values for Nutrient Concentrations and Phytoplankton Biomass

Layer	Nitrate, mmol m ⁻³	Ammonium, mmol m ⁻³	Silicate, mmol m ⁻³	Phytoplankton Biomass	
				Chl, mg m ⁻³	Carbon, mmol m ⁻²
ML	20	1	30	2.5	625
Pycnocline	30	0 ^a	35	0 ^a	0 ^a

^aNote that pycnocline ammonium is always reset to zero so that the pycnocline layer acts as an ammonium sink. Phytoplankton does not cross into the pycnocline layer.

veys. One possible explanation for this relationship is carnivorous feeding by krill on copepods. *Atkinson and Snjyder* [1997] showed that krill removed copepods preferentially in laboratory feeding experiments. Furthermore, this preference appears to be directed at smaller species, such as oithonids, and it is these that show the greatest population increases in years when krill biomass is low. However, it is likely that other processes, such as competition for microplankton food, should be considered when examining the interaction between krill and copepods in the South Georgia system [*Atkinson et al.*, 1999].

[8] Whatever the underlying mechanism, changes in krill abundance around South Georgia may result in significant alteration in the composition of the metazooplankton community, even when overall biomass may vary little. This can be expected to have impacts on the pelagic biological carbon and nitrogen cycles [cf. *Loeb et al.*, 1997; *Perissinotto and Pakhomov*, 1998]. Here, we show the results from a simple model, which represents the major interactions between phytoplankton, copepods, and krill in the South Georgia system. Simulations of a “high krill-low copepod” zooplankton community and a “low krill-high copepod” community will be presented, and the output from these compared with the results of repeat surveys.

2. A Simple Plankton Interactions Model for the South Georgia Pelagic Ecosystem

[9] We have developed a model that includes dissolved inorganic N and Si pools, a single phytoplankton type, a generic copepod and krill (*E. superba*). In the model, copepods feed only on phytoplankton, whereas krill feed facultatively on phytoplankton and copepods. Where possible, parameter values are based on measured values from studies in the South Georgia ecosystem, including nutrient concentrations, plankton biomass and rate processes. The model is run iteratively with 1 hour time steps for 20 days. Some rates, phytoplankton growth, microbial grazing, copepod grazing, krill grazing, and krill predation, are determined by density-dependent functions which include stochastic variability. The model is implemented using MathCad 8 Professional (©MathSoft Inc.), and a full description is given in Appendix A.

2.1. Nutrients and Phytoplankton

[10] All of the biological interactions take place in a 50 m deep surface ML, which is underlain by a 50 m thick “pycnocline” layer which resupplies nutrients by vertical diffusion. Vertical mixing rate is set to 5 cm² s⁻¹, which is within the range of values typical for the South Georgia region. There is no other means to resupply nutrients to the ML. Starting nutrient concentrations and other parameter values are given in Tables 1 and 2. The pycnocline layer is

an ammonium sink, and concentration is reset to zero at each time step.

[11] Initial phytoplankton biomass is 2.5 mg chlorophyll m⁻³, which is an approximate mean value for the South Georgia ecosystem in early summer, and doubling time is 36 hours based on a wide range of Southern Ocean data [cf. *Priddle et al.*, 1997]. Growth rate varies diurnally, following a sine function (modified from the procedure used by *Priddle et al.* [1997]). Phytoplankton growth is modeled initially as carbon incorporation, which is available for grazing by copepods and krill. Nutrient uptake is determined from “gross” production, before biomass loss to grazers, for each time step. The proportion of nitrogen removed from the ML nitrate and ammonium pools is determined by an *f*-ratio, which varies inversely with ammonium concentration. The threshold ammonium concentration at which *f*-ratio decreases to zero is set at 1 mmol m⁻³, which accords with published observations for South Georgia and the Scotia Sea [*Glibert et al.*, 1982; *Owens et al.*, 1991] and elsewhere in the Southern Ocean [*Semeneh et al.*, 1998]. If insufficient nitrogen is available within one of the nitrogen pools, the corresponding carbon accumulation is subtracted from the carbon growth for that time step. The same also applies if the system runs out of silicate.

2.2. Copepods

[12] Copepods function only as grazers in the model, whereas the “real” copepod community also includes

Table 2. Fixed Parameter Values for the Nutrient-Phytoplankton Part of the Model

Parameter	Value
ML thickness	50 m
“Pycnocline” thickness	50 m
Mixing rate for vertical flux	1.8 m ² h ⁻¹ (=5 cm ² s ⁻¹)
Microbial N regeneration rate	0.015 mmol m ⁻³ h ^{-1a}
Phytoplankton mortality, proportion of phytoplankton C	0.0175 h ^{-1b}
Ammonium concentrations for <i>f</i> -ratio = 1 and <i>f</i> -ratio = 0	0 and 1 mmol m ^{-3c}
Phytoplankton doubling time	36 h ^d
Phytoplankton C:N molar ratio (Redfield)	6.625 ^e
Phytoplankton C:Si molar ratio	6.5 ^f

^aLower value from preliminary estimates (R. Sanders, personal communication, 2000).

^bDensity-dependent term includes all mortality except that from the grazers explicitly parameterized in the model. Much of this mortality could be ascribed to microbial heterotrophs. Value is derived empirically.

^cBased on relationships in the studies of *Glibert et al.* [1982] and *Owens et al.* [1991].

^dValue for growth rate used by *Priddle et al.* [1997].

^eRedfield proportions.

^fIn order to simulate a mixed phytoplankton population, this ratio is more carbon rich than the C:Si ratio of 4 determined for particulate matter during one survey near South Georgia [*Priddle et al.*, 1995].

Table 3. Comparison of Parameter Values for Copepods and Krill

Parameter	Final Units	Copepods	Krill
Initial biomass	g FM m ⁻²	variable	variable
Conversion fresh to dry mass	g DM m ⁻²	0.235 ^a	0.235 ^a
Conversion dry mass to carbon	mmol m ⁻²	0.45 ^b	0.576 ^a
Carbon-to-nitrogen ratio	mol mol ⁻¹	5 ^b	6 ^a
BMR, proportion body carbon	h ⁻¹	variable ^c	0.002 ^a
Maximum ingestion rate, proportion of BMR	h ⁻¹	2.5 ^b	5 ^{e,b}
Assimilation efficiency, proportion of ingested carbon	–	0.85 ^d	0.85 ^b
Growth conversion efficiency, proportion of nonrespired assimilated carbon (cf. Figure 2)	–	0.85 ^b	0.85 ^b
Maximum growth rate, proportion of body carbon	h ⁻¹	0.004 ^b	0.001 ^f
Instantaneous mortality, proportion of biomass	h ⁻¹	na	0.0006 ^g
Phytoplankton, threshold biomass	mg chl m ⁻³	0.1 ^b	0.1 ^b
Phytoplankton, optimal biomass	mg chl m ⁻³	6 ^b	5 ^b
Copepods, half-saturation biomass	g FM m ⁻²	na	25 ^b

^aValues derived from data compiled by *Whitehouse et al.* [1999].

