

Primary production and carbon uptake dynamics in the vicinity of South Georgia—balancing carbon fixation and removal

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ABSTRACT: Primary production was measured at a series of stations in austral summer 1996 in the vicinity of South Georgia. Five stations were occupied along a 700 km transect southeastwards towards the western tip of South Georgia. Three stations were located north of the Antarctic Polar Front (PF) with mean primary production of $0.41 \text{ g C m}^{-2} \text{ d}^{-1}$ compared to $0.54 \text{ g C m}^{-2} \text{ d}^{-1}$ for the stations south of the front. Three stations were in the shelf break and off-shelf region to the east of South Georgia where the lowest rates of primary production were recorded (mean $0.34 \text{ g C m}^{-2} \text{ d}^{-1}$). At a further 4 stations northwest of the island, primary production was significantly greater: 0.8 to $2.5 \text{ g C m}^{-2} \text{ d}^{-1}$ (mean $1.5 \text{ g C m}^{-2} \text{ d}^{-1}$). Photoinhibition was a marked feature of the production profiles, resulting in the underestimation of column production by 4 to 16%. An assessment is made of the primary production required to maintain a representative assemblage of metazooplankton around South Georgia composed of $30 \text{ g fresh mass (FM) m}^{-2}$ krill and 20 g FM m^{-2} copepods. The total C requirement of both groups at maximum growth rate is estimated as $0.93 \text{ g C m}^{-2} \text{ d}^{-1}$, with $0.54 \text{ g C m}^{-2} \text{ d}^{-1}$ required to maintain basal metabolism (i.e. for zero growth). Local primary production rates are well in excess of the C demands for basal metabolism by the metazooplankton, and likewise the highest regional values exceed those for maximum metazooplankton growth. It is also estimated that the krill biomass required to sustain higher predators during their breeding season could be supported by local production at plausible maximum krill growth rate. In particular, high primary production found in this study to the northwest of South Georgia appears to be adequate to sustain maximum growth rate by krill when their biomass is 30 g FM m^{-2} , when krill production will exceed predator removal. It is already well known that advection from higher latitudes is important in supplying energy to the South Georgia system. This study adds to the evidence that locally enhanced primary production is also important in supporting the local food web.

KEY WORDS: Primary production · South Georgia · Southern Ocean · Photoinhibition · Nutrients · Carbon flux

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INTRODUCTION

The Southern Ocean is a high nutrient low chlorophyll (HNLC) system, and its overall contribution to global oceanic carbon (C) fixation is only about one-half of that expected from its area (Longhurst et al.

1995, Priddle et al. 1998). A further feature of the Southern Ocean is the high degree of temporal and spatial heterogeneity in the distribution of phytoplankton biomass and production. High values (up to $30 \text{ mg chlorophyll a m}^{-3}$) are often associated with specific physical and hydrographical features. These include neritic areas (Moline & Prézelin 1997), the marginal ice-zone and polynyas (Smetacek et al. 1992, Smith & Gordon 1997), and fronts and other mesoscale features (Heywood & Priddle 1987, Savidge et al. 1995).

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In the Southern Ocean, enhanced phytoplankton biomass and production has been found consistently near several Antarctic and sub-Antarctic islands (Perissinotto et al. 2000, Blain et al. 2001), including South Georgia (Whitehouse et al. 1999, 2000). Satellite imagery further shows that high chl *a* concentrations can extend far downstream of the island (Atkinson et al. 2001). The increased phytoplankton production in this region is of major ecological significance, being associated with a productive food web and valuable commercial fisheries. This has been known for many years (Hardy & Gunther 1935) but the mechanisms for the high productivity have remained unclear (Atkinson et al. 2001). A central question is whether the higher predators at South Georgia depend mainly on locally enhanced primary production and fluxes through the food web, or rather on the Antarctic Circumpolar Current (ACC) in transporting food into their foraging areas. Recent interpretations (Murphy 1995, Murphy et al. 1998) have emphasised the role of advection, although Atkinson et al. (2001) also stressed the importance of enhanced local food web fluxes.

A better understanding of this problem requires a quantification of locally produced C from primary production. There have been surprisingly few estimates of primary production near South Georgia, and these are from a variety of approaches, some indirect, such as nutrient deficits (Whitehouse et al. 1996), nitrogen uptake (Owens et al. 1991) and oxygen flux measurements (Blight 1997). Only Pakhomov et al. (1997b) have made measurements of primary production with the ^{14}C method, and obtained regional coverage near South Georgia.

In this paper, we present primary production data obtained using the ^{14}C technique from the on-shelf, off-shelf and oceanic waters to the north of South Georgia. Firstly, the rates are compared with those from elsewhere in the Antarctic Zone of the Southern Ocean to examine the degree and areal extent of the enhanced productivity. Secondly, in the context of the local food web, we make simple comparisons between the primary production values and the measured consumption rates of higher trophic levels, to examine whether the elevated primary production at South Georgia might enhance food web fluxes sufficiently to support the higher predators.

STUDY SITE

South Georgia is an island with an extensive shelf, forming part of the Scotia Ridge, a mainly submarine island arc bounding the Scotia Sea to the north, east and south. It lies >200 km south of the Polar Front (PF), and is influenced directly by the Southern ACC Front,

and sometimes by high latitude waters that bring cold, silicate-rich waters to the north of the island (Trathan et al. 1997, Brandon et al. 1999, Whitehouse et al. 2000, Atkinson et al. 2001).

