

REVIEW

South Georgia, Antarctica: a productive, cold water, pelagic ecosystem[†]

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ABSTRACT: The South Georgia region is characterised by high biomass and productivity of phytoplankton, zooplankton and vertebrate predators. Important commercial fisheries have been based at the island since the late 1700s, initially exploiting seals and whales, and currently taking krill *Euphausia superba* and finfish. Despite studies dating from the beginning of the last century, the causes of the high productivity remain unclear. The island lies within the Antarctic Zone of the Antarctic Circumpolar Current, to the south of the Polar Front. The offshore waters to its north and east are affected by a northwards deflection of the Southern Antarctic Circumpolar Current Front, together with waters from the Weddell-Scotia Confluence. Despite a retentive circulation over the shelf, the high productivity of phytoplankton and copepods is widespread, occurring far downstream and possibly extending to the Polar Front. High phytoplankton concentrations (>20 mg chlorophyll *a* m^{-3}) may be linked to enhanced supply of iron or reduced forms of nitrogen (up to ~ 3 mmol ammonium m^{-3}). Although macronutrients are generally not limiting in the Antarctic Zone, silicate concentrations of <1 mmol m^{-3} are growth-limiting at South Georgia in some summers. The growth season is long and blooms of >2 mg chl *a* m^{-3} occur for 4 to 5 mo. Biomass of krill plus net-caught zooplankton in summer is around 15 to 20 g dry mass m^{-2} , equally dominated by krill and copepods. This greatly exceeds typical values for Antarctica, and is high compared to productive northern shelves. Zooplankton, and in particular krill, appear to have a pivotal role in regulating energy flow in this food web, through selective grazing and possibly also through nutrient regeneration. Abundances of krill and copepods are negatively related across a wide range of scales, suggesting direct interaction through competition or predation. Evidence suggests that when phytoplankton stocks are low, energy flow through krill is maintained by their feeding on the large populations of small copepods. Metazoans and higher predators at South Georgia can feed across several trophic levels according to prey abundance, and they regenerate substantial quantities of reduced nitrogen. Therefore we suggest that these groups have a controlling influence on lower trophic levels, both stabilising population sizes and maintaining high rates of energy flow. Hydrography, nutrient concentrations, phytoplankton, copepod, and krill biomasses fluctuate between years. Periodically (once or twice a decade), shortages of krill in summer result in breeding failures among many of their predators. This appears to be a downstream effect from wider scale, Scotia Sea phenomena, although the processes involved are unclear. The elevated biomass and energy flows at South Georgia appear to be caused by locally enhanced growth rates; there is no evidence so far for any physical concentration mechanism. Even for krill, which do not breed there, local growth rates are probably of a similar order to the biomass removed by their main land-based predators in summer. Thus the transfer of energy to higher predators depends on local enhancement of fluxes through the food web as well as the supply of plankton to the island by the Antarctic Circumpolar Current.

KEY WORDS: Southern Ocean · South Georgia · Pelagic ecosystem · Food web · Antarctic krill · Zooplankton · Phytoplankton · Nutrients · Island effects

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[†]This paper is dedicated to the memory of Geof Cripps

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1. INTRODUCTION

1.1. The South Georgia ecosystem

South Georgia is a narrow, mountainous island with a broad continental shelf, lying within the open ocean of the Antarctic Zone (AAZ) to the south of the Polar Front (PF) in the Atlantic sector of the Southern Ocean (Fig. 1a). The open ocean of the AAZ is characterised by low productivity compared with marginal ice zones, continental shelves, and frontal systems. However, the ocean around South Georgia does not typify the High Nutrient Low Chlorophyll (HNLC) conditions of the AAZ — phytoplankton blooms are prevalent over both the shelf and in a large area downstream. Zooplankton biomass is also high around the island and downstream, with values roughly 4 to 5 times higher than those more typical of the Southern Ocean. Large colonies of seals and seabirds breed at South Georgia, and the region supports important commercial fisheries for krill and fish. The fisheries interests here underlie the 80 yr history of scientific investigation, making it one of the most intensively studied parts of the Southern Ocean. South Georgia thus provides a case example of a productive, cold water ecosystem.

1.2. Historical perspective

South Georgia has experienced a long history of exploitation, and catches of the various species reflect successive cycles of overfishing and switching to the next most economically viable species. Antarctic fur seals *Arctocephalus gazella* were hunted almost to extinction in the late 1700s and early 1800s (Bonner 1984, Headland 1984) and from 1904 a whaling industry operated from the north coast (Harmer 1931, Kemp

& Bennett 1932). With a sharp decline in whale numbers and the advent of pelagic factory whaling, South Georgia-based operations stopped in 1965 (Moore et al. 1999). In the 1970s, fisheries for icefish and nototheniid fish developed. Again these were overfished, causing population crashes (Kock 1985, Everson 1992). The shelf break north of South Georgia is presently a major site for the winter krill fishery in the Southern Ocean (Everson & Goss 1991, Trathan et al. 1998a). Present catches of krill in Antarctica are not a threat to their stocks, but at South Georgia the fishery is localised (Murphy et al. 1997) and may be in competition with large colonies of krill-dependent predators.

This over-exploitation has continued alongside dedicated research programmes during the last 80 yr. The *Discovery Investigations* were started in the 1920s in order to provide a scientific basis for the management of whaling. These were financed partly from whaling and sealing revenues, and their repeated multi-ship surveys were intensive even by today's standards. The *Discovery Investigations* took an ecosystem approach, aiming to understand the causes of the high primary productivity and how it was linked to fisheries. The *Discovery Reports* covered many topics, from oceanography to whales, and the report on the plankton by Hardy & Gunther (1935) linked the environment and higher trophic levels using some very modern concepts. For example, they suggested that micronutrients contributed to productivity, that diatoms could be detrimental to zooplankton, and that diel vertical migration could influence horizontal transport (see also Hardy 1967). Later *Discovery Investigations* broadened their coverage to include South Georgia as part of the Scotia Sea-Antarctic Circumpolar Current system (e.g. Foxton 1956, Marr 1962, Mackintosh 1973).

Between 1940 and 1970 less scientific work was done at South Georgia, except for mainly Russian investiga-

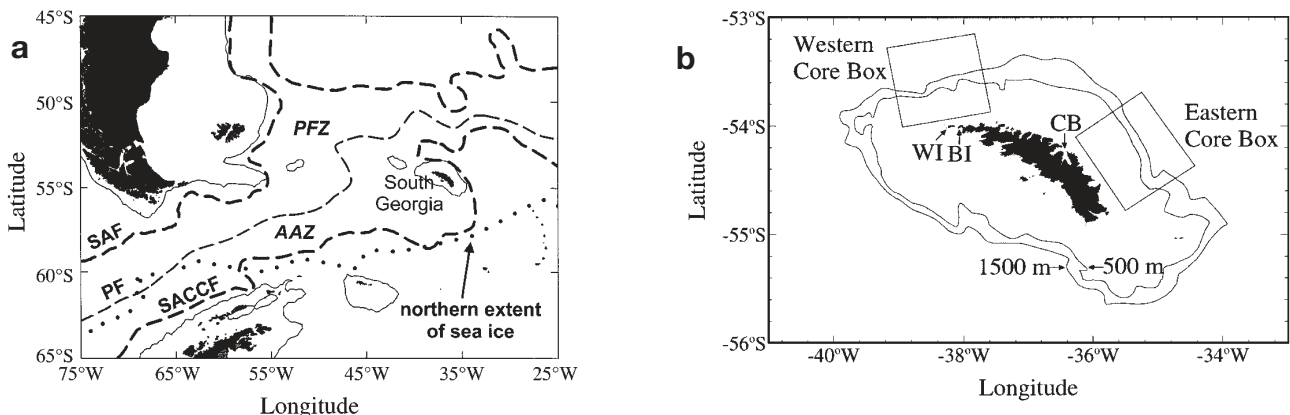


Fig. 1. (a) Atlantic sector of Southern Ocean showing 500 m isobath, major fronts, watermass zones and mean winter northern extent of sea ice. SAF: Subantarctic Front, PFZ: Polar Frontal Zone, PF: Polar Front, AAZ: Antarctic Zone, SACCF: Southern Antarctic Circumpolar Current Front. (b) South Georgia region showing the position of Willis Island (WI), Bird Island (BI), Cumberland Bay (CB) and Eastern and Western Core Box—the focus of a monitoring study by the British Antarctic Survey

tions during the development of the krill fishery (Maslennikov 1972, Vladimirkaya 1978, Maslennikov et al. 1983, Grelowski & Pastuszak 1983, Makarov et al. 1984). In the last 20 to 30 yr attention has been renewed. Several nations have participated, but most work has been done by the British Antarctic Survey (BAS) who started a programme of research there in the 1970s (e.g. Croxall et al. 1988). Thus our detailed knowledge of the South Georgia ecosystem spans the last 80 yr, although it is discontinuous in time.

1.3. Aim of this review

Much data have been published about the South Georgia pelagic region, on topics ranging from hydrography and nutrient chemistry to higher predators and fisheries. This review focusses on interactions mainly within the lower trophic levels. This is because: (1) most of the energy flow is within these levels; (2) despite many studies of certain higher predator species, insufficient data exist for an appraisal of the overall flow of energy into and between the top trophic levels; and (3) the extensive literature on South Georgia seals and seabirds precludes an authoritative summary within the limits of this review. Food consumption by seabirds in the South Georgia system was reviewed by Croxall et al. (1984)—a new synthesis including seals is in preparation (Boyd & Croxall 1996, I. L. Boyd pers. comm.) For recent studies of the higher predators, with special reference to their foraging, we refer the reader to papers by Rodhouse et al. (1996) for squid, North & Ward (1989, 1990), Kock et al. (1994), and Everson et al. (1997) for fish, Trathan et al. (1998b), Rodhouse et al. (1998) and Croxall et al. (1999) for penguins, Harrison et al. (1991), Croxall & Prince (1996), Croxall et al. (1997), Reid et al. (1997a,b), Prince et al. (1999), Berrow & Croxall (1999) for flying seabirds, Reid (1995), North (1996), Reid & Arnauld (1996), Reid et al. (1996), McCafferty et al. (1998) and Brown et al. (1999) for seals, and Moore et al. (1999) and Reid et al. (2000) for whales. Commercial fishing activity in the South Georgia area is summarised by Murphy et al. (1997), Trathan et al. (1998a), Everson et al. (1999) and Moore & Jennings (2000).

In Section 2 we present an overview of the major components of the planktonic system, namely oceanography, nutrients and primary production, microplankton, zooplankton, and krill. Here the assemblages are characterised and placed in a wider, Southern Ocean context. Few studies of South Georgia have encompassed more than 2 trophic levels or functional groups (but see Hardy & Gunther 1935, Everson 1984), and a modern review is lacking. Our second aim is to combine insights from all of the above disciplines to assess

how the system operates. Specifically in Section 3 we examine a key problem in the study of island mass effects, namely whether the high biomasses at every trophic level reflect physical concentration mechanisms or locally enhanced primary production and fluxes within the food web. In Section 4 we summarise our current understanding of interannual variability, a particularly well-studied timescale of change. The concluding discussion in Section 5 is a synthesis of the preceding sections, which identifies features that may be key to understanding the South Georgia food web.

2. MAJOR COMPONENTS OF THE PELAGIC ECOSYSTEM

2.1. Hydrography

2.1.1. Scotia Sea

South Georgia is part of the Scotia Ridge, a mainly submarine arc extending from South America to the Antarctic Peninsula, with surface extensions at Shag Rocks, South Georgia and the South Sandwich, South Orkney and South Shetland Islands (Fig. 1a). This arc forms the northern, eastern and southern boundary of the Scotia Sea, which is bounded to the west by the Drake Passage between South America and the Antarctic Peninsula.