^bCompilation of literature values and BAS unpublished data (see text).

^cHigher BMR used in some model runs to simulate smaller taxa with higher metabolic carbon turnover (see Table 4).

^dMaximum assimilation rate estimated from the study of *Schnack et al.* [1985].

^eMaximum assimilation rate from data in the study of *Pond et al.* [1995].

^f*Clarke and Morris* [1983].

^gValue determined empirically but consistent with uptake by endotherm higher predators [e.g., *Boyd and Croxall*, 1996].

omnivores and carnivores. Their biomass-specific feeding rate is determined as the product of a defined maximum ingestion rate (MIR) and a scaling factor termed “feeding efficiency” (Appendix A). Feeding efficiency increases above a threshold value until it reaches a maximum, and then declines at higher phytoplankton abundance. The phytoplankton abundance at which grazing saturates is 6 mg chl m⁻³, 2.4 times the initial biomass (Table 3). In the model runs discussed here, phytoplankton biomass does not exceed this saturating value, so that grazing increases as phytoplankton abundance increases, but more slowly at higher phytoplankton biomass.

[13] The MIR is defined as a multiple of the basal metabolic rate (BMR), in turn defined as a proportion of total body carbon required per hour (Table 3). There are no direct relationships between ingestion rate and BMR for copepods, but literature values of ingestion rate for the larger copepod species found around South Georgia fall in the range 1.5–27% body C d⁻¹ [*Atkinson et al.*, 1992, 1996], while values for BMR are 3–10% body C d⁻¹ [*Schnack et al.*, 1985]. For smaller taxa such as *Oithona*, the corresponding figures are 24% and up to 100% body C d⁻¹ [*Atkinson*, 1994; *Atkinson et al.*, 1992, 1996]. An average ratio of MIR = 2.5 × BMR is used in the model.

[14] The amount of carbon ingested by copepods at a single time step is the product of the current copepod biomass (time varying), the feeding efficiency (function of phytoplankton biomass), and the MIR (fixed model parameter). The fate of this carbon, and the associated nitrogen incorporation and excretion, is summarized in Figure 2, and resembles the scheme proposed by *Anderson* [1992]. If more carbon is ingested than can be incorporated by a specified maximum growth rate, this “surplus” carbon is egested along with unassimilated carbon. Nitrogen in the model is treated in a simplified version of the scheme of *Anderson* [1992]. Energy demand for both BMR and energetic costs of growth (*Anderson*’s “maintenance” and “growth respiration,” respectively) is assumed to derive solely from carbon; no dietary nitrogenous material is catabolized. Nitrogen from the phytoplankton food is

assimilated in the same ratio to carbon as that in the phytoplankton. Enough of the assimilated nitrogen to satisfy the stoichiometric requirements implied by carbon growth is then incorporated into body tissue. The remaining nitrogen is then excreted (Figure 2).

2.3. Krill

[15] As noted already, krill function in the model as both grazers of phytoplankton and predators on copepods. Their feeding dynamics are treated in the same way as those for copepods (Figure 2), except that there is a different model for density-dependent feeding on copepods, and there is an additional step to allocate carbon and nitrogen intake from phytoplankton and copepods (Appendix A). Values of constant parameters for krill are given Table 3.

[16] Krill feeding on copepods is modeled by Michaelis–Menten (Monod) kinetics. Again, the dependent variable is a feeding efficiency. Because we have no data on the density dependence of krill feeding on copepods, an optimal value for the half-saturation copepod biomass of 25 g FM m⁻² has been determined empirically over a range of model runs. An asymptotic function for krill feeding on copepods was selected because it was considered that raptorial feeding was unlikely to decline at high food abundance in the way commonly observed for filter feeding on phytoplankton [see *Price et al.*, 1988].

[17] The feeding efficiency of krill on phytoplankton is modeled by a parabolic function, as with copepods. Zero efficiency occurs at a phytoplankton chlorophyll biomass of 0.1 mg m⁻³, and grazing saturates at 5 mg m⁻³.

[18] At a single time step in the simulation, efficiencies for krill feeding on the two food sources are evaluated using the current biomasses, applying the biomass of phytoplankton after both microbial and copepod grazing within the time step. The copepod biomass used to compute feeding efficiency is that resulting from the previous time step. A preference index is then calculated on the basis of these two efficiencies (both are scaled 0–1), in a way exactly comparable to an *f*-ratio (Appendix A). The preference indices