METHODS

Data presented here derive from cruise JR11 of RRS 'James Clark Ross' in January–February 1996. The cruise forms part of a long series of studies by the British Antarctic Survey (BAS) around South Georgia, and was the first of a 5 yr programme investigating interannual variability. The present investigation is based on data from 12 stations (Fig. 1). Five stations were occupied along a transect from north of the Maurice Ewing Bank at $47^{\circ} 59' \text{N}$, $43^{\circ} 16' \text{W}$ southeastwards across the PF towards the western tip of South Georgia; 4 were sampled from the shelf break and off-shelf regions to the northwest of South Georgia, while the remaining 3 stations were sampled to the northeast of the island.

Water samples were obtained from 10 l GoFlo bottles mounted on a rosette sampler, integral with a Neil Brown Mk IIIB CTD system. Samples to be used for the estimation of chlorophyll *a* (chl *a*) and nutrient concentrations were taken within approximately 1 h of local

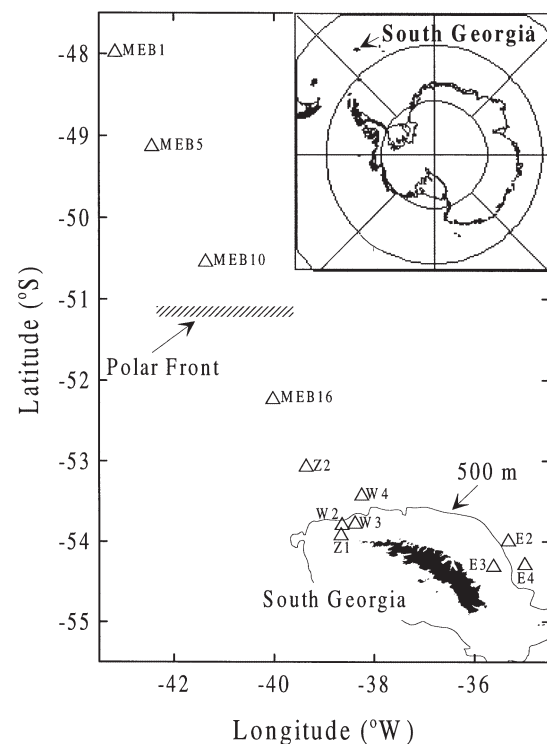


Fig. 1. Study area indicating the 12 primary production stations in the vicinity of South Georgia

dawn at depth intervals of between 10 and 20 m to around 100 m and then at selected intervals to 200 m. Chl *a* concentrations were determined fluorometrically following overnight extraction of the sample in 90% acetone in a refrigerator (Parsons et al. 1984) and nutrients were measured colorimetrically (Whitehouse 1997).

Samples to be used for the productivity estimates were collected from the surface mixed layer at a depth of approximately 40 m from the same CTD cast as the chl *a* and nutrient samples. Productivity was estimated using the ^{14}C technique and deck incubations (see Savidge & Gilpin 1999). Aliquots from the initial sample were dispensed into 60 ml polycarbonate bottles to each of which was added 10 μCi of $\text{NaH}^{14}\text{CO}_3$. Triplicate bottles were incubated on deck in shaded Perspex tubes at 97, 55, 33, 20, 14, 7, 5, 3, 2 and 1% of ambient irradiance, with the tubes cooled by flowing surface seawater. The samples were incubated for 24 h, and the flux of photosynthetically active radiation (PAR) was measured continuously by a Didcot DRP1 sensor mounted on the ship's foremast. At night, the tubes were covered in black polythene or the samples placed in a coldroom in a dark box to avoid interference from deck lighting. Following incubation, each sample was filtered under low vacuum through a 0.2 μm polycarbonate (Nuclepore) filter, fumed for 10 min over HCl, desiccated for several days and stored under cool, dark conditions. On return to the laboratory, 2.5 ml of Optiphase Hisafe III scintillation fluid was added to each filter and ^{14}C fixation established using an LKB scintillation counter. A triplicate set of dark incubations was carried out at each station and the average value was used to correct the light uptake data. Additions of ^{14}C were standardised for each experiment.

This method is based on accepted JGOFS protocols. The duration of the incubation leads to the estimation of net rather than gross production owing to the heterotrophic activity occurring in the bottles. However, in this study this was appropriate since the proportion of primary production available to higher trophic levels was required for subsequent budget calculations.

The corrected uptake data were integrated over the euphotic zone (1% light depth) to provide production values at the 12 stations. Irradiance profiles were not obtained during the cruise and so a comparison was made of PAR attenuation values derived from the empirical equations of Fenton

(1991), Fenton et al. (1994), Mitchell & Holm-Hansen (1991) and Dierssen et al. (2000). The relationship of Fenton (1991) for South Georgia inshore waters and deeper waters offshore to the north ($Kd_{\text{PAR}} = 0.0072[\text{chl } a \text{ concentration}] + 0.0756$; $r^2 = 0.795$, $n = 8$) was used to estimate the euphotic zone depth at each station. Table 1 indicates that the estimates derived using the relationships of the other workers were shallower by an average of 9% (Mitchell & Holm-Hansen 1991), deeper by an average of 27% (Fenton et al. 1994), or varied around the current euphotic depths with an average deviation of 15% (Dierssen et al. 2000).