South Georgia lies in the eastward flowing Antarctic Circumpolar Current (ACC), (Nowlin & Klinck 1986, Orsi et al. 1995). The ACC comprises a series of narrow, high speed frontal jets embedded in broader, slower moving zones (Nowlin & Clifford 1982). South of the Southern Antarctic Circumpolar Current Front (SACCF) the hydrography is complicated by regionally specific conditions. Orsi et al. (1995) defined a circumpolar southern boundary to the ACC which, in the Scotia Sea area, corresponds approximately to the junction between the ACC and the Weddell Gyre. A further complication is the Weddell-Scotia Confluence, as it has unique watermass characteristics and comprises water from the ACC, the Weddell Sea, and the western Weddell Sea shelf (Gordon 1967, Deacon & Moorey 1975, Whitworth et al. 1994). It is most clearly defined near the Antarctic Peninsula and broadens to the east, where, in the region of the Scotia Ridge, it comprises a complex mixing zone of eddies (Patterson & Sievers 1980, Foster & Middleton 1984).

Throughout much of the Southern Ocean the sea ice edge and the ACC's zones and fronts lie roughly parallel, following the lines of latitude. However, to the west of South Georgia, the Scotia Ridge deflects the ACC sharply northwards, after which it resumes its easterly course (Mackintosh 1946, Nowlin & Klinck 1986).

Therefore, despite the cold waters that flow around South Georgia, the island tends to remain to the north of the pack ice. Only in exceptionally cold winters does sea ice extend as far north as South Georgia (Mackintosh & Herdman 1940, Gloerson et al. 1992).

2.1.2. South Georgia in the Antarctic Circumpolar Current

In addition to the general northwards deflection of the ACC near South Georgia, the SACCF as well as the Weddell-Scotia Confluence waters are inflected around the eastern and northern flanks of the island (Fig. 1a). The average positions of the fronts plotted in Fig. 1a mask the degree of large- and meso-scale variability; meandering and eddy-shedding have been described for ACC fronts (e.g. Lutjeharms & Baker 1980, Bryden 1983). In areas of irregular bottom topography such as the northeastern Scotia Sea, the positions of fronts are particularly variable (Gordon et al. 1977, Peterson & Whitworth 1989). Despite this, 90 % of transects in the Atlantic sector have located the PF within 100 km of its mean position (Mackintosh 1946). The positions of fronts and eddies relative to South Georgia thus dictate its watermasses and plankton communities.

The earliest interpretations of South Georgia hydrography (Deacon 1933, Hardy & Gunther 1935) suggested that the island was influenced by 2 watermasses: ACC water of Bellingshausen Sea origin which came from the west, and colder, silicate-rich water of Weddell Sea origin from the south and east. Thus South Georgia appeared to be in a mixing zone of 2 watermasses differing in origin and physical properties. The *Discovery Investigations* documented a pronounced year-to-year variability at South Georgia (Harmer 1931, Kemp & Bennett 1932, Clowes 1938, Deacon 1977). These oscillations are superimposed on climatic changes during the last century in the Scotia Sea region (e.g. Maslennikov & Solyankin 1988, King 1994, de la Mare 1997). Deacon (1977) showed that water temperatures at South Georgia rose during the 1930s, that air and water temperatures were closely linked, and that air temperatures rose $\sim 1^\circ\text{C}$ from the 1930s to the 1970s.

Although this trend has been documented, it is unclear whether changes in temperature and sea ice also affect the positions of the fronts. Bogdanov et al. (1969) found that the frontal zone between the Weddell Gyre and ACC water lay further south of South Georgia than found by Hardy & Gunther (1935). Recent publications have lent further support to the notion of frontal shifts. For example Priddle et al. (1986) suggested that Weddell Water was absent from the region during 1981/1982, and Heywood et al. (1985) and Pakhomov et al. (1997b) proposed that Subantarctic water

influenced the island in 1983 and 1994. These interpretations are not supported by recent findings, which suggest that the PF is consistently > 250 km to the north of South Georgia (Orsi et al. 1995, Trathan et al. 1997, 2000). However, there is some evidence that warm water eddies of PFZ origin may influence the South Georgia region from the west (Atkinson et al. 1990, Whitehouse et al. 1996b).

2.1.3. Local effects at South Georgia

The general circulation patterns around South Georgia are illustrated by the Fine Resolution Antarctic

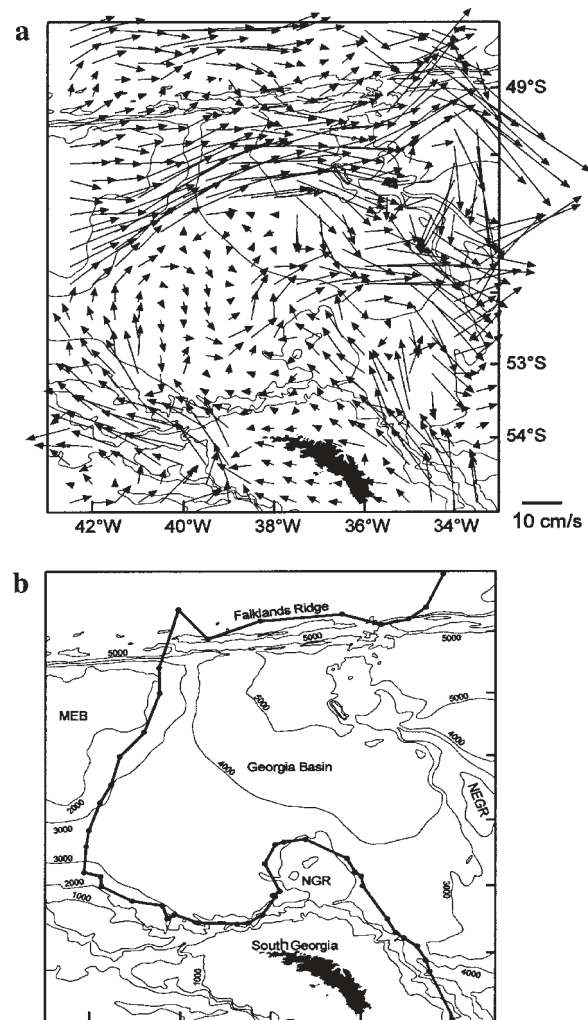


Fig. 2. (a) Current vectors derived from FRAM model (FRAM Group 1991) for South Georgia region and downstream (from Trathan et al. 1997 with permission from author). Note scale bar for velocity vectors. (b) Drift of large iceberg, 31 August to 9 November 1987. Points record position for 45 d during its 71 d transit through study area (from Trathan et al. 1997). MEB: Maurice Ewing Bank, NGR: North Georgia Rise, NEGR: Northeast Georgia Rise

Model (FRAM Group 1991: Fig. 2a). The current vectors it generates fit Eulerian and Lagrangian observations very well (Fig. 2b, Hardy & Gunther 1935, Priddle et al. 1986, Trathan et al. 1997, Brandon et al. 1999, 2000). These confirm a northwesterly flow approximately parallel to the island's northern shelf edge (see also Maslennikov 1979, Latogursky et al. 1990). Two monitoring areas termed the Eastern Core Box (ECB) and the Western Core Box (WCB) have been studied intensively in recent years (Fig. 1b). In the ECB the shelf break is a shear zone between fast oceanic currents and slower shelf currents, with a shelf-break front between them (Brandon et al. 1999). No pronounced shelf-break front was found in the WCB (Brandon et al. 2000), so transfer across the shelf break is probably variable, both regionally and temporally (Murphy et al. 1998, Brandon et al. 1999). To the west of South Georgia the FRAM also concurs with field observations. The consensus (Hardy & Gunther 1935, Trathan et al. 1997, Brandon et al. 2000) is that this area is a variable mixing zone between the ACC waters approaching from the west and a colder, more saline current approaching from the east, along the north side of the island.

As well as deflecting the ACC, the broad shelf around South Georgia further influences the water masses. The shelf water in summer is often slightly warmer and is locally fresher than its surroundings (Priddle et al. 1986, Brandon et al. 2000). The lower salinity is due to local runoff and the higher temperature is possibly due to greater solar heating of the resident waters compared with the surrounding ocean water recently advected from colder latitudes.

2.2. Nutrients and primary production

2.2.1. Nutrient availability and phytoplankton biomass

The *Discovery Investigations* laid the foundations for our understanding of phytoplankton growth and nutrient use at South Georgia. Hardy & Gunther (1935) and Hardy (1967) correlated locally reduced phosphate concentrations with elevated phytoplankton biomass, suggesting that phosphate depletion provided a time-integrated 'memory' of primary production. Clowes (1938) showed summer silicate and phosphate reductions, possible year to year variation in phytoplankton utilisation, and suggested that silicate concentrations may, in some years, limit phytoplankton growth. The latter has since been supported for ACC waters, although Weddell Sea waters in the vicinity of the island are always replete in silicate (Whitehouse et al. 1996a). A wider scale context was provided by Hart (1934, 1942), who noted the general failure of Antarc-

tic marine phytoplankton to deplete fully the abundant pools of macronutrients in the surface waters: now known as the HNLC paradox.

This inability of phytoplankton to utilise fully the available nutrients has subsequently been attributed to a variety of factors: low temperature and physiological inefficiency of nutrient uptake, deep vertical mixing, lack of trace elements, and zooplankton grazing pressure (see Chisholm & Morel 1991, Smith et al. 1996, Priddle et al. 1998b). However, within the Southern Ocean there are several areas where high primary production rates do occur. These are certain marginal ice zones (e.g. Smith & Nelson 1985, Nelson et al. 1989), fronts (e.g. Lutjeharms et al. 1985, Jacques & Panouse 1991) and neritic regions (e.g. Boden 1988, Holm-Hansen & Mitchell 1991, Perissinotto et al. 1992). South Georgia lies in the ice-free AAZ which epitomises HNLC conditions. Productivity is generally very low in this zone (maximum chl *a* $\sim 1 \text{ mg m}^{-3}$), and although it may be greater in the Scotia Sea, even here it is usually $< 2.5 \text{ mg chl } a \text{ m}^{-3}$ (Rönnner et al. 1983, Jacques 1989, Tréguer & Jacques 1992). Thus the $> 20 \text{ mg chl } a \text{ m}^{-3}$ blooms at South Georgia are exceptional (Whitehouse et al. 1996a, 1999). These blooms are not confined to neritic areas, but occur regularly in deep oceanic water to the north of the island ($> 12 \text{ mg chl } a \text{ m}^{-3}$), as well as at the PF ($> 8 \text{ mg chl } a \text{ m}^{-3}$; Fryxell et al. 1979, El-Sayed & Weber 1982, Whitehouse et al. 1996b, 2000).

The *Discovery* scientists were aware that macronutrients were not usually the key factors limiting phytoplankton growth. Hardy (1967) suggested that the krill-rich 'area of dead water' on the northern (lee) side of the island was productive because it was a mixing zone of 2 currents of different origin, each supplying a micronutrient which was deficient in the other. Since then, several of the potentially limiting nutrients in this region have been identified, namely iron (de Baar et al. 1995) and ammonium (Owens et al. 1991, Priddle et al. 1997, Whitehouse et al. 1999). However we are still some way from elucidating how nutrients modulate primary production rates at South Georgia. This topic is revisited in Section 3.1.

2.2.2. Primary production

There are few measurements of primary production from South Georgia (Table 1), and the variety of methods used makes comparison difficult. However, the rates seem to be genuinely variable, both temporally and spatially. The values, particularly in the WCB, appear to be high compared to the rest of the AAZ, although they are typical of inshore regions (Table 1).