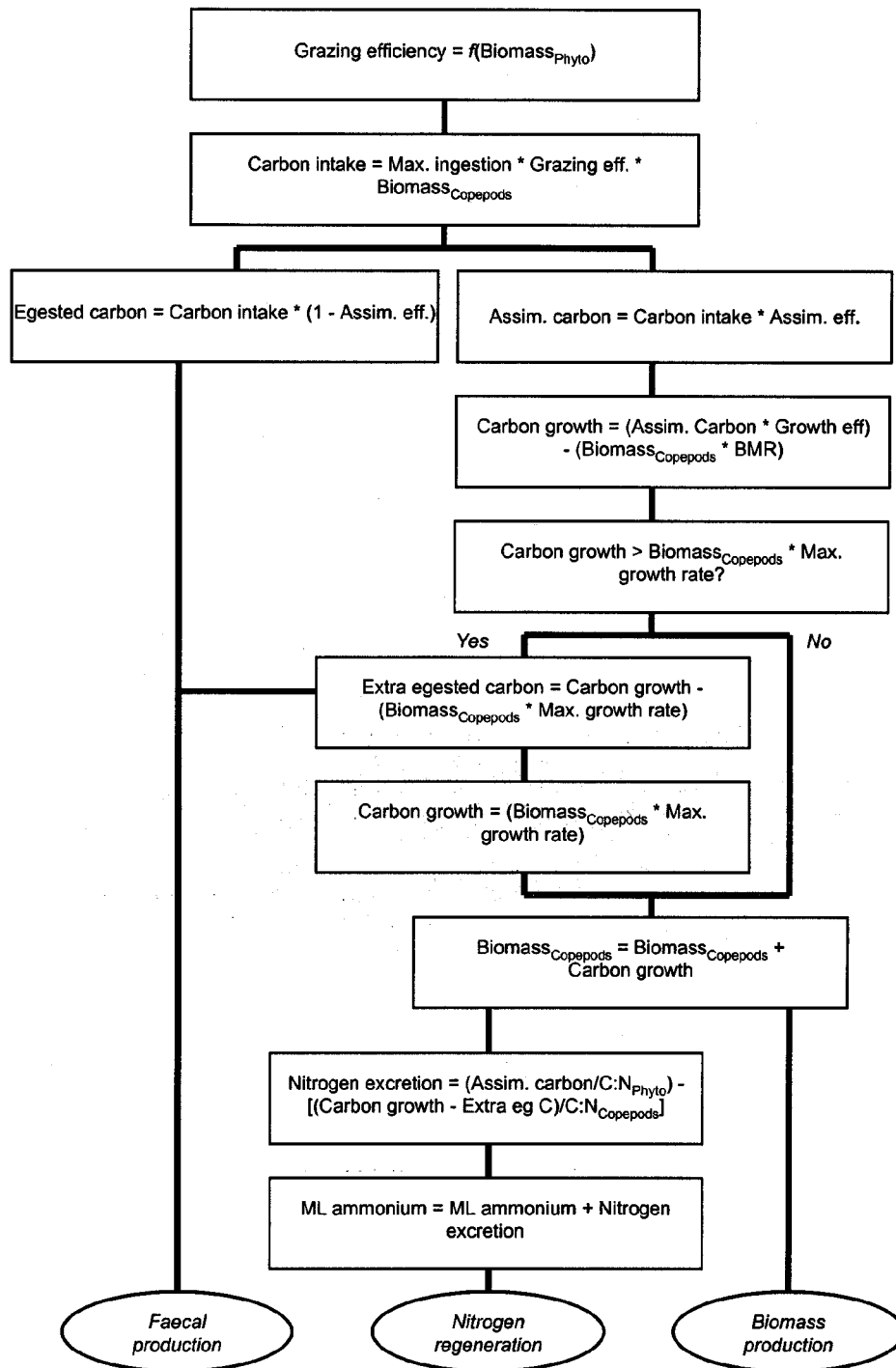


Figure 2. Simplified flow diagram summarizing the fate of carbon and nitrogen ingested by copepods in a single time step in the model.

for copepods and phytoplankton are used to scale the carbon ingestion from the respective food sources.

[19] Carbon and nitrogen uptake from the two food sources is evaluated separately at each time step, as an amount of phytoplankton ingested and an amount of copepods. Nitrogen assimilation is computed from the net growth of krill and the krill C:N ratio. Any residual assimilated nitrogen is excreted. For both krill and copepods, if net growth is ≤ 0 then excretion is zero and it is

assumed that carbohydrate and lipid are catabolized to fuel metabolism in excess of carbon assimilation within a time step.

[20] There is an explicit density-dependent mortality for krill. The value has been determined empirically as $0.0006 \times \text{biomass h}^{-1}$, or ca. 1.4% biomass per day. This would equate to a removal of $0.4 \text{ g FM m}^{-2} \text{ d}^{-1}$ for a krill biomass of 30 g FM m^{-2} (around the average biomass value from survey data in the study of *Brierley et al.* [1999b]).

Table 4. Parameter Values and Selected Output Data (Mean Plus Range) for 10 Simulations of Each of Two Scenarios for the South Georgia Plankton System^a

	"HK-LC"	"LK-HC"
Initial krill biomass (g FM m ⁻²)	27	8.5
Initial copepod biomass (g FM m ⁻²)	12	32
Copepods: BMR, proportion body C (h ⁻¹)	0.004	0.01
Final phytoplankton biomass (mmol C m ⁻²)	273 (254–297)	923 (815–1003)
Average gross primary production (mmol C m ⁻² d ⁻¹)	207 (190–222)	357 (336–380)
Final ML ammonium concentration (mmol N m ⁻³)	0.91 (0.87–0.96)	0.75 (0.69–0.81)
Average total zooplankton excretion (mmol N m ⁻² d ⁻¹)	3.63 (3.29–3.91)	17.0 (15.9–18.0)
Final ML nitrate concentration (mmol N m ⁻³)	19.2 (18.5–19.9)	16.0 (14.9–16.9)
Final ML silicate concentration (mmol Si m ⁻³)	20.5 (19.7–21.4)	12.1 (10.9–13.4)
Fecal production as proportion GPP (%)	4.7 (4.3–5.1)	20.1 (18.6–21.8)

^a"HK-LC" indicates "high krill-low copepod" scenario and "LK-HC" is "low krill-high copepod." In both cases, model runs are for 20 days with 1 hour time steps. All initial values and constants as Tables 1–3, unless stated otherwise.

Such removal is easily consistent with known predation pressure from endotherm higher predators alone [cf. *Boyd and Croxall*, 1996]. There is no corresponding separate mortality term for copepods; predation by krill is the only loss term for copepod biomass in the model.

3. Results of Two Model Simulations

[21] The model has been run initially using a variety of krill and copepod biomass, to optimize some of the empirical parameter values. Here we present the results of two simulations using biomass estimates for copepods and krill for two scenarios: a "high krill-low copepod" community and a "low krill-high copepod" community. The "high krill" data are average values from two field studies in 1995 and 1997 [see *Atkinson et al.*, 1999]. The designation "high krill" refers to their abundance relative to copepods; the krill biomass from these 2 years was not especially high for the South Georgia system [*Brierley et al.*, 1999b]. The "high copepod" data derive from a single study in 1994.

3.1. "High Krill-Low Copepod" Scenario

[22] For this simulation, initial krill biomass was set at 27 g FM m⁻² and copepod biomass at 12 g FM m⁻². Assuming that the krill–copepod interactions described by *Atkinson and Snýder* [1997] and *Atkinson et al.* [1999] would have resulted in a predominance of larger copepod taxa and stages, copepod BMR was set at 10% body C d⁻¹ [cf. *Schnack et al.*, 1985].