RESULTS

Transect stations north of the PF

The PF was located between Stns MEB10 and MEB16 along the transect (Trathan et al. 2000). Surface temperature values at Stns MEB1, MEB5 and MEB10 ranged between 7.85°C at MEB1 and 5.61°C at MEB10 (Table 2). Density was controlled by temperature in the surface water and a shallow surface mixed layer, deepening from 20 m at MEB1 to 38 m at MEB10 (Table 2, Fig. 2) was evident at all 3 stations. Surface silicate (Si) concentrations were low, in the range 2 to 6 mmol m^{-3} , with nitrate (NO_3) concentrations of the order of 15 mmol m^{-3} . The low Si concentrations together with the physical properties characterise the presence of sub-Antarctic surface water (SAW) at these locations. Chl *a* concentrations in the surface

Table 1. Comparison of the 1% light depths estimated using the Kd_{PAR} vs chlorophyll relationships of Mitchell & Holm-Hansen (1991), Fenton et al. (1994) and Dierssen et al. (2000) with the 1% LDs used in the text as derived using data from Fenton (1991)

Stn	% deviation of estimated 1%LD from value derived using Fenton (1991)		
	Mitchell & Holm-Hansen (1991)	Fenton et al. (1994)	Dierssen et al. (2000)
MEB1	7.05	-29.81	-3.30
MEB5	7.55	-29.07	0.76
MEB10	7.12	-29.72	-2.74
MEB16	9.38	-26.43	11.36
Z2	5.95	-31.43	-15.45
Z1	10.58	-24.70	16.13
W4.1.N	16.05	-16.80	28.26
W3.1.S	11.25	-23.72	18.33
W2.1.S	17.30	-15.01	29.80
E2.1.N	5.33	-32.31	-25.60
E3.1.S	7.18	-29.62	-2.21
E4.1.N	5.26	-32.41	-26.97
Average ^a	9.17	26.75	15.08

^aCalculated ignoring the sign of the deviation

Table 2. Physical and biological characteristics of the productivity stations: position, surface temperature, depth of surface mixed layer (as defined by depth of initial $0.05\sigma_t$ change in density) and euphotic zone, typical mixed layer (ML) concentration of dissolved reactive silicate, nitrate, ammonium and chl *a*

Region	Stn	Latitude (°S)	Longitude (°W)	Surface temp (°C)	Mixed layer – ML (m)	Euphotic zone (m)	ML silicate (mmol m ⁻³)	ML nitrate (mmol m ⁻³)	ML ammonium (mmol m ⁻³)	ML chl <i>a</i> (mg m ⁻³)
Transect N of PF										
	MEB1	-47.96	-43.18	7.85	20	58	2.4	18.87	0.4	0.57
	MEB5	-49.11	-42.44	5.54	32	57	6.5	17.16	0.38	0.65
	MEB10	-50.52	-41.37	5.61	38	58	2.9	15.54	0.66	0.58
Transect S of PF										
	MEB16	-52.21	-40.02	3.68	55	56	9.5	18.7	0.69	0.96
	Z2	-53.05	-39.36	4.69	58	59	0.56	18.91	0.95	0.4
W shelf break										
	Z1	-53.90	-38.67	2.98	58	55	21.9	20.83	1.11	1.18
	W4	-53.40	-38.25	3.28	45	50	10.1	17.41	0.43	2.40
	W3	-53.75	-38.38	3.17	35	54	21.7	18.76	1.36	1.31
	W2	-53.77	-38.65	2.99	40	48	21.8		0.83	2.74
E shelf break										
	E2	-53.97	-35.33	1.94	60	59	30.0	25.79	1.22	0.31
	E3	-54.29	-35.62	2.30	50	58	25.3	21.73	1.61	0.59
	E4	-54.27	-35.00	1.91	60	59	31.9	24.69	0.6	0.30

mixed layer were typically 0.6 mg m^{-3} at each station (Table 2), with these concentrations extending to depths of between 60 and 100 m (Fig. 2). A mean value of primary production $0.41 \text{ g C m}^{-2} \text{ d}^{-1}$ was recorded for these transect stations (Fig. 3).

Transect stations south of the PF

At Stns MEB16 and Z2, the vertical temperature profile exhibited a distinct subsurface minimum (mean 0.71°C , Fig. 2) associated with the winter surface mixed water (Whitehouse et al. 1996). The density profile in the upper 80 m at the 2 stations essentially reflected the temperature profile with the principal surface mixed layer extending down to approximately 60 m (Fig. 2). At depths greater than 80 m, density increased monotonically, closely reflecting changes in salinity. Surface Si concentrations of approximately 10 mmol m^{-3} were recorded at MEB16 but a marked decrease to 0.56 mmol m^{-3} was recorded at Z2 (Table 2). The decrease was assumed to be indicative of active diatom growth at this location. The corresponding NO_3 concentrations increased slightly to 18.7 mmol m^{-3} south of the PF. There was a marked subsurface ammonium (NH_4) concentration maximum in the range 1 to 2 mmol m^{-3} , with corresponding surface concentrations between 0.4 and 1.0 mmol m^{-3} .

Chl *a* concentrations in the surface mixed layer were in the range 0.4 to 1.0 mg m^{-3} (Table 2). In contrast to transect stations to the north of the PF, the southern

stations had a pronounced subsurface chl *a* maximum (SCM) located some 10 m below the base of the surface mixed layer (Fig. 2) with concentrations at least double those observed in the surface layer. The presence of SCMs has been reported from the Southern Ocean (Yamaguchi et al. 1985, Whitehouse et al. 2000, Wright & van den Enden 2000) whereas Whitehouse et al. (1993) remarked specifically on the absence of SCMs in South Georgia waters during 3 summer surveys. The reasons for the presence or absence of SCM are not clear since there was no evidence of a more sharply defined pycnocline or of reduced vertical mixing at either station compared to other stations studied during the cruise. The depth of the euphotic zone was comparable to that of the mixed layer (Table 2) indicating that active phytoplankton growth was not occurring in the SCM and that it may have resulted from sedimentation. Subsurface ammonium maxima were generally located below the SCM, suggesting that they were generated by the remineralisation of organic matter sedimenting from the SCM. The mean rate of primary production recorded for these stations was $0.54 \text{ g C m}^{-2} \text{ d}^{-1}$, slightly higher than that to the north of the PF (Fig. 3).