Annual rates of primary production at South Georgia have been estimated from seasonal nutrient deficits

Table 1. Primary production values for the Eastern Core Box (ECB) and the Western Core Box (WCB) at South Georgia, compared with some other Southern Ocean zones

Region	Time of year	Primary production (g C m ⁻² d ⁻¹)	Primary production (g C m ⁻² d ⁻¹) mean (range)	Source
South Georgia (ECB)	Dec–Feb	1.2 1.2	0.57 (0.069–1.2)	Owens et al. (1991)
	Feb–Mar	0.15 0.069		Pakhomov et al. (1997a,b)
	Jan	0.45 0.7 0.25		British Antarctic Survey (unpubl. data)
South Georgia (WCB)	Dec–Feb	2.12 0.742 0.536 0.464	1.72 (0.323–8.9)	Owens et al. (1991)
	Jan	8.9 ^a		Atkinson et al. (1996)
	Feb–Mar	0.37 0.323 1.66 0.444		Pakhomov et al. (1997a,b)
	Jan	1.9 1.45 2.75 1.0 1.4		British Antarctic Survey (unpubl. data)
Neritic regions	Summer		2.8	Horne et al. (1969)
	Summer		3.2	El-Sayed (1967)
	Jan–Mar		0.374	Helbling et al. (1995)
	Spring–summer		(1.08–6.58)	Moline & Prézélin (1996)
Antarctic open ocean zone	Nov–Jan		0.55 (0.29–1.33)	Mathot et al. (1992)
	Jan–Feb		0.256 (0.162–1.12)	Rönnner et al. (1983)
Seasonal ice zone	Spring		1.13 (0.61–1.4)	Mathot et al. (1992)
	Spring		0.49 (0.17–0.98)	Smith & Nelson (1990)
	Nov–Dec		0.8	Boyd et al. (1995)
	Summer		2.1	Park et al. (1999)
	Jan		(0.179–1.61)	Alcaraz et al. (1998)

^aGross microbial production based on oxygen flux measurements

(Whitehouse et al. 1996a). Estimates based on several seasons of phosphate and silicate data suggest a value of 30 to 40 g C m⁻² yr⁻¹. This value, albeit based heavily on a season of unusually low productivity and including an unproductive area south of the island, is no higher than overall Southern Ocean estimates (Savidge et al. 1996, Priddle et al. 1998a). However, we stress that errors inherent in the nutrient budget technique (e.g. non-stoichiometric uptake, vertical mixing and diffusion, recycling of nutrients) all tend to underestimate annual primary production.

2.2.3. Seasonal succession

Seasonal sampling is limited by logistics, but remote sensing offers an alternative view. Heavy cloud cover in this area restricts satellite imagery, but SeaWiFS chl *a* maps, averaged on a monthly basis to reduce the problem of cloud cover, are instructive (Fig. 3a,b). The high chl *a* values to the north of South Georgia, and sometimes also far downstream, contrast with the low biomass in the Scotia Sea. The other clear feature is the long growing season. The SeaWiFS images and

Fig. 3 (a) SeaWiFS monthly composite images of Atlantic sector of Southern Ocean from successive months during 1998/1999. Provided by SeaWiFS Project, NASA/Goddard Space Flight Center and ORBIMAGE. Black areas where cloud-cover/sea-ice have obscured image. Central outlined box encloses South Georgia region. (b) Closeup of monthly SeaWiFS images from the central outlined box in (a)

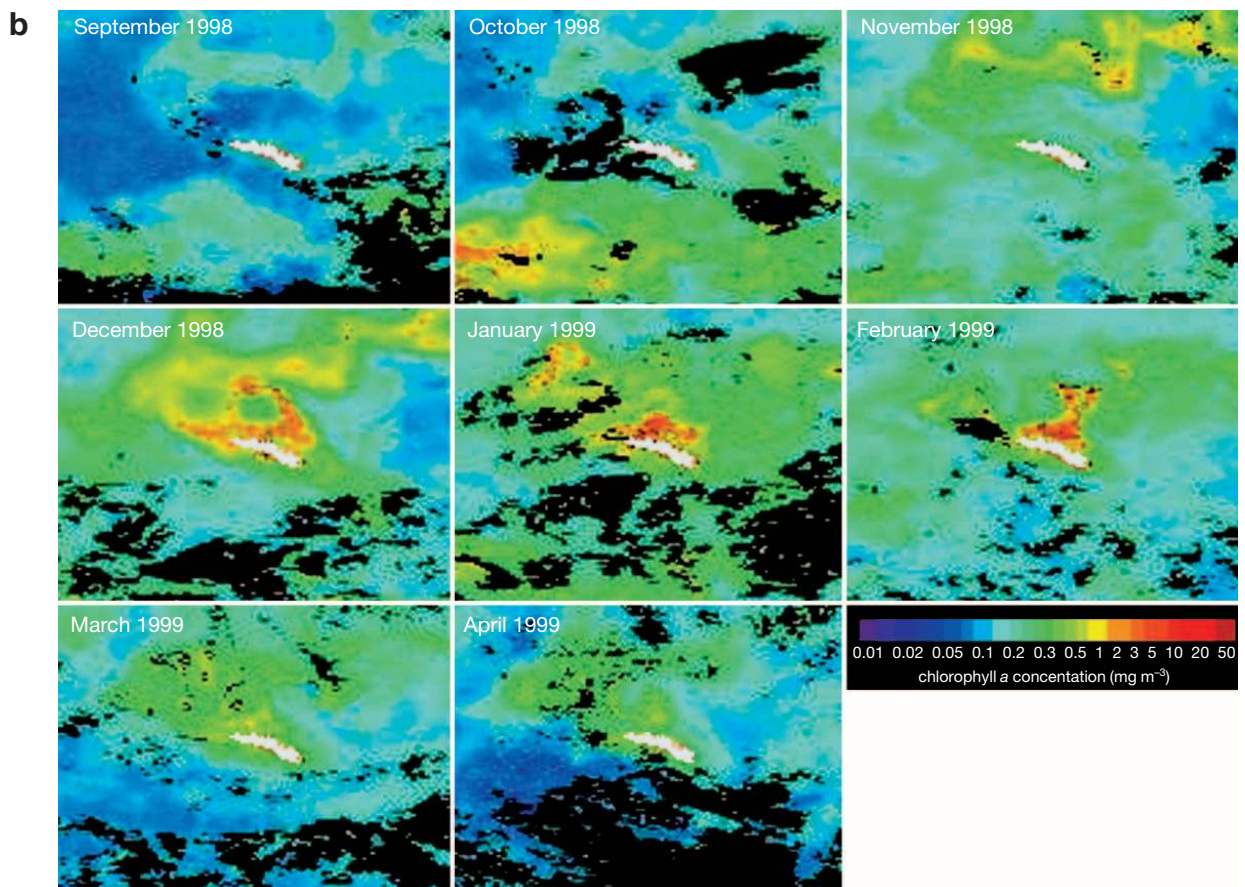
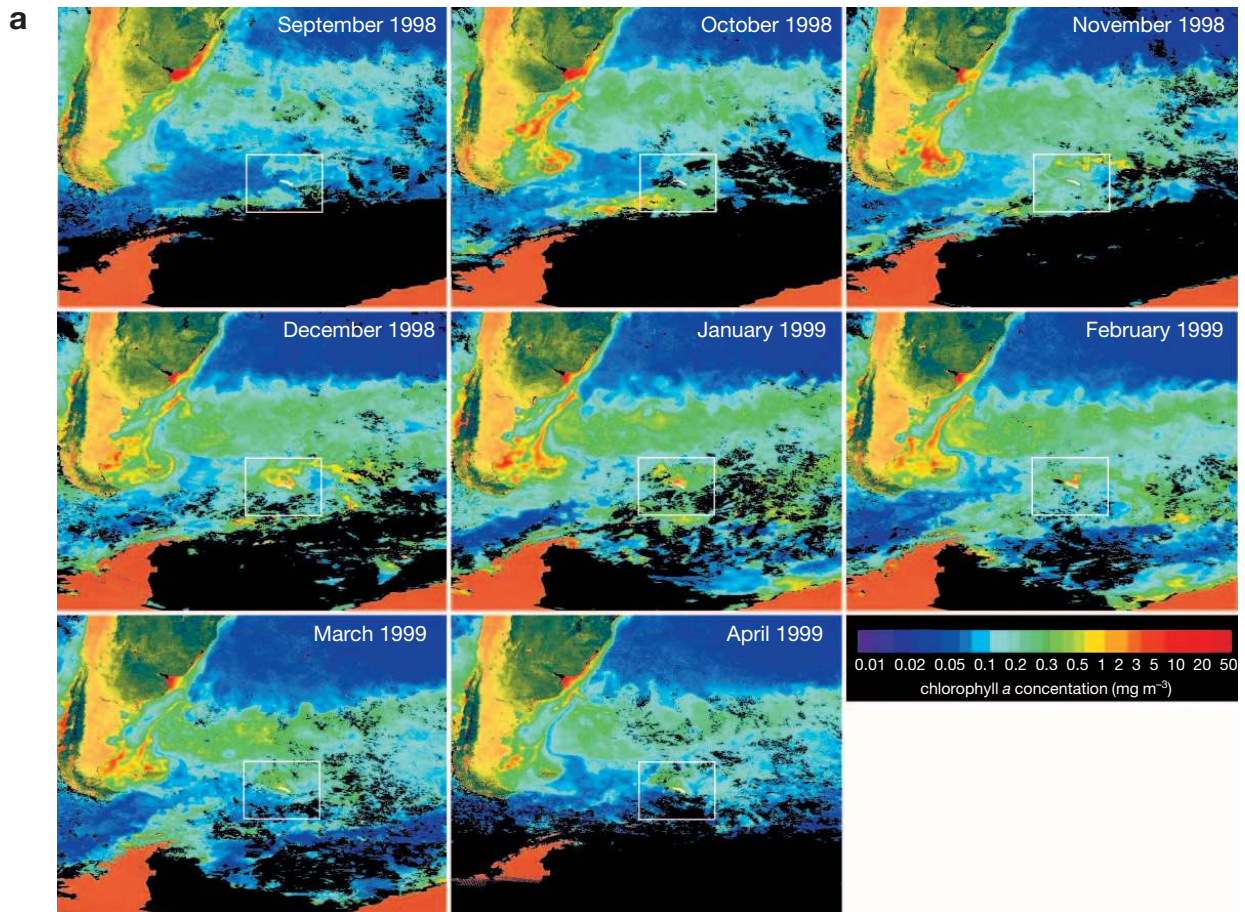


Table 2. Seasonal changes in the South Georgia area. SeaWiFS satellite imagery and conventional near-surface (≤ 30 m) measurements of chl *a*, nutrients and temperature. South Georgia zone survey (SGZS) for entire island, other measurements to the north. SGZS silicate presented separately for Antarctic Circumpolar Current (ACC) and waters of Weddell-Scotia Confluence origin (WSC). No data for May/June