[23] Both krill and copepod biomass remained more or less stable over the course of the simulation, although both (especially copepods) were beginning to decline at the end in response to decreasing phytoplankton biomass. Phytoplankton biomass decreased by 56% in 20 days, to 1.1 mg chl m⁻³ (Table 4). Average gross primary productivity (GPP) was ca. 2.5 g C m⁻² d⁻¹. The final ammonium concentration in the ML was 0.9 mmol m⁻³. The total ammonium excretion by both copepods and krill averaged 3.6 mmol m⁻² d⁻¹, ca. 10% of average phytoplankton nitrogen demand based on GPP. *Atkinson and Whitehouse* [2000] found that excretion by krill may be up to 6 nmol mg⁻¹ DM h⁻¹. For the krill biomass in this simulation, this excretion rate would supply ca. 1 mmol m⁻² d⁻¹. Krill dominate the metazooplankton biomass in this scenario, but it is likely that biomass-specific excretion rate by copepods would be higher. Thus it appears that ammonium production

rate in this model scenario is realistic. The modest phytoplankton growth rate and low *f*-ratio (resulting from ammonium concentration at or near the threshold value), together with nitrate replenishment from the pycnocline layer, meant that ML nitrate concentration only fell very slightly, from 20 mmol m⁻³ at the start of the simulation to 19.2 mmol m⁻³ at the end. Similarly, ML silicate concentration changed from 30 mmol m⁻³ at the start to 20.5 mmol m⁻³ at the end. Production of fecal pellets by copepods and krill together equated to <5% of GPP (0.12 g C m⁻² d⁻¹), and krill and copepods produced similar amounts.

3.2. "Low Krill-High Copepod" Scenario

[24] For this simulation, initial krill biomass was reduced to 8.5 g FM m⁻² and copepod biomass increased to 32 g FM m⁻². The overall metazooplankton biomass is very similar in the two scenarios. Because the low abundance of krill would favor small copepod taxa [cf. *Atkinson et al.*, 1999], BMR was increased to 25% body C d⁻¹ to simulate the more energetic small taxa. Both copepod and krill biomass increased slightly in this scenario.

[25] Phytoplankton biomass increased by 48% during the simulation to 3.7 mg chl m⁻³, and GPP averaged 4.3 g C m⁻² d⁻¹ (Table 4). Final ML ammonium concentration was less than that in the "high krill" scenario, at 0.75 mmol m⁻³. On the other hand, excretion by zooplankton was higher, averaging 17.0 mmol m⁻² d⁻¹, ca. 30% of phytoplankton nitrogen demand. This apparent mismatch between lower ML ammonium and higher excretion rates arose from a combination of factors. Uptake of ammonium by phytoplankton was high in direct relationship to the higher primary production. Meanwhile, production of ammonium by metazooplankton was also high. Copepods dominate the metazooplankton biomass and have high metabolic rates, while krill have higher mass-specific excretion in this scenario because of greater surplus nitrogen in the diets of N-rich copepods than N-deplete phytoplankton. Because ammonium concentration was lower overall, *f*-ratio did not fall below 0.25, resulting in increased nitrate draw-down. Final ML nitrate concentration was 16.0 mmol m⁻³, and final ML silicate decreased to 12.1 mmol m⁻³. A higher proportion of primary production, ca. 20%, was converted to fecal pellet production and overall detrital carbon production was greatly increased (0.86 g C m⁻² d⁻¹). In absolute terms, the production of copepod fecal pellets was about 3 times that in the previous scenario, whereas

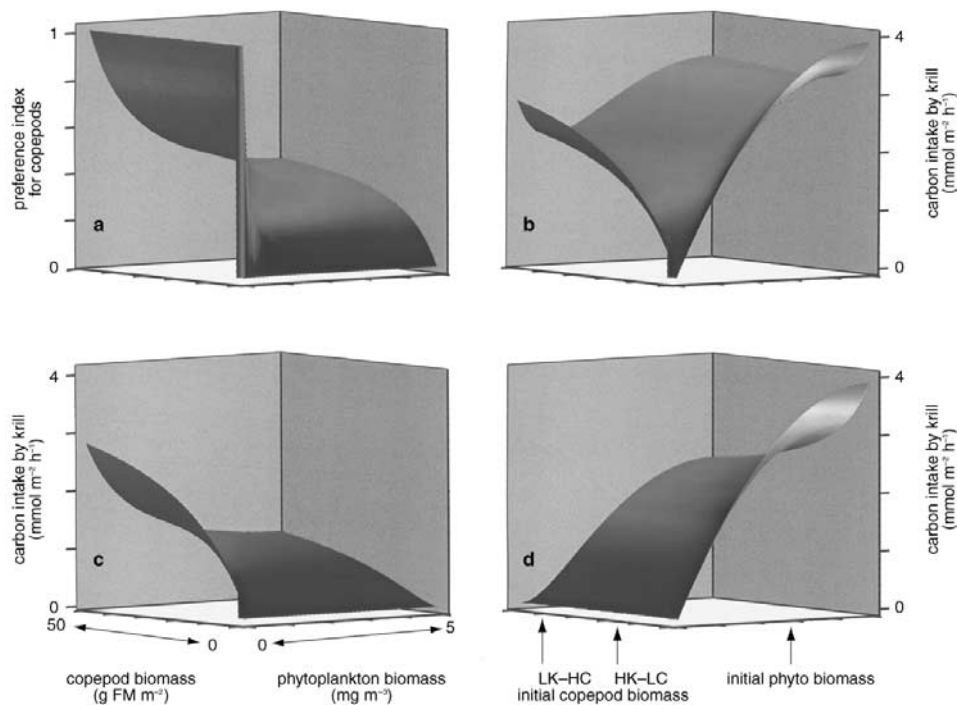


Figure 3. Visualization of the effects of feeding preference on the carbon intake of krill with varying biomass of copepods and phytoplankton. The x and y axes of these isometric plots are the biomass of the two food items and are keyed on panel (c). Panel (a) shows the preference index for krill feeding on copepods (see Appendix A for a description of the index). An index of 1 indicates that all of the diet is copepods, while an index of 0 indicates that krill feed exclusively on phytoplankton. Panel (b) shows the total carbon intake by a krill biomass of 30 g FM m^{-2} , feeding on various combinations of copepod and phytoplankton biomass. Panels (c) and (d) show the contributions of copepods and phytoplankton, respectively, to the overall carbon intake shown in panel (b). The functional relationships between feeding efficiency (see Appendix A) and prey biomass are apparent on panels (c) and (d) when the alternate prey item has zero biomass. Initial prey biomass for the two model scenarios (see text) is keyed on panel (d) (“HK-LC” is “high krill-low copepod” and “LK-HC” is “low krill-high copepod”). Panels (b)–(d) show the increasing impact of krill herbivory on phytoplankton at low copepod biomass.

fecal pellet production by krill tended to be only slightly less.