Western shelf break area

At Stns W4, W3, W2 and Z1, a subsurface temperature minimum was present between 80 and 110 m, with temperatures in the range 0.24 to 0.41°C (Fig. 2). A surface mixed layer extending down to approxi-

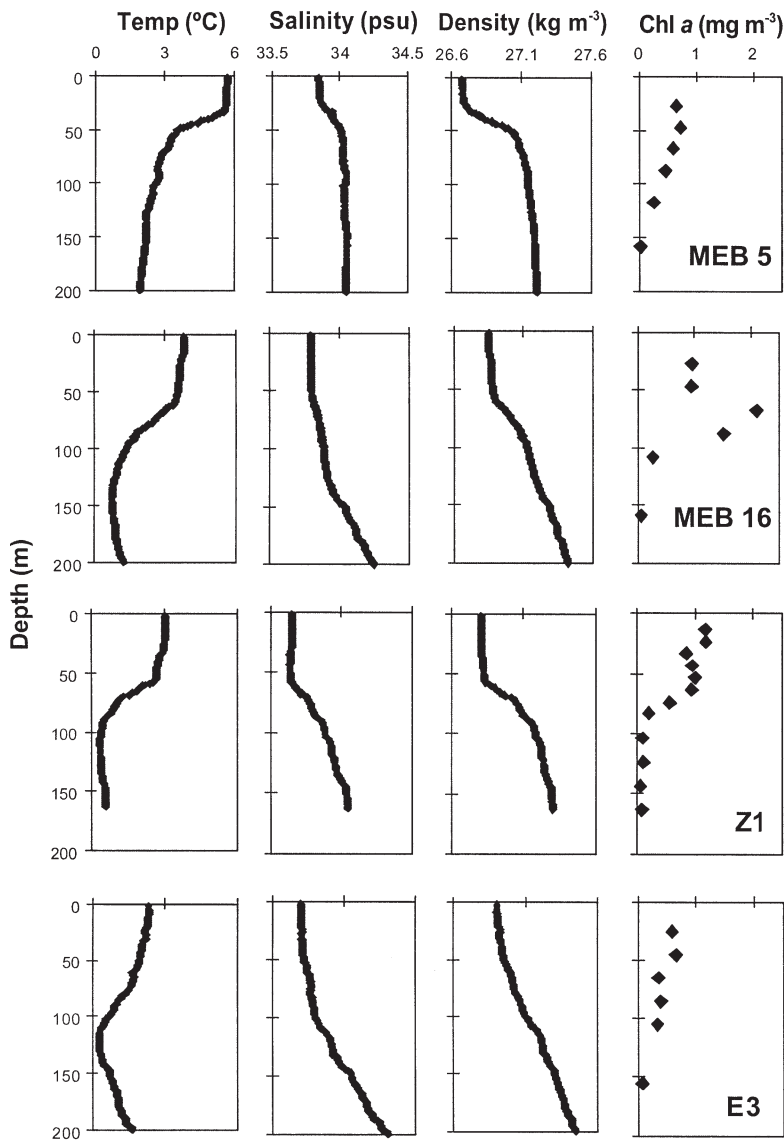


Fig. 2. Vertical distribution of potential temperature, salinity, potential density (σ_t) and chl *a* concentration at stations representative of the 4 regions described in this study

mately 30 m was present at all stations. Between approximately 30 and 60 m, a complex density structure was evident with a density gradient $>0.1\sigma_t$ units at the 3 W stations, although density increased by only $0.03\sigma_t$ units at Stn Z1 (Fig. 2).

Surface Si and NO_3 concentrations were high at the 4 stations at around 20 and 17 mmol m^{-3} , respectively, except at W4 where the Si concentration was 10 mmol m^{-3} (Table 2). NH_4 concentrations were maximal in the surface mixed layer and were generally in the range 1.0 to 1.5 mmol m^{-3} . At the majority of stations, the high NH_4 values extended well below the surface mixed layer, suggesting active remineralisation of

organic material sedimenting out of the surface layer. The highest surface chl *a* concentrations of the cruise were all from this region, with values in the range 1.18 to 2.74 mg m^{-3} (Table 2). Concentrations either decreased steadily with depth from the surface to 100–150 m, as observed at Stns W4 and W3, or decreased rapidly below 60 m, as at W2 and Z1. Primary production in this region was the highest recorded during the cruise, with a mean value of 1.52 $\text{g C m}^{-2} \text{d}^{-1}$ (Fig. 3).

Eastern shelf break area

Although a marked subsurface temperature minimum averaging 0.07°C was present at Stns E2, E3 and E4, the density profile reflected the salinity profile, with a surface mixed layer extending down to approximately 40 m (Fig. 2). Surface Si concentrations at all 3 stations were in the range 25 to 32 mmol m^{-3} (Table 2) while NO_3 concentrations were in the range 20 to 25 mmol m^{-3} . NH_4 concentrations at E2 and E3 were high in the upper 100 m (1.0 to 1.6 mmol m^{-3}), decreasing to $<0.1 \text{mmol m}^{-3}$ at 200 m. A similar distribution was also evident at E4, although surface concentrations were lower with a mean of 0.6 mmol m^{-3} NH_4 . The generally high NH_4 concentrations in the surface layer at these stations suggest an excess of organic nitrogen remineralisation over NH_4 uptake in this horizon. Surface chl *a* concentrations, ranging between 0.3 and 0.6 mg m^{-3} (Table 2), were evenly distributed throughout the mixed layer, with no SCM evident. Beneath the mixed layer, chl *a* concentrations decreased steadily to depths between 100 and 150 m. Primary production was low, with a mean value of 0.34 $\text{g C m}^{-2} \text{d}^{-1}$ (Fig. 3).