Month	Phytoplankton biomass (mg chl <i>a</i> m ⁻³) SeaWiFS 1998/1999	Field data 1980–1999	Nutrients (mmol m ⁻³), temperature (°C) Field data 1980–1999
Jul/Aug	No data	SGZS ^{2,10} 0.23 (0.11–0.38) Values of $\sim 0.3^5$, similar to Scotia Sea ⁴	SGZS ^{2,10} phosphate 2.0 (1.6–2.5), silicate ACC 26 (18–36) WSC 48 (35–76), nitrate 23 (17–27), temp 0.5 (–0.8 to 1.8)
Sep/Oct	Low around South Georgia, possibly higher close inshore Higher concentrations to the southwest possibly related to the seasonally retreating ice-edge or the SACCF	SGZS ^{2,10} 0.70 (0.20–2.78) NW island ² 1.6 (0–6.9) High biomass recorded in fjords ^{2,3} Offshelf NW island Oct ⁹ ≤ 3	SGZS ^{2,10} phosphate 2.0 (1.3–2.5), silicate ACC 29 (11–40) WSC 52 (43–65), temp 0.4 (–1.0 to 1.8) NW island ² phosphate 1.9 (1.5–2.3), silicate 32 (23–42), nitrate 27 (24–29), nitrite 0.25 (0.2–0.3), ammonium 0.34 (0.1–0.8), temp 0.5 (0.3 to 0.8)
Nov/Dec	Bloom develops at the PF and around South Georgia, with high values inshore and to the north downstream of the island, and between it and the PF	SGZS ^{2,6,10} 0.8 (0.13–4.54) N island end Dec ^{2,10} 5.3 (0.5–30) Blooms recorded N&W island ^{3,9,12}	SGZS ^{2,10} phosphate 1.5 (0.5–2.2), silicate ACC 19 (2–45) WSC 37 (22–55), nitrate 22 (16–29), temp 1.1 (–1.0 to 3.0) N island end Dec ^{2,10} phosphate 1.6 (1.1–2.0), silicate 14 (<1–31), nitrate 21 (13–29), nitrite 0.3 (0.2–0.4), ammonium (0.1–2.7), temp 2.6 (1.4 to 3.5)
Jan/Feb	Dense blooms (>10) inshore to the north of South Georgia, with large patches >2 downstream of island	Jan 1999 N&W island ² 5.1 (0.4–17.3) SGZS ^{2,10} 2.26 (0.14–29.0) N island ² 3.3 (0.2–22.3) Dense blooms frequently recorded NW of island ^{1,7,8,11,12,13}	Jan 1999 N&W island ² phosphate 1.2 (0.6–2.2), silicate 12 (2.2–50), nitrate 20 (16–30), nitrite 0.3 (0.2–0.5), ammonium 0.7 (0–1.9), temp 2.7 (2.1 to 4.0) SGZS ^{2,10} phosphate 1.4 (0.5–2.2), silicate ACC 13 (<1–37) WSC 27 (1–52), nitrate 21 (13–31), temp 2.7 (0.8 to 4.5) N island ² phosphate 1.3 (0.3–2.3), silicate 15 (1–50), nitrate 19 (10–30), nitrite 0.3 (0.2–0.5), ammonium 0.8 (0–1.9), temp 2.8 (1.2 to 4.5)
Mar/Apr	Large patches >1 remain near the island and downstream of it	SGZS ^{2,10} 0.35 (0.03–1.0)	SGZS ^{2,10} phosphate 1.4 (0.9–1.7), silicate ACC 8 (2–25) WSC 24 (10–36), nitrate 22 (21–23), temp 3.0 (1.9 to 4.2)

¹ Atkinson et al. (1996), ²British Antarctic Survey (unpubl. data), ³Hart (1934), ⁴Heywood et al. (1985), ⁵Morris & Priddle (1984), ⁶Priddle et al. (1986), ⁷Priddle et al. (1995), ⁸Shreeve & Ward (1998), ⁹Ward & Shreeve (1999), ¹⁰Whitehouse et al. (1996a), ¹¹Whitehouse et al. (1999), ¹²Whitehouse et al. (1993), ¹³Whitehouse et al. (1996b)

ground observations for various years both show that blooms around South Georgia can occur for 4 to 5 mo, and regularly exceed 10 mg chl *a* m⁻³ (Table 2). Blooms may be seeded close inshore (Hart 1934, Whitehouse et al. 1999), with elevated chl *a* concentrations found in fjords as early as September (BAS unpubl.). SeaWiFS data (Fig. 3b) also suggest this, although the low spatial resolution of the data prevents firm conclusions around the convoluted coastline.

2.2.4. Microplankton composition

Phytoplankton blooms around South Georgia invariably comprise large colonial diatoms, mainly centric

forms such as *Eucampia antarctica*, *Odontella weissflogii*, *Chaetoceros socialis* and *Thalassiosira* spp. (especially *T. scotia* and *T. tumida*). Several of these have been found in late winter blooms inshore, suggesting that they formed a seed population for growth later on. Many of the colonies are clearly visible to the naked eye, and about half of the chl *a* may be retained on a 200 μ m sieve (Priddle et al. 1995, Atkinson et al. 1996) and around 80 to 90% retained on a 20 μ m sieve (von Bröckel 1981, Priddle et al. 1995).

Although phytoplankton biomass at South Georgia is patchy over scales of 10 to 20 km, spatial coherence in community structure appears to be a recurring feature (Hardy & Gunther 1935, Priddle et al. 1986, Froneman et al. 1997). The summer pattern shows a distinct

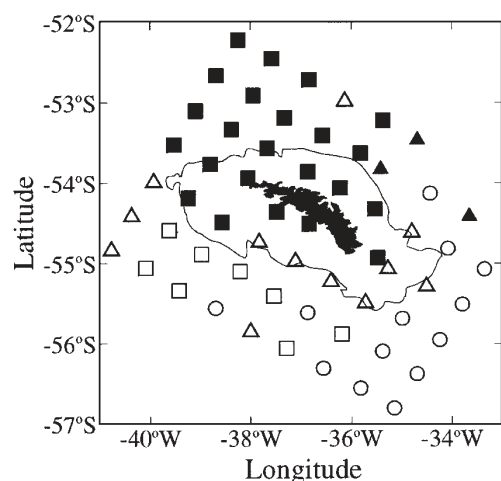


Fig. 4. South Georgia region showing 500 m isobath and 5 assemblages of net (>20 μm) diatoms from a survey in November/December 1981 (redrawn from Theriot & Fryxell 1985). Symbols represent assemblages of diatoms identified by Principal Components Analysis (Theriot & Fryxell 1985), most distinct separation is between northern assemblage (■) and remaining stations

group of species on the shelf and in the northwest area, which contrasts with a colder water group to the south and east (Fig. 4). This general pattern appears to pervade, despite more subtle differences within these regions (Froneman et al. 1997).

The patchy diatom blooms appear to be superimposed on a more constant background of smaller autotrophs and heterotrophs, dominated by small diatoms, with prymnesiophytes and dinoflagellates also contributing. The fact that bacterial numbers were unrelated to phytoplankton biomass (B. W. Mullins & J. Priddle unpubl.) suggests that the microbial food web is at least partly isolated from that involving large diatoms (see also Karl et al. 1996). The limited data for South Georgia (von Bröckel 1981, Dodge & Priddle 1986, Priddle et al. 1995) suggest a rich and substantial community of microheterotrophs, comparable to the highest values in other regions of Antarctica (see Garrison & Mathot 1996). Priddle et al. (1995) provided a breakdown of microbial composition at 3 sites during a declining January bloom (2 to 3 mg chl a m^{-3}). Of the total microbial biomass of 2.3 to 4.5 g C m^{-2} in the upper mixed layer, heterotrophic nanoplankton and microplankton comprised about 20% of total microbial biomass at shelf and shelf-break stations, but >50% at the oceanic station. Of the heterotrophic fraction, between 15 and 60% were bacteria, the remainder being mainly dinoflagellates. Although the data are limited, the biomass of protozoans are at the upper end of the range of Antarctic summer values (e.g. von Bröckel 1981, Garrison 1991, Garrison & Mathot 1996, Edwards et al. 1998), underlining their importance in

microbial community functioning. Likewise, the bacterial biomass in this study (~10% of total microbial biomass) is within the upper range of Antarctic values (Hodson et al. 1981, Hanson et al. 1983, Karl et al. 1991).

There are too few data to support firm conclusions regarding seasonal succession of the microbial community, but in Jan/Feb silicate concentrations fall to values which could stress some of the large diatoms. Small colonies of *Phaeocystis* spp. may occur late in the season, but unlike other regions of Antarctica, blooms of this species, or of dinoflagellates, have never been recorded at South Georgia.

2.3. Metazooplankton

2.3.1. Biomass

Regional comparisons of zooplankton biomass require care, due to the differences in methods and times of year of sampling. Nevertheless, when comparisons are made from equivalent depths, nets and times of year (Table 3), mesozooplankton biomass is clearly much greater at South Georgia than elsewhere in the Southern Ocean. Indeed, it is at the high end of the range for productive northern shelves such as the North Sea (Hay 1995), Bering Sea (Vidal & Smith 1986) and Georges Bank (Wiebe et al. 1996). The South Georgia values are mainly from catches with 200 μm ring nets, which do not retain the important small fraction (Hopkins 1985, Franz & Gonzalez 1997). Macroplankters such as krill, which avoid such nets, are also not included. Eight years of acoustic surveys north of the island gave a mean krill biomass of ~59 g wet mass m^{-2} (Brierley et al. 1999b), or ~14 g dry mass m^{-2} , which is a similar value to that for mesozooplankton (Table 3). South Georgia is in the northern part of the AAZ, a zone where mesozooplankton reach a maximum near the PF (Foxton 1956, Pakhomov & McQuaid 1996, Atkinson & Sinclair 2000), but where krill are near their northern limit (Marr 1962). The abundance of krill at South Georgia means that the combined biomass of krill and mesozooplankton far exceeds that elsewhere in Antarctica.

Furthermore this area of high biomass is extensive, and covers a much wider area than just the island shelf. The values in Table 3 are from oceanic as well as shelf stations and transects from here to the PF show high copepod numbers well downstream of the island (Ward et al. 1996, Atkinson et al. 1999). Mackintosh (1934) depicted the whole of the Scotia Arc region as having a higher biomass than the Scotia Sea, Antarctic Peninsula area or the Weddell Sea. Thus at South Georgia, and possibly downstream, there may be regional enhancement associated with parts of the Scotia Ridge.

Table 3. Mesozooplankton biomass at South Georgia compared to other Southern Ocean zones. Comparative data selected from spring/summer surveys with nets (mainly $\leq 200 \mu\text{m}$), sampling deep enough to encompass most biomass. Note that macroplankton or micronekton (e.g. krill) are under-represented in these estimates (see text)