3.3. Comparison of the Two Model Scenarios: Contrasts in the Behavior of the Metazooplankton

[26] It is clear that the major differences between the two model scenarios arise from the differential impact of the zooplankton community on phytoplankton, which in turn determines the levels of dissolved nutrients. Examination of the model suggests that there is a fine balance between phytoplankton production and removal by grazing. Metazooplankton biomass in the two scenarios is similar, but in one scenario the biomass is dominated by an omnivore (krill) while in the other an obligate herbivore (copepods) represents most of the biomass. The preference index for copepods ($PI_{copepods}$) (see Appendix A) was typically around 0.25 (predominantly herbivorous) in the krill-dominated scenario but 0.45 (omnivorous) in the copepod-dominated scenario. The different feeding ecology of krill in the two scenarios impinges on phytoplankton in contrasting ways. When krill biomass is high relative to copepods, krill acts as an effective herbivore and the total metazooplankton community is predominantly herbivorous. However, when copepod biomass is high relative to

krill, the omnivorous feeding by krill reduces both the contribution by krill to overall grazing impact and also the biomass, and thus grazing impact, of copepods. Figure 3 visualizes these interactions. The preference index for krill feeding on copepods tends to be <0.5 for all combinations of copepod and phytoplankton biomass except at very low phytoplankton biomass (Figure 3a). Carbon uptake by the krill is a function of both feeding efficiency (food biomass dependent) for the two food sources, and on feeding preference. Total carbon intake by the model krill is highest at a combination of high phytoplankton biomass and low copepod biomass, where feeding preference is shifted strongly to herbivory (Figures 3a and 3b). An increase in copepod biomass at the phytoplankton biomass used as the starting condition in the model simulations results in reduced carbon intake (Figure 3b). Hence feeding preference is shifted toward omnivory but feeding efficiency on copepods is insufficient to make up the shortfall in carbon intake from phytoplankton (Figures 3c and 3d). Note that the figure is based on a notional and constant krill biomass of 30 g FM m^{-2} . The lower krill biomass used for the LK-HC scenario would reinforce the decreased grazing pressure on phytoplankton (Figures 3b and 3d).

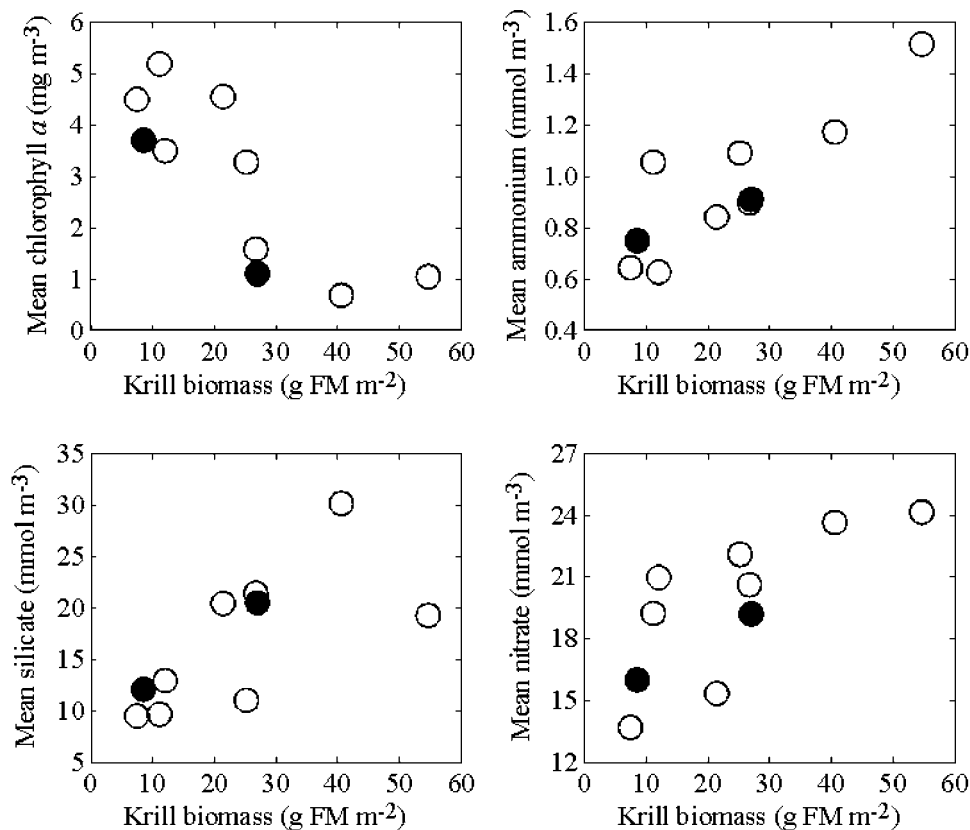


Figure 4. Plots of chlorophyll biomass and nutrient concentrations versus krill biomass (mean values from mesoscale acoustic surveys). Open symbols are mean values from observations from surveys (derived from all water bottle data in the top 50 m) and filled symbols are mean final values after 20 day simulations for each of the two zooplankton community scenarios described in the text.

[27] Thus krill in the “high krill-low copepod” scenario act as effective herbivores and reduce phytoplankton biomass, whereas in the low krill-high copepod scenario the impact of krill on phytoplankton is reduced not only because of their lower biomass but also because their feeding preference is shifted toward a more evenly omnivorous diet. We should emphasize that this behavior is a property of the model and its parameter values, a few of which are poorly constrained by measurements. The model is simply a tool for exploring interactions, rather than being designed to produce a faithful simulation of the South Georgia pelagic ecosystem. However, the model provides a useful pointer toward possible trophic interactions in the metazooplankton which influence phytoplankton production and nutrient cycling. We shall show later that the contrast between the two scenarios is also counterintuitive, given the likely carbon demands of the two metazooplankton groups. However, we first test our model output against field observations.

3.4. Comparison of Model and Field Data

[28] As noted already, the South Georgia region has been the site of a long series of extensive biological oceanographic studies. *Brierley et al.* [1999b] present data on krill abundance estimated using acoustic techniques for the period 1981–1998. However, during this period both equipment and data processing have changed. Here we restrict

our attention to a recent series of BAS cruises, for which acoustic estimates of krill biomass are of high quality, are consistently ascribed to krill rather than to other scatterers using multifrequency techniques (Δ MVBS) [*Madureira et al.*, 1993], and come from repeated, randomized survey designs. For all of these cruises, the two mesoscale survey grids (one to the northwest of the island, Western Core Box, and one to the northeast, Eastern Core Box) contain hydrographic stations, which provide estimates of phytoplankton (chlorophyll) biomass and nutrient fields. We have added data for a more recent cruise in this series, JR38 in 1999 [*Brierley and Goss*, 1999], together with data for the western survey region from an earlier cruise, JR06 in 1994 [*Brierley and Watkins*, 1996]. We have omitted the data for the ECB in 1998 (cruise JR28) because the very high mean krill abundance was generated by a small patch of exceptionally high biomass; we felt that comparison of this (high variance) biomass estimate with (time and space averaged) biogeochemical properties would be meaningless. Thus, we have eight averaged values for krill biomass (along-track mesoscale survey), chlorophyll biomass, ML ammonium, nitrate, and silicate (mean of all water bottle data over the top 50 m, typically 20–40 individual measurements per survey box).