Column production at the survey stations ranged from 0.18 to 2.48 $\text{g C m}^{-2} \text{d}^{-1}$, with the highest values being found in the western shelf break area and lowest values in the eastern shelf break (Fig. 3). The relationship between column production P ($\text{g C m}^{-2} \text{d}^{-1}$) and column chl *a* (mg m^{-2}) using all available station data was $p = 0.0113 \text{ chl } a, r^2 = 0.35, n = 11$. However, Stn MEB16 lay off the line of best-fit and its removal yielded an r^2 of 0.62; $p = 0.0139 \text{ chl } a$ (Fig. 4) suggest-

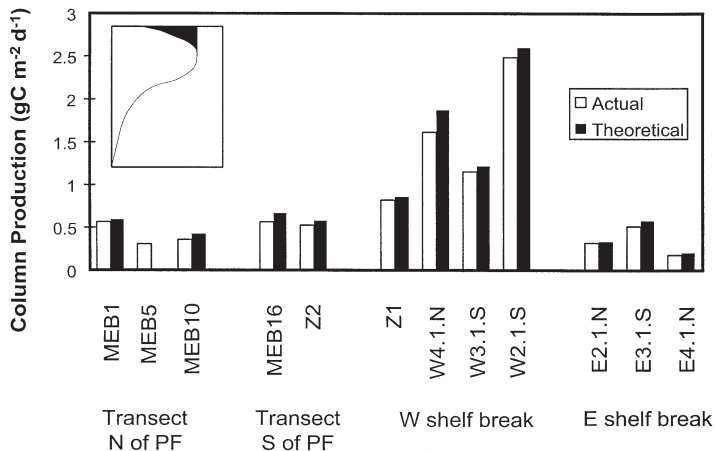


Fig. 3. Column production derived from actual data including photo-inhibition and from theoretical calculations using P_{max} and assuming no photoinhibition. Stations grouped for each region as discussed

ing that primary production was closely related to phytoplankton biomass. Similar conclusions were derived indirectly by Mathot et al. (1992) for samples taken from ACC water along meridional transects at 47°W and 49°W.

DISCUSSION

Primary production measurements in a regional context

The range of primary production measured during this survey encompasses all previous estimates for the region. Values from earlier studies, using a range of techniques, vary from 0.1 to 1.9 g C m⁻² d⁻¹ (Owens et al. 1991, Priddle et al. 1995, Blight 1997, Pakhomov et al. 1997b). The value of 30 to 40 g C m⁻² yr⁻¹ for annual production inferred by Whitehouse et al. (1996) from differences between winter and summer nutrient concentrations suggests that average primary production rates for the South Georgia zone tend to be at the lower end of the range of measured daily rates. However, their estimate should probably be taken as a minimum value as no additional nutrient input to the system was assumed during summer.

Only a limited number of direct estimates of primary production have been made previously in the water masses encountered during the present survey, making comparison difficult. The mean value recorded on the transect to the north of the PF (0.41 g C m⁻² d⁻¹) is higher than that re-calculated from Allanson et al. (1981) for January 1981 from the SAW for longitude 20° 24' E (0.13 g C m⁻² d⁻¹) assuming an 18 h irradiance day. Similarly, a lower value was derived from these authors for the ACC (0.09 g C m⁻² d⁻¹) compared to the

mean of 0.54 g C m⁻² d⁻¹ in the present study for the transect stations south of the PF. In contrast, the mean production derived by Mathot et al. (1992) from the ACC at 47° and 49°W (0.55 g C m⁻² d⁻¹) in December 1988 agreed closely with the corresponding value for the present study. However, samples taken from both ACC and Weddell Sea water from a 6°W transect in November 1992 (Jochem et al. 1995) gave consistently lower values in the range 0.2 to 0.3 g C m⁻² d⁻¹, highlighting the variability recorded for the region. Although Rönner et al. (1983) demonstrated daily production of the order of 1 g C m⁻² d⁻¹ in the Weddell-Scotia Confluence based on ¹⁵N uptake measurements, values obtained from open waters of the Scotia Sea were observed to decrease to 0.2–0.3 g C m⁻² d⁻¹ eastwards towards South Georgia. Comparable values in late summer quoted by El-Sayed

& Weber (1982) for the Scotia Sea were in the range 0.1 to 0.3 g C m⁻² d⁻¹, although these authors indicate that isolated high values may also be observed. From the present data set, it thus appears that production in the waters immediately adjacent to the South Georgia land-mass are generally higher than in the adjacent upstream and downstream open ocean waters. This is consistent with the elevated biomass observed both from ship-based studies and more recently by satellite ocean-colour measurements. Data from the SeaWiFS ocean colour sensor suggest that phytoplankton may be concentrated along the northern side of the island between December and March (Atkinson et al. 2001). Here the potential growing season is likely to be of the order of 4 mo with phytoplankton biomass commonly around 2 mg chl a m⁻³. This high phytoplankton productivity clearly has important implications for the

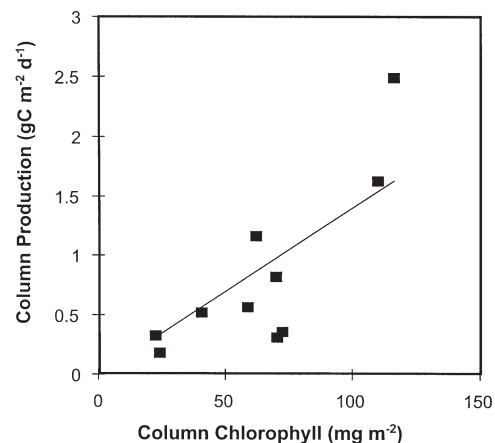


Fig. 4. Relationship between column production and column chl a concentration

higher trophic levels of the local pelagic ecosystem in the vicinity of South Georgia.