Zone	Region	Time of year	Sampling net and depth	Biomass, g dry mass m^{-2}	Main contributors to net-caught biomass	Source
South Georgia waters	Shelf and oceanic monitoring sites	Jan	200 μm mesh net, 0–200 m, 0–700 m	13	Copepods	Ward et al. (1995)
	Shelf monitoring site	Jan	200 μm mesh net, 0–200 m	12	75% copepods	Atkinson et al. (1996)
	Shelf and oceanic monitoring sites	Oct/Nov	200 μm mesh net, 0–150 m, 0–1000 m	6.5–16	81–98% copepods	Ward & Shreeve (1999)
Near/within Polar Front	Average of all sectors, 50–55° S	Nov–Apr	N70V net (~200 μm), 0–1000 m	3.6 ^{a,c}	(Not analysed)	Foxton (1956)
	Pacific sector	Jan	202 μm Bé net, 0–1000 m	4.1	70% copepods	Hopkins (1971)
	North of South Georgia	Feb	200 μm net, 0–200 m	6.3	65% copepods	Atkinson (1996)
	6° W	Oct/Nov	64 and 200 μm nets, 0–500 m	6.1 ^c	84–87% copepods	Franz & Gonzalez (1997)
	Indian sector	Dec	N70V net (~200 μm), 0–500 m	0.68 ^c	(Not presented)	Kawamura (1986)
Antarctic Zone	Average of all sectors, 55–65° S	Nov–Apr	N70V net (~200 μm), 0–1000 m	2.3 ^{a,c}	(Not analysed)	Foxton (1956)
	Pacific sector	Jan	202 μm Bé net, 0–1000 m	2.1	67% copepods	Hopkins (1971)
	6° W	Oct/Nov	64 and 200 μm mesh nets	2.6 ^b	75–81% copepods	Franz & Gonzalez (1997)
	15° W	Feb	Compiled from bottles, plankton nets and pelagic trawl	2.0 ^c	75% copepods	Voronina et al. (1994)
	Indian sector	Dec	N70V net (~200 μm), 0–500 m	2.5 ^c	No data	Kawamura (1986)
East Wind Drift /near continent	Average of all sectors, 65–70° S	Nov–Apr	N70V net (~200 μm), 0–1000 m	1.8 ^{a,c}	(Not analysed)	Foxton (1956)
	Lützow-Holm Bay	May–Dec	Parasol net (350 μm), 0–660 m	1.1 ^{a,c}	Copepods dominate	Fukuchi et al. (1985)
	Croker Passage	Apr	162 μm net, 0–1000 m	3.1	>75% copepods	Hopkins (1985)
	Ross Sea	Feb	162 μm net, 0–800 m	1.5–3.4	Copepods and pteropods dominate	Hopkins (1987)
	Western Weddell Sea	Mar	162 μm net and water bottles	1.1–1.3	Copepods (biomass ~trebled if euphausiids and salps included)	Hopkins & Torres (1988), Lancraft et al. (1989)
	Eastern Weddell Sea	Feb	Bottles, plankton net, trawl in top 200 m	1.5 ^c	77% copepods	Voronina et al. (1994)

^aValues converted from displacement volume to wet mass using 1 ml = 1 g (Hopkins 1971)

^bValues converted from ash free dry weight (AFDW) to dry mass (DM) using AFDW = 0.9 DM

^cValues converted from wet mass (WM) to dry mass using WM = 4 DM

2.3.2. Composition

Krill comprise about half of the overall zooplankton biomass at South Georgia, so they are described separately and in more detail in Section 2.3.3. Here we describe the remaining zooplankton. Copepods comprise >60% of the biomass caught with ring nets at South Georgia, in common with other Antarctic zones (Table 3). Also in common, the rest is mainly small euphausiids, pteropods, amphipods (mainly *Themisto gaudichaudii*) and chaetognaths (Atkinson & Peck 1988, Ward et al. 1995, Pakhomov et al. 1997b). However, salps are not so prominent as in higher latitudes (e.g. Hosie 1994, Ross et al. 1996, Perissinotto & Pakhomov 1998). Foxton (1966) described the AAZ zone as the main habitat of *Salpa thompsoni*, the most abundant salp in Antarctica. 'Salp years' are being reported with increasing frequency in the Southern Ocean (Loeb et al. 1997, Perissinotto & Pakhomov 1998), but at South Georgia they have only been prominent in 3 of the last 15 summers (BAS unpubl.), and even during these they are not so pervasive as during 'salp years' further south (e.g. Ross et al. 1996, Loeb et al. 1997). Salps appear to be most successful in offshore regions (Hosie 1994) and

at intermediate chl *a* concentrations ($\sim 1 \text{ mg m}^{-3}$; Perissinotto & Pakhomov 1998). This may explain the comparative rarity of salps at South Georgia.

Copepod biomass is dominated by the large Antarctic and Subantarctic species, *Calanoides acutus*, *Rhinocalanus gigas* and *Calanus simillimus*, reflecting the mixture of cold and warmer water species typical of the northern part of the AAZ. Their relative abundance reflects the origin of the watermasses—for example, warm water areas, possibly eddies from the APF, were inhabited by predominantly Subantarctic assemblages (Atkinson et al. 1990). Small species, particularly of the genera *Oithona* and *Ctenocalanus*, are moderately abundant around the island, but their numbers are much lower than those near the PF (Atkinson et al. 1999). However the small neritic species *Drepanopus forcipatus* is very numerous, particularly close to the island. This clausocalaniid has a patchy distribution (Hardy & Gunther 1935, Fig. 5) and can comprise 70% of the net-caught biomass (Ward & Shreeve 1999).

The neritic community is more prominent at South Georgia than at most other isolated islands in the Southern Ocean (cf. Perissinotto 1989, Pakhomov & Froneman 1999 for Marion Island). This is probably

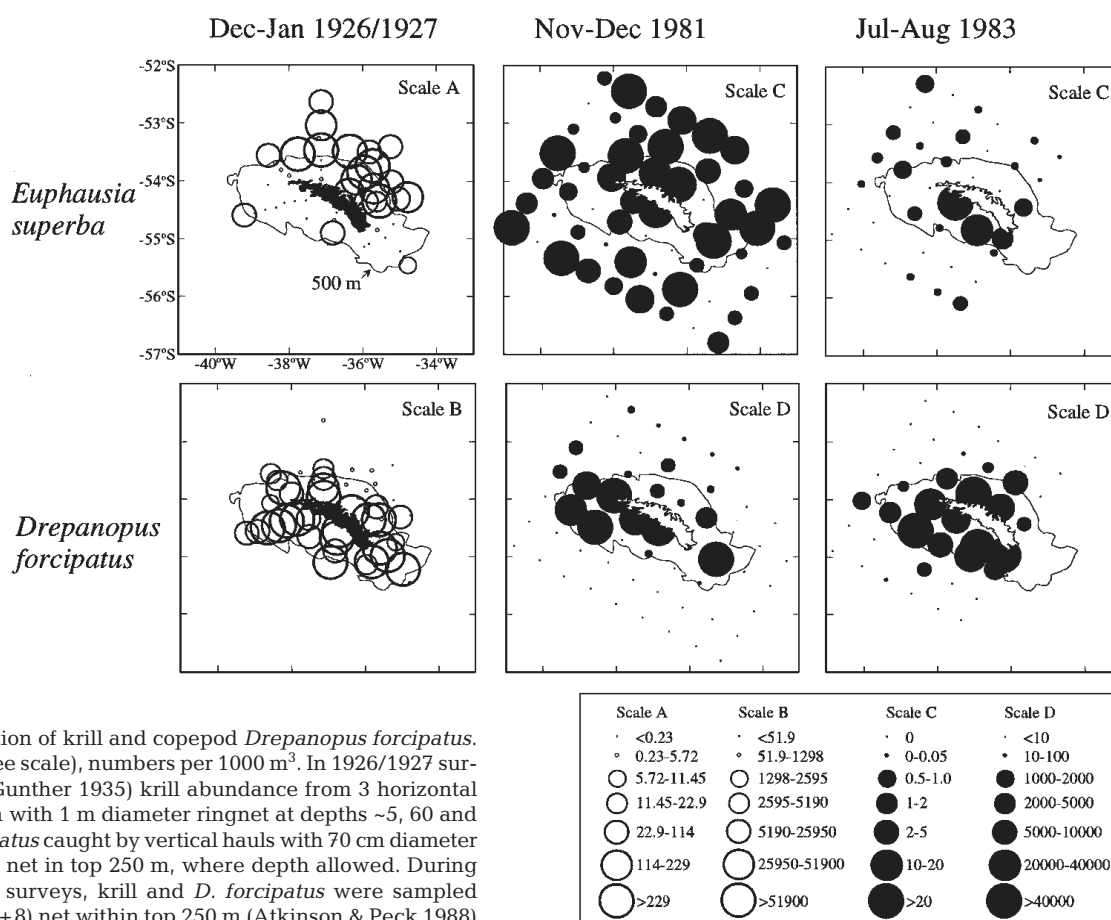


Fig. 5. Distribution of krill and copepod *Drepanopus forcipatus*. Abundances (see scale), numbers per 1000 m^3 . In 1926/1927 survey (Hardy & Gunther 1935) krill abundance from 3 horizontal tows of $\sim 1.8 \text{ km}$ with 1 m diameter ringnet at depths ~ 5 , 60 and 120 m. *D. forcipatus* caught by vertical hauls with 70 cm diameter Nansen closing net in top 250 m, where depth allowed. During 1981 and 1983 surveys, krill and *D. forcipatus* were sampled with an RMT (1+8) net within top 250 m (Atkinson & Peck 1988)

because of the broader shelf, with a more retentive circulation pattern (Atkinson & Peck 1990, Brandon et al. 2000). *Drepanopus forcipatus* is the major neritic species, but the coasts and fjords are also spawning and nursery grounds for commercially exploited fish, in particular the mackerel icefish *Champoscephalus gunnari* (North & Murray 1992), which is reliant on *D. forcipatus* for food (North & Ward 1989, 1990).

2.3.3. Krill (*Euphausia superba*)

Krill are a species of the seasonal sea ice zone, so South Georgia is an atypical habitat, being near the northern limit of their distribution and almost always free of pack ice. The lack of early larvae at South Georgia led Marr (1962) to suggest that they do not breed successfully here, a finding since supported by Ward et al. (1990). Although it has long been known that South Georgia krill come from upstream (Marr 1962), the source regions, and how and when they arrive at the island, are of continued debate.

The most reliable place to find krill at South Georgia is the shelf break to the north of the central region of the island (e.g. Hardy & Gunther 1935, Elizarov 1971, Mackintosh 1973, Pakhomov et al. 1997a, Murphy et al. 1997). However, they are much more widely distributed; schools are found throughout the region, often with no clear link to bathymetry or hydrography (Murphy et al. 1991, Goss & Everson 1996; see Fig. 5). The central northern shelf break was the site of the largest catches of baleen whales (Kemp & Bennett 1932, Everson 1984) and is now one of the major sites for the winter krill fishery (Trathan et al. 1998a). Marr (1962) attributed this distribution directly to hydrography. The coldest water, described by Deacon (1933) and Hardy & Gunther (1935) as being of Weddell origin, was to the north and east of the island and was invoked as the main source of krill (Marr 1962, Maslennikov & Solyankin 1988).

Recently, Marr's (1962) suggestion that waters of mainly Weddell Sea origin supply krill to South Georgia has not been supported by Hofmann et al. (1998). Their model of larval transport across the Scotia Sea suggested that populations west of the Antarctic Peninsula provide the source. Perhaps this conflict can be reconciled if we consider that mesoscale transport is pronounced in the Southern Ocean (Huntley & Nisler 1995). Iceberg drift directions certainly show that Weddell water can arrive at South Georgia (Trathan et al. 1997, Murphy et al. 1998; Fig. 2b). Watkins et al. (1999) found that the smallest krill tended to occur towards the east end of the island, in water which they identified as 'Weddell' in origin, whereas at the western end, with greater influence of 'Bellingshausen'

water, an additional, larger, year class sometimes occurred. They suggested that this reflected the differing age structures from 2 distinct source regions, as well as possibly different conditions during their transit to, and while at, each end of South Georgia. Thus the transport of krill to South Georgia is probably discontinuous and from several distinct sources.

The origin and fluctuations in krill stocks at South Georgia are currently areas of active research interest. Since the SACCF lies adjacent to the krill-rich area north of the island (Fig. 1a), its role as a transport pathway to the island is being addressed. A degree of connection between the southern Scotia Sea and South Georgia krill populations was suggested by Brierley et al. (1999a). They linked interannual fluctuations in krill biomass at South Georgia with same-season fluctuations in the Elephant Island area. This compares with a ~5 mo transit time from the Antarctic Peninsula to South Georgia estimated by Hofmann et al. (1998). Interannual fluctuations in South Georgia krill stocks, and how they relate to those in the source regions, is a topic revisited in Section 4.1.3.