[29] The data are presented in Figure 4. It is clear that the trends in the data are the same as seen in the two model scenarios: surveys with high krill biomass tended to have

low mean chlorophyll concentrations but higher ammonium, nitrate, and silicate concentrations. Given that the data are simple averages, the relationships appear remarkably robust.

[30] We can compare the field data with output from the model. The averaged final concentrations of chlorophyll and three nutrients derived from the model are the result of a 20 day simulation for each of two scenarios. By contrast, the observed data have an uncertain previous history, and will include the effects of mesoscale processes which have not been included in our model. However, average data from the two model scenarios, plotted against their respective krill biomass, coincide well with observation (Figure 4).

4. Discussion and Conclusion

[31] Observations from a series of surveys suggest that measurable differences in biogeochemical properties of the South Georgia pelagic ecosystem can be linked to large-scale (mesoscale up to interannual) variation in krill abundance. The output from the model suggests that these differences arise from the relative impact of krill and copepods on phytoplankton, whose growth in turn regulates nutrient cycles.

[32] We have suggested that the behavior of our model system and the observed natural system variability arise from changes in trophic structure in the metazooplankton, especially in the way krill shift from omnivorous to herbivorous diet as their biomass increases. This parallels earlier observations based on modeling studies which suggested that zooplankton community composition, and especially predation on grazers, is a major determinant of phytoplankton biomass and community structure [Steele and Frost, 1977; Steele and Henderson, 1992]. If interactions within the metazooplankton were insignificant, we would have an intuitive expectation that the metazooplankton community dominated by small copepods would have a larger carbon demand than the community dominated by larger krill. We can use physiological and biomass data for our zooplankton communities to estimate overall carbon demand. These calculations include other metazooplankton (some of which are predators) but exclude protist grazers, for which we lack adequate data. The carbon demand for the “high krill-low copepod” community would be ca. $0.35 \text{ g C m}^{-2} \text{ d}^{-1}$, while the “low krill-high copepod” community would have a significantly higher carbon demand of ca. $1.45 \text{ g C m}^{-2} \text{ d}^{-1}$. The main reason for the higher carbon demand for the “low krill-high copepod” community is the greater energetic requirements of copepods than krill. Although total biomass is similar in the two scenarios, the predominance of small taxa with greater metabolic rates [Peters and Downing, 1984; Atkinson, 1996] increases the carbon requirement. Thus, on physiological grounds, we would expect higher grazing impact, and thus lower phytoplankton biomass, when krill biomass is low and copepod biomass is high and dominated by small taxa, if we assume that the carbon demand is directed solely at phytoplankton.

[33] So, simple changes in carbon demand do not explain changes in phytoplankton dynamics. Clearly, the impact of krill in the system is to shift part of the carbon demand of the metazooplankton community away from direct impact on phytoplankton to impact on part of the zooplankton. The model suggests that the observed variability in biogeochem-

ical cycles reflects quite subtle differences in grazing impact by contrasting metazooplankton communities. In the real ecosystem, parallel effects are likely to exist, but their temporal evolution is undoubtedly more complex.

[34] We have used natural changes in community composition to explore the role of metazooplankton in determining the character of biogeochemical cycles in a pelagic ecosystem. Both a simple model and field observations show that changes in metazooplankton community composition impinge on phytoplankton biomass and production, on nutrient drawdown and on nitrogen recycling. The model suggests further differences, especially in the production of detrital material, for which we have no direct supporting evidence. Multiyear data from this pelagic ecosystem provide a useful test bed for exploring key interactions and feedbacks in the cycles of carbon and other elements. In particular, the analysis may provide a means of improving our ability to predict the effects of community shifts arising from long-term secular change.

Appendix A: Model Description

[35] The model is iterative, and evaluates state and rate variables at regular time steps. The ordering of calculations in the following description is that implemented in the model for a single time step. As a result, this section can be viewed as an informal flowchart for the model as a whole. Stochasticity is introduced to five calculations in order to highlight any predominant feedbacks in the dynamics of the system. In all cases, a random number has been calculated from the uniform distribution function in MathCad, and this is used as a scaling factor. In the description below, the convention $Rnd(x_1, x_2)$ is used to denote a random number selected from a uniform distribution with the limits $x_1 \leq Rnd \leq x_2$.

A1. Compute New Phytoplankton Biomass and Growth Increment

[36] Phytoplankton growth is assumed to be exponential, with a constant intrinsic doubling time. This growth rate equation is modified by a sine function scaling factor, which varies growth rate according to the time of day, T . Growth is also varied stochastically. The standard expression for exponential growth is

$$P_T = P_{(T-t)} \exp(k \cdot t)$$

where P_T and $P_{(T-t)}$ are the phytoplankton biomass at times T and $(T - t)$, respectively, and k is a constant related to growth rate. The exponent can be made to vary with time of day, so that growth rate is zero at midnight, and twice the nominal value at midday. This is a crude simulation of the light dependence of phytoplankton growth, used by Priddle *et al.* [1997]. A diurnally varying scaling factor is calculated by

$$phase = \left(1 + \sin \left(T \cdot \frac{2\pi}{24} + 1.5\pi \right) \right)$$

Stochastic variability is also included, so that

$$P_T = P_{(T-t)} \exp(k \cdot phase \cdot Rnd(0.75, 1.25) \cdot t)$$

Growth increment, used to compute nutrient uptake, is given by $\delta P_T = P_T - P_{(T-t)}$. Note that $P_{(T-t)}$ is final phytoplankton biomass from the preceding time step after grazing and other losses (during that time step).