Photoinhibition

A marked and consistent feature of the ^{14}C uptake data was the demonstration of photoinhibition. Since the samples were incubated under ambient, thus variable, irradiance conditions, we have not derived values of the parameter β , defined as the slope of the photoinhibited portion of the $P:I$ curve (Platt et al. 1980). We have quantified the influence of photoinhibition on column production by comparing the actual experimental data with theoretical values calculated using the value of maximum production (P_{\max}) and assuming no photoinhibition. The reduction in column production ranged widely, from 3.9% at Stn MEB1 to 15.5% at Stn MEB10 (Fig. 3). These values lie within the range of inhibition of column production derived by Platt et al. (1990) from fundamental considerations.

Photoinhibition has frequently been observed in high latitude phytoplankton samples (e.g. Yamaguchi et al. 1985, Sakshaug & Holm-Hansen 1986, Smith et al. 1991, Dower et al. 1996, Moline & Prézelin 1997) and has generally been related to the magnitude of vertical mixing in the surface mixed layer inducing low light adaptation in the phytoplankton populations (Platt et al. 1982). It is possible that the degree of photoinhibition in the present observations has been enhanced by the extended incubation period to which the samples had been subject. However, the degree of photoinhibition in the sample incubated at 97% irradiance compared to P_{\max} ranged between 40 and 80%, similar to that recorded from other comparable high

latitude studies based on short-term constant irradiance incubations (Dower et al. 1996). The degree of photoinhibition was linearly related to ambient PAR ($r^2 = 0.86$; $n = 11$; $p < 0.001$ Fig. 5). A similar relationship was noted previously by Takahashi et al. (1971). Although photoinhibition experienced by the surface phytoplankton samples under constant irradiance may be severe, the overall influence on column production estimates is limited.

Primary production in relation to South Georgia food web fluxes

The mean daily production rate across all stations was $0.80 \text{ g C m}^{-2} \text{ d}^{-1}$ with highest rates to the northwest of South Georgia and lowest to the east. These values are fairly high for the Southern Ocean, but not in a global context. However, the South Georgia region supports a productive pelagic ecosystem and major fisheries (see Hardy & Gunther 1935, Everson 1984, Atkinson et al. 2001). Phytoplankton blooms north of South Georgia are often apparent from satellite data in spring and summer, and this may help to explain the high biomass (20 to $40 \text{ g fresh mass [FM] m}^{-2}$) of metazoan zooplankton (metazooplankton) typical of the region in summer (Atkinson et al. 2001). This in turn is assumed to support a high biomass of apex predators.

The high biomass of consumers in the South Georgia pelagic system has been known for a long time, but there is uncertainty over the relative importance of advection and local production in sustaining this (Marr 1962, Croxall et al. 1985, Trathan et al. 1995, Atkinson et al. 2001). This study has added to the sparse data currently available on primary production in this system, and allows an appraisal of whether the locally enhanced production is significant compared to consumer demands.

Carbon flux to grazers

The metazooplankton grazers comprise a variety of taxonomic groups, but copepods and euphausiids predominate in terms of biomass. The copepods are represented by a large number of species, whilst Antarctic krill, *Euphausia superba*, may contribute more than half of the metazooplankton biomass. Krill do not appear to breed around South Georgia (Marr 1962, Ward et al. 1990) and the population is maintained by advection of animals from breeding populations around the Antarctic Peninsula and Weddell-Scotia area (Marr 1962, Hofmann et al. 1998, Murphy et al. 1998). This recruitment process exhibits marked interannual variability, giving rise to significant

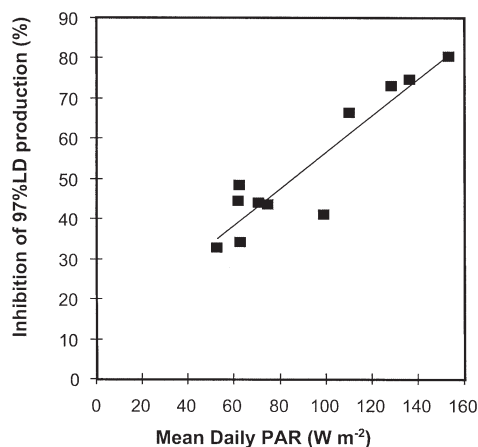


Fig. 5. Relationship between inhibition of carbon uptake for the sample incubated at 97% ambient irradiance and mean daily PAR

Table 3. Parameter values used to estimate carbon demand by krill and copepods in the South Georgia pelagic ecosystem (derived values are shown in bold)

Parameter or variable	Units	Krill	Copepods
Biomass, fresh mass	(g FM m ⁻²)	30	20
Convert fresh mass to dry mass (DM/FM)	–	0.235 ^a	0.235 ^a
Convert dry mass to carbon (C/DM)	–	0.4 ^a	0.45 ^b
Biomass, as carbon	(g C m ⁻²)	2.8	2.1
Assimilation efficiency	–	0.85 ^c	0.85 ^d
BMR (prop. body C)*	(d ⁻¹)	0.05 ^e	0.15 ^f
C required for BMR	(g C m ⁻² d ⁻¹)	0.17	0.37
Growth conversion efficiency	–	0.85 ^b	0.85 ^b
Maximum growth rate (prop. body C)	(d ⁻¹)	0.035 ^g	0.1 ^h
C required for growth	(g C m ⁻² d ⁻¹)	0.14	0.25
Total C requirement	(g C m ⁻² d ⁻¹)	0.31	0.62

^aValues derived from data compiled by Whitehouse et al. (1999)
^bCompilation of unpublished BAS data
^cMaximum assimilation rate estimated from Pond et al. (1995)
^dMaximum assimilation rate estimated from Schnack et al. (1985)
^eBased on C ration at low phytoplankton concentration near South Georgia (Pakhomov et al. 1997a)
^fAveraged value for a range of Antarctic copepod taxa (Schnack et al. 1985, Atkinson 1996)
^gBased on estimates of krill growth at South Georgia (Clarke & Morris 1983, Reid 2001)
^hMean of direct measurements on copepodite stages of 2 species (Shreeve & Ward 1998)
*Body C-ration for zero growth, expressed as proportion of body C per day

changes in the composition of the metazooplankton community. Krill and copepods also interact directly, either through competition for food or through predation (Atkinson et al. 1999). Evidence from three surveys indicates that total metazooplankton biomass at South Georgia varied only slightly between years (Atkinson et al. 1999), but krill biomass is known to vary 10-fold (Brierley et al. 1999). Here we estimate the C flux to a metazooplankton community, the composition of which represents the average values derived from several repeat surveys; krill biomass 30 g FM m⁻² (Brierley et al. 1999) and copepod biomass 20 g FM m⁻² (Pakhomov et al. 1997b, Atkinson et al. 1999, Ward & Shreeve 1999).