3. INTERACTIONS

The previous sections describe substantial biomasses of phytoplankton, microheterotrophs, mesozooplankton and krill at South Georgia. The island also supports valuable commercial fisheries and large numbers of higher predators. Here we examine the interactions leading to the high biomasses: do they reflect physical concentration mechanisms or high local productivity? The biomass of an organism in a defined area, for example over the South Georgia shelf, is a function of the additive processes, i.e. the rate of advection into the area, the local rate of growth and reproduction, minus the losses; local mortality and advection from the area. These are considered in turn for phytoplankton, copepods and krill.

3.1. Controls on phytoplankton

3.1.1. Factors enhancing primary production

The blooms at South Georgia do not typify the HNLC waters of the AAZ. So which controls have been lifted to allow algal growth? Potential controls on primary production in the Southern Ocean include limitation by nutrients, low temperatures, light and vertical mixing (Chisholm & Morel 1991, Tréguer & Jacques 1992, Smith et al. 1996). These are considered in turn.

Nutrients. The South Georgia data set for the major macronutrients, nitrogen, silicon and phosphorus, sug-

gests that these are only rarely limiting to phytoplankton growth (Whitehouse et al. 1996a, Section 2.2.1). Of the other nutrients which restrict phytoplankton growth in the Southern Ocean, iron has received much attention recently (de Baar & Boyd 2000). Although required only in trace quantities, iron is a key constituent in many systems in algal cells, including components of the photosynthetic electron transport system (Geider & La Roche 1994). Low iron availability appears to be characteristic of much of the Southern Ocean (de Baar et al. 1995). While iron availability near South Georgia is unknown, it was suggested to promote phytoplankton growth downstream of the island (de Baar et al. 1995). These authors found low phytoplankton biomass in the AAZ coincident with iron/phosphate ratios well below those critical for growth, while the more productive adjacent PF waters had more iron, the source for which was suggested to be the Northeast Georgia Rise (see Fig. 2b). Given the extent of glaciation and island run-off at South Georgia, and the communication between shelf and offshore waters (Brandon et al. 1999, 2000), it is likely that much of the island's shelf water, and that downstream, is iron-replete. Further indirect evidence of South Georgia waters being replete in iron is the abundance of large diatoms which characterise its local and downstream blooms—algae of a size probably under most iron stress (Hudson & Morel 1990, Sunda & Huntsman 1997).

Iron availability will also impinge on the active transport of nutrients into the cell. In the case of nitrate, low iron availability will diminish the cell's ability to synthesise the enzymes needed to convert nitrate into ammonium (Timmermans et al. 1994). In addition to the effects of iron on nitrate utilisation, other factors may determine *f*-ratio, i.e. the ratio: (nitrate assimilation)/(nitrate + reduced nitrogen assimilation). High concentrations of ammonium may reduce nitrate utilisation, possibly through inhibition of uptake (Flynn et al. 1997). Armstrong (1999) has suggested that the degree of ammonium inhibition of nitrate utilisation is determined by iron availability. An inadequate iron supply appears to decrease nitrate utilisation, and thus decreases the ammonium concentrations at which very low *f*-ratios occur. Studies in the Southern Ocean suggest that the effect of ammonium inhibition on nitrate utilisation varies spatially (Glibert et al. 1982, Owens et al. 1991, Mengesha et al. 1998, R. Sanders pers. comm.). Although Owens et al. (1991) noted the importance of reduced forms of nitrogen around South Georgia, they measured average *f*-ratios of ~0.5 (ranging from 0.96 inshore at Cumberland Bay to 0.29 at the shelf-break to the northeast). Recent studies suggest that, although at least part of this system is probably replete in iron, the observed under-utilisation of nitrate is due to a preference by phytoplankton for reduced

nitrogen, and may be a consequence of low water temperatures (R. Sanders pers. comm.). The nitrate affinity of several algal species was found to be dependent on temperature, while their affinity for ammonium appeared unrelated to temperature (Priddle et al. 1998b, Reay et al. 1999, in press).

Therefore despite typically high concentrations of nitrate in the waters around South Georgia, the supply rates of reduced nitrogen (e.g. ammonium) has an important role in dictating phytoplankton growth rates (Owens et al. 1991, Priddle et al. 1997, Whitehouse et al. 1999). A tight coupling between the processes of uptake and resupply is suggested by observations, made during several seasons, of a diel cycle in ammonium concentrations in the upper mixed layer (Priddle et al. 1997). Although the major regenerators of nitrogen are generally microheterotrophs and bacteria (Glibert et al. 1992, Miller & Glibert 1998), the high concentrations of metazooplankton and higher predators at South Georgia also appear to have a role. Excretion rates of copepods and krill measured at South Georgia suggested that they could supply ~50 to 80 % of the ammonium required for phytoplankton growth in the ECB (Atkinson & Whitehouse 2000, in press, see Fig. 1b for the location of the ECB). We stress that these are averages over a wide area: the patchy distribution of krill would mean wide fluctuations about these values. However, in the WCB, where krill biomass is generally lower and primary production higher, copepods and krill were estimated to supply <20 % of the required ammonium.

At this western end of the island, land-breeding predators, in particular macaroni penguins *Eudyptes chrysolophus* and Antarctic fur seals, are abundant (Boyd 1996, Prince & Poncet 1996). Their high metabolic costs result in rapid recycling of dietary nitrogen. When their foraging ranges are constrained during the breeding season, their excretion effectively concentrates nitrogen near their breeding site. From models of their biomass, foraging activity and physiology, Whitehouse et al. (1999) suggested that these 2 species were effective redistributors of nitrogen, and that run-off of guano and excretion from the colony areas could provide a 'point source' of ammonium to trigger in-shore blooms. Such a scenario has been proposed for the high productivity observed near other Southern Ocean islands, such as the Prince Edward Island group (Burger et al. 1978, Ismail 1990, Perissinotto & Duncombe Rae 1990).

Other nutrients also appear to modulate phytoplankton growth in the waters to the north of South Georgia. During some seasons, silicic acid concentrations in waters of ACC origin fall to <1 mmol m⁻³, which is likely to limit diatom growth (Clowes 1938, Whitehouse et al. 1996a, 2000). Silicon limitation may there-

fore operate as a secondary control at certain times, or in regions of high productivity. The demand for silicon differs between diatom species, and it may dictate a succession of progressively more tolerant algae as concentrations fall. Whitehouse et al. (2000) found elevated chl *a* levels coincident with apparently large silicic acid depletions in the off-shelf waters to the north of the island. South Georgia is influenced by the SACCF and silicic acid-replete waters from higher latitudes—this may replenish locally depleted waters.

Temperature. On an interannual scale, there appears to be a link between temperature and phytoplankton growth at South Georgia. Anomalously cold seasons (e.g. 1981/1982) were characterised by delayed and probably low primary production, while warmer seasons (e.g. 1985/1986) tended to be more productive (Whitehouse et al. 1996b). Whether this is a direct or indirect effect is unknown. Temperature affects physiology directly and thus could lead to higher primary production rates in warmer seasons or warmer parts of a species' range. Q_{10} values for microbial respiration obtained from sites between the Falklands and South Georgia lay in the range 1 to 3 (Robinson & Williams 1993), similar to literature values for photosynthesis. It appears that in the Southern Ocean, temperature compensation of algal photosynthesis is poor and rates are below the maxima attainable for these species (see Smith et al. 1996). The source regions of the phytoplankton at South Georgia are from higher latitudes with less seasonal warming, so locally higher temperatures ($>4^{\circ}\text{C}$), for example over the shelf and northwest of the island, could enhance primary production, although temperature alone is unlikely to be the main factor promoting phytoplankton blooms.

Temperature may have important indirect effects: both on the environment, such as in promoting thermal stratification (Smith et al. 1996, Priddle et al. 1998b) and on algal physiology, such as their nutrient preference (see previous section 'Nutrients'). Although temperature may thus modulate primary production rates, the patchy nature of the blooms and high range of primary production rates across small temperature ranges suggest that it is a secondary control factor at South Georgia.

Light and vertical mixing. The high primary productivity in some regions of the marginal ice zone has been attributed to high irradiance within shallow meltwater lenses (e.g. Smith & Nelson 1990, Cota et al. 1992). Likewise at South Georgia the fjords and inlets are surrounded by glaciers and high mountains, which provide both shelter from the prevailing westerlies and a source of meltwater to enable shallow stratification. This combination has been suggested to promote phytoplankton growth by seeding from fjords (Hart 1934), and indeed elevated chl *a* concentrations have

been recorded inshore as early as September (BAS unpubl.). However, high primary production rates are often found well offshore, in the prevailing westerlies and in no more stratified conditions than in low productivity parts of the AAZ. Although the release from light limitation may be important in generating inshore blooms, its effect seems too local to be more than a contributing factor.

3.1.2. Mortality

Grazing. With the exception of salp blooms and krill schools, Southern Ocean metazooplankton generally have a minor grazing impact on phytoplankton stocks (Schnack et al. 1985, Atkinson 1996, Dubischar & Bathmann 1997, Swadling et al. 1997, Razouls et al. 1998). However, protozoans may at times be important grazers (Garrison 1991, Burkill et al. 1995). At South Georgia the high biomasses of metazooplankton and protozoans would suggest high grazing losses. While there are no estimates for protozoans, the assemblage caught in 200 μm ring nets could alone exert a significant grazing impact (Table 4).

Variability in the calculated grazing impact reflects that of primary production more than that of zooplankton biomass or grazing rate. Thus the impact found during a bloom (Atkinson et al. 1996) was much lower than that post-bloom in the same season (Pakhomov et al. 1997a,b). In these post-bloom conditions of small cells, Pakhomov et al. (1997a) found a higher impact on the primary production of cells $>20 \mu\text{m}$. Small cells are possibly not eaten so readily by metazooplankton (Quetin & Ross 1985, Berggreen et al. 1988), and are under control from protozoans (Garrison & Gowing 1993, Karl et al. 1996). However this still requires a proper appraisal at South Georgia, as the ratios between grazer size and food size vary greatly, both among copepods (e.g. Lampitt 1978) and among protozoans (Jacobsen & Anderson 1993). For example, in the South Georgia area the tiny *Oithona* spp. are fully capable of eating the large, bloom forming diatoms (Atkinson 1994, 1996).