A2. Compute f -Ratio

[37] The share of phytoplankton nitrogen nutrition between ammonium and nitrate at a given time step is determined by ammonium concentration.

$$f\text{-ratio} = 1 - \frac{[NH_4]_{ML}}{[NH_4]_{threshold}}$$

where $[NH_4]_{ML}$ is the ML ammonium concentration, and $[NH_4]_{threshold}$ is the ammonium concentration above which f -ratio is zero. These special conditions apply

$$f\text{-ratio} = 0 \text{ when } [NH_4]_{ML} > [NH_4]_{threshold}$$

$$f\text{-ratio} = 0 \text{ when } [NO_3]_{ML} < 0.1 \text{ mmol m}^{-3}$$

A3. Compute Nutrient Uptake by Phytoplankton

[38] Nutrient uptake is calculated from the growth increment for phytoplankton (note that this is before any grazing) and stoichiometric C:N and C:Si. For nitrogen, the f -ratio calculated previously defines the allocation of nitrogen uptake between the nitrate and ammonium pools.

$$\delta Si(OH)_4 = \delta P / C / Si$$

$$\delta NO_3 = \delta P \cdot f\text{-ratio} / C : N$$

$$\delta NH_4 = \delta P \cdot (1 - f\text{-ratio}) / C : N$$

[39] There are no nutrient uptake kinetics in the model. However, if the amount of nutrient available is insufficient for the (carbon) growth increment, growth is reduced. For silicate, insufficient nutrient resets the carbon growth for the time step to zero: phytoplankton do not grow if there is insufficient silicate. For the two nitrogenous nutrients, carbon growth is reduced by the amount sustained by that nutrient-limited phytoplankton growth can proceed if one of the two nutrients is present in an adequate quantity.

[40] In the model runs presented in this paper, nutrients never become limiting for growth, either in the sense discussed here (near-total removal of a nutrient) or in the sense of more classical nutrient kinetics in which the concentration of nutrient(s) determines growth rate.

[41] There is a single phytoplankton type, with a fixed C:N:Si stoichiometry. Given the short model runs, we have not implemented any shift in phytoplankton community, and thus change in nutrient requirement. Specifically, the C:Si uptake ratio is typical of the mixed phytoplankton assemblage seen at South Georgia during the summer, and includes the silicon demand of both nondiatom taxa and diatoms with a typically low C:Si ratio (≈ 4) [Priddle et al., 1995].

A4. Copepod Feeding and Metabolism

[42] In this model, all copepods are herbivorous. The total amount of carbon ingested from a given food source is defined as the product of the biomass of copepods, the MIR, and the feeding efficiency on the food source. MIR is a

linear function of the BMR (see Table 2). The feeding efficiency is in turn defined by the biomass of the food source.

[43] Feeding on phytoplankton is modeled by a parabolic (quadratic) function [cf. Mullin, 1963; Carlotti et al., 2000]. This belongs to the Holling type 2 family of relationships, in which feeding efficiency increases initially with food biomass until an asymptote value is reached, after which efficiency decreases. A generalized quadratic model of the form

$$y = a_0 + a_1x + a_2x^2$$

can be rewritten in terms of the values of the vertex (x_1, y_1) , thus

$$(y - y_1) = (x - x_1)^2$$

[44] For the relation between feeding efficiency, E_p , and phytoplankton biomass, P , we define two points on the parabola: the threshold biomass, P_{th} , at which efficiency is zero, and the optimal biomass, P_{opt} , at which efficiency = 1. Then for a given phytoplankton biomass P , the feeding efficiency is given by

$$E_p = 1 + \frac{-1 \cdot (P - P_{opt})^2}{(P_{th} - P_{opt})^2}$$

The value of E_p varies between 0 and 1 (negative values are set to zero in the model). It simulates a feeding mechanism where feeding on low biomass of a food source increases rapidly as food supply increases, then gradually approaches an asymptote value. At food biomass above the asymptote value, feeding efficiency declines, mimicking saturation and inhibition in filter feeders.

[45] The carbon flux (C_{ingest}) to the copepod population (carbon biomass = $B_{copepod}$) at a given time step is given by

$$C_{ingest} = B_{copepod} \cdot MIR \cdot E_p \cdot Rnd(0.5, 1.5)$$

where MIR is maximum ingestion rate, which is in turn scaled to BMR expressed as a proportion of body carbon metabolized per unit time. Ingested carbon is set to zero if the amount calculated in the model exceeds the phytoplankton carbon biomass. Note that stochasticity is included.

[46] The fate of ingested carbon has been summarized in Figure 2. A proportion of the ingested carbon is assimilated. Any of the carbon assimilated can be devoted to growth (with a specified conversion efficiency), up to a defined maximum growth rate. Any surplus carbon is egested, as is the carbon that is not assimilated. Assuming that there is sufficient phytoplankton carbon to support the modeled ingestion, carbon growth is given by

$$G_{copepod} = e_{growth} \cdot ((C_{ingest} \cdot AR) - (BMR \cdot B_{copepod}))$$

when $G_{copepod} \leq G_{max}$. If $G_{copepod} > G_{max}$, $G_{copepod} \rightarrow G_{max}$. The parameter e_{growth} is a growth conversion efficiency, and AR is assimilation efficiency. Note that $G_{copepod}$ will be

negative if the assimilated carbon is insufficient to fuel BMR.

[47] The carbon egested is calculated from the difference between the ingested carbon and that used for growth:

$$C_{egest} = C_{ingest} - G_{copepod}$$

[48] Excretion is calculated from stoichiometric relationships for both the C:N ratio of the ingested food, and that for the new copepod tissue. Excretion is described by

$$Ex_{copepod} = \frac{C_{assim,phyto}}{C : N_{phyto}} - \frac{G_{copepod}}{C : N_{copepod}}$$

where $C_{assim,phyto}$ is the phytoplankton carbon assimilated, after allowing for any extra egestion to “dump” carbon surplus to maximum growth rate. All assimilated nitrogen which is not used for growth is excreted.

[49] There is no independent mortality term for copepods in the model; all loss of copepod biomass is through predation by krill.

A5. Adjust Phytoplankton Biomass for Copepod Grazing

[50] Within the time step, a new (ungrazed) phytoplankton biomass has been calculated, and used to compute nutrient drawdown in the ML. Copepod grazing reduces phytoplankton biomass, and this reduced biomass is calculated before krill feeding is computed.

$$P^* = P - C_{ingest}$$

If this calculation results in negative phytoplankton biomass, this is reset to a small positive value.

A6. Krill Feeding and Metabolism

[51] In the model, krill feed on phytoplankton and copepods. Feeding on phytoplankton is modeled in the same way as for copepods feeding herbivorously, although parameter values differ slightly (see Table 2).