Measured values for physiological rates (Table 3) have been used to derive 2 values for C demand for this metazooplankton community—one for the maintenance of 'basal metabolism' alone (here defined as the C intake to balance respiration loss when growth is zero), and a second to sustain maximum growth rate. The C required to maintain the basal metabolic rate (BMR) of krill biomass of 30 g FM m⁻² (2.8 g C m⁻²) is estimated to be 0.17 g C m⁻² d⁻¹ with a further 0.14 g C m⁻² d⁻¹ required to support maximum growth. For a copepod biomass of 20 g FM m⁻² (2.1 g C m⁻²), BMR consumes 0.37 g C m⁻² d⁻¹ whilst maximum growth would consume a further 0.25 g C m⁻² d⁻¹. These values yield a gross growth efficiency (i.e. production divided by C intake) at maximum growth rate of 0.33, a reasonable value.

These estimates of C uptake by grazers can be compared with values of primary production to examine whether locally enhanced primary production may be a significant factor in the enhanced food web fluxes at South Georgia. The total C requirement estimated for BMR of metazooplankton is ~0.5 g C m⁻² d⁻¹, lower than the mean primary production rate of 0.8 g C m⁻² d⁻¹. Likewise, the estimate for maximum growth is ~0.9 g C m⁻² d⁻¹, lower than the regional maximum average primary production of 1.5 g C m⁻² d⁻¹. Obviously this is a simple and crude comparison. Only a proportion of the total C rations of zooplankton is phytoplankton (Hopkins & Torres 1989, Atkinson & Snjyder 1997, Pakhomov et al. 1997a) and conversely there are other, unmeasured sinks of phytoplankton such as grazing by microzooplankton (Burkill et al. 1995) or sedimentation. The point we are making is that the values of C uptake and removal are of the same magnitude, implying that autochthonous production is important in supporting the substantial grazer biomass at South Georgia.

The values used for the physiological parameters obviously influence the C demand calculations. South Georgia data have been used where available and where extrapolations are made, for example, in the case of BMR, we have used data at the high-end of the spectrum of published literature values. Using lower values reduces grazer carbon demand, reinforcing our conclusion that locally high primary production is a significant factor in sustaining consumers.

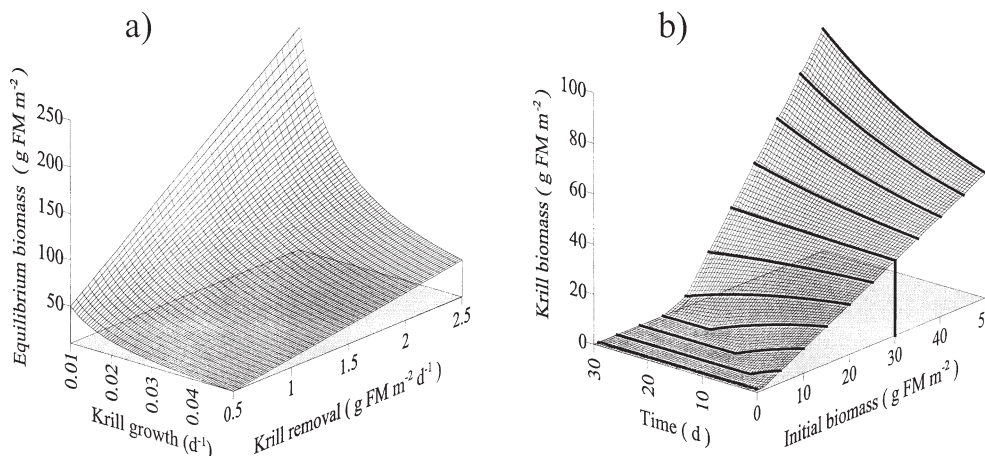


Fig. 6. Relationship between krill biomass, krill growth rate and rate of removal by predators: (a) contour plot of equilibrium biomass (at which production equals removal—see text) for a range of rates of proportionate growth rate (% biomass d^{-1}) and removal by predators; (b) time course, over 30 d, of krill biomass for a range of initial biomass levels (0 to 50 g fresh mass [FM] m^{-2}), at a production rate of 3.5% biomass d^{-1} and predator removal of 1 g FM $\text{m}^{-2} \text{d}^{-1}$. Note that biomass neither increases nor decreases over the 30 d simulation for initial biomass 30 g FM m^{-2}

Carbon flux to predators

Land-breeding birds and seals are a conspicuous element of the pelagic ecosystem around South Georgia and they act as predators at various levels in the island–ocean ecosystem. Indeed, it was their abundance in such areas which helped perpetuate the now discredited view of the entire Southern Ocean as a highly productive system. A feature of the biology of land-breeding predators is the closely circumscribed foraging range during the breeding season, determined by the need to be able to return to feed offspring (Murphy 1995, Croxall et al. 1999). This means that the C demand of breeding adults can be allocated to a specific area, and also that they are very sensitive to any major changes within their foraging range (Croxall et al. 1988). Boyd & Croxall (1996) estimated that the annual food requirement of South Georgia bird and seal predators is $1.6 \times 10^7 \text{ t FM yr}^{-1}$ or about $1.6 \times 10^{12} \text{ g C yr}^{-1}$.