Sedimentation. The rich benthos on the South Georgia shelf suggests substantial export of organic material from the epipelagic. Although there are no direct estimates of sedimentation rate, the composition of this material has been determined (Priddle et al. 1995, G. C. Cripps unpubl.). Recognisable krill faecal strings were a predominant item, and these formed roughly half of the material (maximum 70%). This contained useful dietary material, such as polyunsaturated fatty acids, in contrast to the remainder which was highly degraded and amorphous. However, generalisations about the relative importance of mass sedimentation of

Table 4. Available estimates of zooplankton biomass, grazing rate and grazing impact in relation to net primary production rates at South Georgia. Estimates only included if grazing rates and primary production rates measured directly in same area and season

Region and time	Biomass of zooplankton whose grazing impact estimated (g dry mass m ⁻²)	Total zooplankton biomass (g dry mass m ⁻² in top 200 m)	Maximum chl <i>a</i> concentration (mg m ⁻³)	Primary production rate (g C m ⁻² d ⁻¹)	% of primary production removed	Comments on grazing impact measurements
Oceanic monitoring site in WCB Jan 1990	6.3 ¹¹ Herbivorous copepods and small euphausiids in upper mixed layer and thermocline	13 ¹¹ in top 800 m, including carnivorous species but excluding krill	1.2 ⁹	0.45 based on ¹⁵ N method ⁶	25 ¹¹	Copepod values based on bottle incubations ¹ , but small euphausiid carbon rations assumed as 20%
Oceanic monitoring site in WCB Jan 1994	9.2 ³ Copepods	12 ³ excluding krill	19 ³	8.9 ³ Gross microbial production based on oxygen flux measurements	1.2–1.3 ³	Values based on gut fluorescence and bottle incubations. Impact on net primary production will be higher, but still less than 5 %
South Georgia shelf and oceanic sites Feb/Mar 1994	8 ⁸ Total mesozooplankton excluding krill	~10–15 total for mesozooplankton and krill	1.2 ⁸ median of 8 sites	0.45 ⁸ ¹⁴ C method, median of 8 sites	26 ⁹ median of 7 values	Gut fluorescence used for large copepods and small euphausiids. Literature values for pteropods and small copepods
South Georgia shelf Feb/Mar 1994	7.7 ⁷ Krill only, based on acoustics and converted to dry mass ⁵	~10–15 total for mesozooplankton and krill	0.67 ⁷ median of 4 sites, and converted from depth integrated measurements	0.31 ⁷ ¹⁴ C method, median of 4 sites	27 ⁷ median of 4 sites	Gut fluorescence. Regional average will be lower as the stations used had high krill densities
South Georgia region, shelf and oceanic sites Jan/Feb 1996	8.3 ² Krill only, based on acoustics ⁴ and converted to dry mass ⁵	9.6 ² total for krill and copepods	1.7 ¹⁰	Mean ~1.0 ¹⁰ range 0.44 in ECB to 1.88 in WCB	1.4 ² based on gut fluorescence	Gut fluorescence, using regional average krill biomass. Incubations in ambient seawater ² yield an impact of ~2.2 % of primary production d ⁻¹

¹Atkinson (1994), ²Atkinson & Snýder (1997), ³Atkinson et al. (1996), ⁴Brierley et al. (1997), ⁵Morris et al. (1988), ⁶Owens et al. (1991),

⁷Pakhomov et al. (1997a), ⁸Pakhomov et al. (1997b), ⁹Pridde et al. (1995), ¹⁰British Antarctic Survey (unpubl.), ¹¹Ward et al. (1995)

blooms and krill grazing should be avoided—long time-series of trap data in the Bransfield Strait (von Bodungen et al. 1986, Wefer et al. 1988) suggest that sedimentation can be highly pulsed, and vary annually in both amount and composition.

Vertical distributions of nutrients, chl *a* and C and N have been measured at South Georgia, and these give some insights into vertical loss processes. Chl *a* profiles suggest that phytoplankton biomass in summer is distributed fairly uniformly through the upper mixed layer, which is typically 50 to 70 m deep. Subsurface chl *a* maxima are rare. Where phytoplankton biomass is high (e.g. $>5 \text{ mg chl } a \text{ m}^{-3}$), the biomass maximum is shallow, although the mixed layer may extend beneath this. This contrasts with ammonium maxima frequently found at the base of the mixed layer, suggestive either of remineralisation there or faster uptake above (Priddle et al. 1995, Whitehouse et al. 1999). Furthermore, Priddle et al. (1995) found that C:N ratios at their 3 South Georgia sites increased with depth, suggesting that C and N are not exported stoichiometrically. In other words, N was remineralised in the upper layers but C was exported. C:N ratios are generally fairly stable with depth elsewhere, which allows the use of nitrate uptake to set an upper limit on C export (Dugdale & Goering 1967). However, both increases and decreases in C:N ratios with depth have been found before (Sambrotto et al. 1993, Karl et al. 1996). The fact that they have been found to increase with depth at South Georgia suggests that the C and N cycles are partially decoupled, allowing the possibility for regenerated N to fuel C export in this system.

3.1.3. Advection

Doubling times of algae are measured in days, so compared to slower growing organisms such as krill, local growth and mortality are likely to be more important in dictating algal biomass around South Georgia. From the FRAM vectors (Fig. 2a) we have estimated a mean current speed of $\sim 4 \text{ cm s}^{-1}$ over the northern shelf, based on the mean of all current vectors there. It would therefore take ~ 2 mo for water to travel from one end of the island to the other. FRAM vectors are not ideal for estimating current velocity in shallow water, but the slow currents suggested are supported by direct observations using an Acoustic Doppler Current Profiler (ADCP; Brandon et al. 2000). This suggests that phytoplankton biomass over the shelf will be determined by local production and losses rather than critically dependent on advection. Even in the offshore ocean currents, the rate of advection through the system is ~ 2 to 3 wk (Fig. 2b), which is long relative to phytoplankton doubling times.

Satellite data (Fig. 3 and Sullivan et al. 1993) suggest that the South Georgia system generates phytoplankton biomass which is then exported downstream. However, advection from the shelf area is likely to be by mesoscale processes and possibly intermittent, so it will be hard to quantify. During the early summer of 1981 the phytoplankton community composition was similar over the shelf and downstream (Fig. 4). This suggests that, at least intermittently, these regions are connected hydrographically and allow phytoplankton from the shelf to be lost to the north. A site for such a shelf/ocean exchange was found near the northern shelf break (Brandon et al. 2000). Summer chl *a* values are often high in the large region north (i.e. downstream), between the island and the PF (Fryxell et al. 1979, El-Sayed & Weber 1982, Whitehouse et al. 1996b, 2000). These downstream blooms may be of both gradually ageing populations (Fryxell et al. 1979) and of actively growing cells (Whitehouse et al. 1996b, 2000). A fast frontal jet, the SACCF, flows westwards near South Georgia's northern shelf before turning eastwards (Fig. 1a). The oceanic blooms just north of the island, and a meandering stream of high chl *a* water following the position of this front (Fig. 3), suggest that the SACCF may advect blooms rapidly from this system.

3.1.4. Conclusions

Interpretations of the HNLC paradox have moved from the search for single limiting factors towards understanding the interaction of complex multiple controls (Tréguer & Jacques 1992, Marchant & Murphy 1994, Priddle et al. 1998b). At South Georgia, all the major controls on primary production, except for grazing, are reduced, so a combination of factors would appear to enhance phytoplankton growth. These include: (1) possibly enhanced supplies of iron; (2) rapid recycling of N; (3) temperatures that can be elevated over the shelf due to seasonal warming; and, (4) local inshore conditions providing shallow stable stratification for bloom formation. All of these conditions are most favourable either close inshore or downstream, where chl *a* values are highest. Phytoplankton doubling times are probably fast enough for biomass to be built up within the system, despite fairly fast currents off the shelf. Nevertheless, fast frontal jets and extensive blooms downcurrent suggest that South Georgia influences a very large area. Despite the frequent blooms, the mesozooplankton and krill exert some control on phytoplankton biomass. This suggests a large flux to these grazers, so that within the same system, enhanced plant growth can be translated into enhanced animal growth.

3.2. Controls on copepods

3.2.1. Growth and reproduction

The accumulation of copepod biomass in a retentive system lasting possibly from weeks (offshore) to months (onshore) should reflect the rates of both reproduction and growth. These are related to food availability and temperature, both of which are locally high at South Georgia compared with other parts of the AAZ. Given that food needs to be above a threshold value for positive growth to take place, the prolonged bloom season here would benefit copepods for a large part of their life cycle.

However, regional comparisons of chl *a* concentration and the rates of copepod egg production and growth do not show quite such a clear picture. While growth rates of *Calanoides acutus* were strongly related to chl *a* concentrations, those of *Rhincalanus gigas* were not (Shreeve & Ward 1998), and their egg production rates were only weakly correlated (Ward & Shreeve 1995). As well as the problem of time/space effects in this analysis, chl *a* can be a poor proxy for food (e.g. White & Roman 1992, Pond et al. 1996, Ross et al. 2000). A 'balanced diet' including protozoans seems to help zooplankton growth and development (see Stoecker & Capuzzo 1990, Kleppel 1993). The protozoan community appears to be both diverse and substantial at South Georgia, but studies of food quality are still at an early stage here (Pond et al. 1993, Cripps et al. 1999). Experiments have suggested that, even during blooms, some copepods (*Calanus simillimus*, *C. propinquus*, *Metridia gerlachei*) cleared protozoans faster than diatoms of similar size, whereas *C. acutus* and *R. gigas* cleared them at similar rates (Atkinson 1994, 1995, Atkinson et al. 1996). As in other regions (e.g. Gifford 1993, Ohman & Runge 1994) there is a significant flow of energy from the microbial network to zooplankton at South Georgia.

Calanoides acutus is a dominant copepod at South Georgia, and work on it illustrates a copepod's response to blooms. This mainly herbivorous species is fully capable of ingesting bloom-forming diatoms, even though they are often dominated by cells and colonies >500 µm long (Atkinson 1994, 1995, Atkinson et al. 1996). The rates of feeding, growth and egg production at high chl *a* concentrations fit into a plausible energy budget. The daily ration of copepodite stage V (CV) and adults during South Georgia blooms ranged from 10 to 27% of body C d⁻¹ (Atkinson et al. 1992, 1996), which fits with a respiration rate of 3.8% (Schnack et al. 1985) and egg production rates of 1.2 to 4.5% (Lopez et al. 1993, Ward & Shreeve 1995), measured at high chl *a* concentrations. Somatic growth rates are not available for these late copepodites, but those of early cope-

podites were fast—a mean of 14% of body C d⁻¹ for stages CI to CIV (Shreeve & Ward 1998).

Thus copepods can respond rapidly to enhanced microplankton biomass at South Georgia. On the time-scale of water circulation around the island, growth rates measured for *C. acutus* would have time to produce a significant increase in biomass.

3.2.2. Mortality

Copepod mortality is probably high due to the large populations of a wide array of predator. These include vertebrates, such as prions and diving petrels (Goss et al. 1997, Reid et al. 1997a,b), as well as fish larvae (North & Ward 1989, 1990) and a wide range of invertebrates. The latter include euchaetiid copepods (Øresland & Ward 1993), the amphipod *Themisto gaudichaudii* (Pakhomov & Perissinotto 1996), and also krill. Krill are known to be omnivorous (Price et al. 1988, Hopkins et al. 1993a,b) but are considered to be mainly herbivorous in summer (see Miller & Hampton 1989, Quetin et al. 1994). However, evidence is accumulating that South Georgia krill eat other zooplankton during non-bloom conditions. This has been indicated by a variety of methods, including: gut content analysis (Nishino & Kawamura 1994, Pakhomov et al. 1997a), feeding experiments (Atkinson & Snýder 1997) and lipid biomarker analysis (Cripps et al. 1999, Cripps & Atkinson 2000). Indeed the feeding rates on 1 to 3 mm copepods found in large volume incubations suggest that when krill do feed on copepods, they could have a major predatory impact (Atkinson & Snýder 1997).

The biomass of krill at South Georgia far exceeds that of any of the better known copepod predators. Furthermore, distribution studies suggested that copepod abundance was severely affected by the presence of krill (Atkinson et al. 1999). In this respect, krill would appear to be the most important single 'top-down' control on copepod abundance. At a fine scale, krill schools coincided with very low copepod numbers but dispersed krill were associated with elevated concentrations of copepods. At the mesoscale, areas of high krill abundance were not clearly related to hydrographic features. This disassociation provided the opportunity to separate the affects of krill and environmental parameters as predictors of copepod abundance (Atkinson et al. 1999). Copepod abundance was found to be linked more closely to that of krill than to any environmental variable measured.

Such analyses require care when interpreting cause and effect. For example krill sometimes concentrate at shelf breaks (Agnew & Nicol 1996, Quetin et al. 1996) and in such cases, negative relationships with other zooplankton could be explained by their different

habitat preferences (see Hosie 1994). This cannot explain the South Georgia results, as krill swarms are found throughout the region, and the krill-copepod interaction was more widespread than a shelf break effect (Atkinson et al. 1999). Instead there appears to be a direct interaction between the 2 taxa, but whether this is through competition or predation is unclear. Whatever the nature of this interaction, the notion that copepod abundance is influenced so strongly by another species is unusual. Until recently (e.g. Huntley et al. 1989, Loeb et al. 1997) most Southern Ocean studies have examined zooplankton from the perspective of environmental (i.e. bottom-up) factors, rather than from top-down controls. Clearly a direct interaction between krill and copepods would have profound implications for the South Georgia food web.