[52] Krill feeding efficiency on copepods is related to copepod biomass by a hyperbolic Michaelis–Menten model. This suggests that feeding efficiency is zero at zero prey abundance, increases rapidly and then gradually approaches an asymptote value. The shape of such a curve is defined by the maximum value of the dependent variable (here feeding efficiency, where $E_{max} = 1$) and the half saturation constant, the value of the independent variable where the dependent variable is half of the asymptote value. Thus for efficiency of krill feeding on copepods of biomass $B_{copepod}$

$$E_c = \frac{B_{copepod}}{(B_{copepod} + C_{half-sat})}$$

[53] Because krill consume food from two sources, the model needs to allocate carbon uptake between the two. Feeding efficiency on both phytoplankton and copepods is scaled between 0 and 1, and this can be used to calculate a preference index under a range of different biomass for each prey item. For krill feeding on phytoplankton, the preference index is calculated as

$$PI_p = \frac{E_p}{E_c + E_p}$$

The corresponding index for krill feeding on copepods is $(1 - PI_p)$. This can now be used to determine the carbon ingested from the two food sources. Again, for phytoplankton

$$C_{ingest,p} = B_{krill} \cdot MIR \cdot E_p \cdot PI_p \cdot Rnd(0.5, 1.5)$$

As before, there is a stochastic element in the calculation. A large value of the preference index will mean that the value of $C_{ingest,p}$ will approach the value calculated if krill feed on phytoplankton alone.

[54] Similarly, carbon ingested from copepods is calculated (again with the same stochastic scaling). In either case, if the prey biomass is insufficient to sustain consumption, carbon ingested from that source is set to zero.

[55] The fates of ingested carbon and nitrogen are calculated in a similar way to that for copepods feeding on a single food source. However, it is necessary to retain a “memory” of the relative amounts of each prey type. This is for two reasons. First, because any assimilated carbon, which exceeds the requirements for growth, will be egested, the egested carbon will derive from each food source in the same proportion as that in which it was ingested. Second, the two food sources differ in their C:N stoichiometry, and consequently excretion of nitrogen (relative to assimilated carbon) will depend on the amount of each food source ingested.

[56] Carbon growth of krill is described by

$$G_{krill} = e_{growth} \cdot (((C_{ingest,p} + C_{ingest,c}) \cdot AR) - (BMR \cdot B_{krill}))$$

Again, if $G_{krill} > G_{max,k}$, $G_{krill} \rightarrow G_{max,k}$ and “surplus” carbon is egested. This surplus carbon is partitioned between phytoplankton- and copepod-derived carbon in proportion to the division of total food ingested between the two food sources. Note that this is not the same as the feeding preference index.

[57] The carbon egested is calculated from the difference between the ingested carbon and that used for growth:

$$C_{egest} = C_{ingest} - G_{krill}$$

[58] For excretion, the nitrogen ration from each food source needs to be evaluated separately. For phytoplankton, the nitrogen assimilated can be calculated as

$$N_p = \frac{C_{assim,p}}{C : N_p}$$

where, again, $C_{assim,p}$ is the net phytoplankton carbon assimilated by krill. Similarly

$$N_c = \frac{C_{assim,c}}{C : N_c}$$

Excretion by krill is then calculated by

$$Ex_{krill} = N_p + N_c - \frac{G_{krill}}{C : N_{krill}}$$

If net growth of krill is zero, excretion is also zero.

A7. Compute Final Biomass Changes

[59] Phytoplankton biomass was already reduced by copepod grazing, prior to the calculations for krill. The

remaining losses from the phytoplankton are grazing by krill and a biomass-specific mortality term M_p that will include, among other things, grazing by microbial plankton.

$$B_{phyto} \rightarrow (B_{phyto} - C_{ingest,p,k}) \cdot (1 - (M_p \cdot Rnd(0.75, 1.25)))$$

Copepod mortality in the model is due solely to predation by krill, so that the copepod biomass at the end of the time step is the product of the biomass in the previous time step, the growth in the time step (which can be negative), and loss through predation

$$B_{copepod} \rightarrow B_{copepod} + G_{copepod} - C_{ingest,c}$$

For krill, there is a small density-dependent mortality term, M_k

$$B_{krill} \rightarrow (B_{krill} + G_{krill} \cdot (1 - M_k))$$

A8. Compute Changes in Nutrient Concentrations in ML and Pycnocline

[60] Changes in nutrient concentration are controlled by uptake (and production for ammonium) in the ML and exchange between the ML and the underlying “pycnocline.” Uptake of silicate, nitrate, and ammonium by phytoplankton have already been calculated, as have ammonium production by copepod and krill excretion. A fixed value for microbial ammonium production is assumed.

$$Si(OH)_{4ML} \rightarrow Si(OH)_{4ML} - \delta Si(OH)_4$$

$$NO_{3ML} \rightarrow NO_{3ML} - \delta NO_3$$

$$NH_{4ML} \rightarrow NH_{4ML} - \delta NH_4 + Ex_{copepod} + Ex_{krill} + Ex_{microb}$$

[61] The physics of the model are very simple. It comprises two slabs, of thicknesses h_{ML} and h_{pycno} . Exchange between them is governed by the gradient in nutrient concentration and the mixing rate. Using silicate as an example, the gradient is given by

$$\Delta Si(OH)_4 = \frac{[Si(OH)_4]_{pycno} - [Si(OH)_4]_{ML}}{0.5 \cdot (h_{pycno} + h_{ML})}$$

Vertical flux between the pycnocline and ML is the product of $\Delta Si(OH)_4$ and the mixing rate, K_v . Flux from the pycnocline to the ML is positive, adding nutrient to the ML pool and depleting the pycnocline. Thus

$$Si(OH)_{4ML} \rightarrow Si(OH)_{4ML} + \Delta Si(OH)_4 \cdot K_v$$

$$Si(OH)_{4pycno} \rightarrow Si(OH)_{4pycno} - \Delta Si(OH)_4 \cdot K_v$$

Calculation for nitrate is identical. For ammonium, the pycnocline is modeled as an ammonium sink. The vertical flux is always negative, because

$$\Delta NH_4 = \frac{0 - [NH_4]_{ML}}{0.5 \cdot (h_{pycno} + h_{ML})}$$

[62] **Acknowledgments.** We are grateful to Graham Savidge (Queen’s University, Belfast), Richard Sanders (Southampton Oceanography Centre), and Bettina Fach (Old Dominion University) for discussion on earlier versions of the plankton interaction model. We also thank Eileen Hoffman and an anonymous referee for their helpful comments on the original manuscript. Reprint requests should be sent to Mick Whitehouse at mjwh@bas.ac.uk.

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- M. A. Brandon, Department of Earth Sciences, Open University, Milton Keynes, MK7 6AA, UK.
- A. S. Brierley, Gatty Marine Laboratory, University of St. Andrews, St. Andrews, KY16 8LB, UK.
- J. Priddle, STEP, Scolt House, 59 High Street, Barrington, CB2 5QX, UK. (julian.priddle@ntlworld.com)