This annual average value conceals considerable within-year variability in the local C demand of land-breeding predators. Demand for food is increased, and the average foraging area diminished, in the middle of the breeding season when the adult population is feeding close to the colony to provide food for themselves and their young. In a recent krill budget calculation, Atkinson et al. (2001) estimated removal of krill by fur seals and macaroni penguins at the major colonies to the northwestern end of the island alone, of the order of $32 \times 10^3 \text{ t FM d}^{-1}$ ($3 \times 10^9 \text{ g C d}^{-1}$) in January. Atkinson et al. (2001) base their calculation on an area extending tens of kilometres from the colony, which encompasses most of the foraging range of the 2 predator species and has an area of the order of

41 000 km^2 ($4.1 \times 10^{10} \text{ m}^2$). Their best estimate for krill removal in this region at the time of peak demand is thus $\sim 1 \text{ g FM m}^{-2} \text{ d}^{-1}$ ($\sim 0.1 \text{ g C m}^{-2} \text{ d}^{-1}$).

The question is whether this rate of krill removal can be sustained by local production, or whether it is dependent on continual input of krill biomass through advection. We can calculate the biomass of krill for which production equals removal by predators, for a range of possible production and removal rates. The equilibrium biomass of krill, B_{equil} (g FM m^{-2}), is related to proportionate growth rate, PGR (d^{-1}), and biomass removal by predators, R_{pred} (g FM $\text{m}^{-2} \text{d}^{-1}$), by

$$B_{\text{equil}} \times \text{PGR} = R_{\text{pred}}$$

Then

$$B_{\text{equil}} = \frac{R_{\text{pred}}}{\text{PGR}}$$

A contour plot of equilibrium biomass for a range of rates of growth (1–5% biomass d^{-1}) and removal by predators (0.5–2.5 g FM $\text{m}^{-2} \text{d}^{-1}$) shows that a best estimate value of krill predation of 1 g FM $\text{m}^{-2} \text{d}^{-1}$ and maximum production of 3.5% biomass d^{-1} (values measured at South Georgia by Clarke & Morris 1983, Reid 2001) can be sustained by a krill biomass of at least 30 g FM m^{-2} (Fig. 6a). This krill biomass corresponds to that of our ‘typical’ metazooplankton community used previously to estimate grazer C demand. Having indicated that primary production in the region of maximum predator feeding to the NW of South Georgia was potentially sufficient to sustain maximum production of both krill and copepods, these calculations suggest that the krill biomass produced under such conditions may be sufficient to support typical predator demands.

Interannual changes in krill biomass provide an indication of the relationship between krill availability and the success of krill-dependent predators. There appears to be a threshold krill biomass below which predator demand cannot be fully supported, and measures of predator feeding and reproductive success decline (Boyd & Murray in press). This critical value for krill biomass is ca. 30 g FM m⁻², which is, perhaps not coincidentally, the mean value of krill biomass around the island (Brierley et al. 1999). We can visualise the relationship between production and predation for different initial krill biomass levels based on values of proportionate production (3.5% biomass d⁻¹ at maximum growth rate) and predator removal (1 g FM m⁻² d⁻¹) used previously (Fig. 6b). This shows that, assuming these rates of krill removal and production, a krill biomass of at least 30 g FM m⁻² would be sustained or experience net growth. However, when krill biomass is less than this critical value, predation exceeds production. This is a simplistic calculation, but is compatible with observation of krill and predator dynamics over more than a decade in a region exhibiting strong inter-annual variability.

SUMMARY AND CONCLUSIONS

Primary production measured during summer in several regions around South Georgia and near the Antarctic PF varied from 0.34 to 1.52 g C m⁻² d⁻¹. The highest regional rates (mean 1.52, range 0.9 to 2.5 g C m⁻² d⁻¹) were recorded at stations to the northwest of the island. Photoinhibition of production in the near-surface layer decreased column production by 4 to 16%.

Estimates of C demand by the 2 main groups of metazooplankton—Antarctic krill and copepods—suggest that ~0.5 g C m⁻² d⁻¹ would be needed to sustain basal metabolism. This value is less than the measured primary production rate at most stations around South Georgia. Combined C demand for the 2 groups at maximum growth rate was estimated to be 0.93 g C m⁻² d⁻¹; primary production rates higher than this were only found in more productive regions to the northwest of the island.

Maintenance of the krill population at South Georgia appears to depend on advection of animals from higher latitudes. This krill stock supports large populations of predators. However, the degree to which the food supply for predators is replenished by advection and how much is provided by local krill production has been uncertain. Taking typical values for removal rates of krill by predators, and krill production rates and biomass, we suggest that krill production may equal or exceed the predator demand under some conditions.

When krill biomass exceeds the long-term mean value of ~30 g FM m⁻² (Brierley et al. 1999), we calculate that growth at the maximum rate used in our calculations (3.5% body mass d⁻¹) is adequate to sustain removal by predators. Combining this with our estimates of C demand by metazooplankton suggests that primary production measured in this study met the requirements for maximum growth rate at some stations.

Our observations and calculations support those of Atkinson et al. (2001) that autochthonous production can make a significant contribution to the South Georgia food web. Our estimate of optimal krill biomass based on production criteria agrees with the threshold value for breeding success by krill-dependent, land-based predators (Boyd & Murray 2001). This and the co-location of the region of highest homiothermic predator foraging with the highest primary production in this study may point to complex relationships within the local system (cf. Whitehouse et al. 1999, Atkinson et al. 2001).

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