3.2.3. Advection

Compared to the short doubling times of phytoplankton, generation times of Southern Ocean copepods are typically 0.5 to 2 yr (Marin 1988, Schnack-Schiel & Mizdalski 1994, Metz 1996), so advection will be relatively more important in dictating their local biomass. We cannot yet quantify advection rates of zooplankton into the South Georgia area, or whether there may be physical mechanisms such as convergent fronts around the island that might concentrate biomass (e.g. Franks 1992). A shelf break front was found in the ECB (Brandon et al. 1999), but whether it acts as a local concentration mechanism is unknown. However, the distribution, age structure and abundance of copepods give some insights into the circulation and residence times of water.

The neritic copepod *Drepanopus forcipatus* is abundant not just inshore but over a large extent of the shelf (Fig. 5). Shelf/oceanic contrasts in abundance also occur for seasonal vertical migrants and mesopelagic species (Fig. 6). Atkinson & Peck (1990) suggested that this combination of patterns could be explained by a restricted exchange of water between the shelf and the surrounding ocean. This is supported by ADCP data (Brandon et al. 1998, 2000) and FRAM vectors (Fig. 2a). Brandon et al. (2000) found a distinct water mass over the shelf, which infers that, in this region at least, local processes have time to influence copepod growth and reproduction.

Advection could remove copepods from this local South Georgia region. Occurrences of the neritic copepod *Drepanopus forcipatus* off the shelf edge (Fig. 5) provide evidence for advection, particularly downstream to the north. Mackintosh (1934) found high zooplankton biomass in a broad region along the Scotia Arc, and high copepod numbers have been found

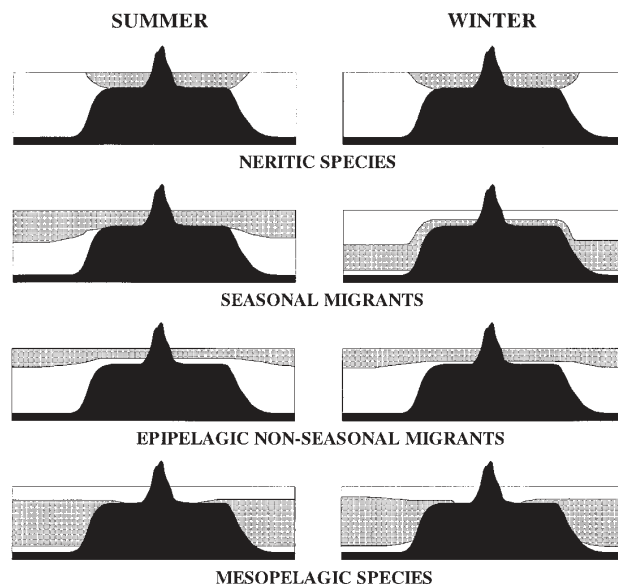


Fig. 6. Schematic representation of onshelf-offshelf zooplankton distribution for summer and winter surveys. Black areas represent cross sections through South Georgia and stippled areas represent distributions of major groups of species in relation to shelf and ocean in summer and winter

downstream of South Georgia to the north (Ward et al. 1996, Atkinson et al. 1999). Thus the enhancement, like that of algae, may be over a large area, although whether this represents advection or continued high production in downstream blooms is unclear.

3.2.4. Conclusions

Zooplankton grazing can account for a significant fraction of primary production (Table 4), which implies efficient energy transfer between trophic levels. There are not enough data to quantify energy flows through the microbial food web, but the importance of protozoans as dietary items for both copepods and krill in this area suggests a significant flow of energy out of the microbial network. Thus the retention time of water within this system is likely to allow the enhanced primary production to be channelled up the food web and to enhance zooplankton production. Given that krill and copepods have roughly similar overall biomass at South Georgia, secondary production by copepods will far exceed that of krill for allometric reasons. However, little is known about how copepods are incorporated into the food web. Krill appear to be the major single factor influencing their abundance, and the numerous small copepods may provide an alternative food source for krill during non-bloom periods. This may be an important trophic link given the large biomasses involved, and warrants further investigation.

3.3. Controls on krill

Several studies have suggested that the rates of krill removal by land-based predators are high relative to the krill stocks at South Georgia (Croxall et al. 1984, 1985, Trathan et al. 1995, Boyd & Croxall 1996). Recent interpretations (Murphy 1995, Murphy et al. 1998) have emphasised the importance of the ACC in supplying krill to within the foraging ranges of these predators. Boyd & Croxall (1996) calculated that there must be a replenishment of the entire krill population every month to support the land-based predators, which were suggested as the major cause of mortality of older krill (>40 mm length) at South Georgia. Their calculations do not include the krill removed by pelagic predators such as fish, squid and whales, implying that the water turnover rate needs to be even faster than 1 mo. A large part of the foraging of these predators is over the shelf, so the suggested fast turnover of water and krill conflicts with the evidence for a long residence time of shelf water presented in Section 3. The previous krill budgets have emphasised the preliminary nature of the calculations, particularly with regard to krill standing stock estimates. We have also constructed a simple krill budget with current best estimates. Unlike the other sections, the loss processes are the best known so we start with those.

3.3.1 Factors reducing krill biomass

Although loss rates of krill due to advection or migration are unknown, we do have estimates for losses to higher predators breeding on South Georgia. These are from the western end of South Georgia (Fig. 1b) where colonies of krill-eating predators are most numerous (Boyd 1996, Prince & Poncet 1996). This end of the island is thus the best place for a krill budget, although we stress that it will overemphasise the impact from land-breeding predators compared to the rest of the system. Our estimate is for Antarctic fur seals and macaroni penguins, which together consume >75% of the total for land-based predators (Croxall et al. 1985). Based on Boyd's (1993) survey, 95% of South Georgia's fur seal breeding population is based on its westernmost 60 km. Trathan et al. (1998b) show that 91% of the breeding population of macaroni penguins are based on the Willis Islands at South Georgia's westernmost tip. Our budget is an average for January when there is most information, being when BAS krill monitoring surveys most often take place and predator breeding studies are underway. Boyd & Croxall (1996) assessed the demand for krill of fur seals and macaroni penguins from a combination of physiological data and sampling from Bird Island. From their model for Janu-

ary, the average demand for krill by the South Georgia populations of both species was 32 000 tonnes fresh mass d^{-1} .

Estimates of foraging range of Antarctic fur seals and macaroni penguins are constrained by lack of information on the non-breeding individuals. These comprise >50% of their populations and are not tied to feeding around the island. So instead we have defined 2 areas, the first described by a radius of 100 km from the Willis Islands for the macaroni penguins and the second by a radius of 100 km from the westernmost 60 km of the island for the fur seals. These areas encompass most of the foraging by the breeding adults of the 2 species, which need to return regularly to the island to feed young (Boyd 1998, Boyd et al. 1998, Trathan et al. 1998b). The 100 km radius from Willis Island, where the foraging by both species overlaps, is the defined area of our krill budget. For this area, we calculate a total food removal by both species of 0.94 g fresh mass $\text{m}^{-2} \text{d}^{-1}$.

The estimated krill demand can be compared with a mean krill biomass of 30 g fresh mass m^{-2} . This is derived from acoustic monitoring surveys in the area of the krill budget, mainly in the 6400 km^2 WCB ($n = 5$ yr, range of annual means = 21 to 45 g fresh mass m^{-2} ; Brierley et al. 1999b). The comparison suggests that in this region the rate of removal of standing stock is, on average, ~3% d^{-1} .

This estimate is subject to several sources of variation or bias. Our defined area encompasses most, but not all, of the feeding area for those fur seals and macaroni penguins that are breeding and have to return regularly to land. A large proportion of the foraging by adult fur seals from Bird Island was found to occur well outside this 100 km radius (Boyd et al. 1998), so their impact would be less than that calculated. The fact that >50% of the populations of both species are non-breeders, which may not be so in the South Georgia system, would also mean that their actual predation pressure is substantially less than our calculated value. Although these 2 species are responsible for >75% of the krill eaten by land-based predators at South Georgia, other species, mainly white-chinned petrels *Procellaria aequinoctialis* and prions *Pachyptila* spp., are not tied to feeding within the area of our budget, and so their additional impact is probably small. Also, we have assumed that the mean krill biomass sampled within a portion of the budget area is representative of that of the whole. From limited data (Priddle et al. 1986), this does not appear to be an unreasonable or biased assumption.

Our calculated predation impact is superficially similar to that calculated by Boyd & Croxall (1996). However, our generous assumptions about the foraging ranges of the 2 species (see above) means that their

removal of krill from the budget area is probably less than our estimate. Also, Boyd & Croxall's (1996) budget was for the whole South Georgia system, whereas ours is just for the end of the island where most of the land-based krill predators breed. Thus for the South Georgia system as a whole, and also outside of the breeding season, the land-based predators are likely to crop a smaller krill biomass per km² than our estimate suggests. Future measurements will refine this simple budget, but at this stage it appears that each day the land-based predators remove a percentage of the krill biomass which is in low single figures.

3.3.2. Factors enhancing krill biomass

The estimate of krill removal at the western end of the island can be compared with rates of local growth and physical flux through the area. The only local measurements of krill growth are from Clarke & Morris (1983). Their rates, equivalent to ~3.5% of body mass d⁻¹, were questioned by Quetin et al. (1994) for being higher than other literature values, but they suggested that growth rates in this food rich, warm water area may indeed be higher than those further south. Growth rates equivalent to ~2% of body mass d⁻¹ were found by Rosenberg et al. (1986) in the Scotia Sea-South Georgia region. These are more representative of the higher range of values from further south. Considering the phytoplankton blooms, and temperatures reaching as much as 4°C, growth rates of ~2 to 4% d⁻¹ are not unreasonable. They fit krill rations of ~13 to 25% of body C d⁻¹ in high food concentrations (Clarke et al. 1988, Perissinotto et al. 1997) and with growth rates inferred from Antarctic fur seal diets (Reid 2001). Whatever the exact values, a krill growth rate of a few percent of biomass per day is probably of a similar order to our best estimates of their removal by land-based predators during their breeding period.

Since krill do not appear to breed at South Georgia, advection has long been known to be important in supplying them to the area (see Everson 1984, Murphy et al. 1998 for reviews). The area of our krill budget covers 2 zones of contrasting hydrographic conditions. In the inner, or shelf zone, advection is much slower than in the outer, or oceanic zone. However, even the sluggish currents over the shelf are likely to supply a substantial amount of krill to the budget area, compared to their rate of removal by land-based predators. Based on a 4.2 cm s⁻¹ current speed (see Section 3.1) over a ~60 km wide northern shelf, ~0.7% of the water in the budget area would be replaced each day. Currents over the southern shelf would also help to resupply krill to this end of the island, as would exchanges between the fast oceanic currents and the shelf. A site for such an ex-

change was noted in the vicinity of a Taylor column over an area of shallow topography in the WCB (Brandon et al. 2000). Therefore we suggest that advection, when combined with local growth, would easily meet the demands of local land-based predators.

3.3.3. Conclusions

Our conclusions contrast with those from previous studies (Croxall et al. 1984, 1985, Murphy 1995, Trathan et al. 1995, Boyd & Croxall 1996). The budget suggests that there does not need to be either a fast turnover of krill or an efficient concentration mechanism to meet the demand from predators based on South Georgia. Their impact in summer probably accounts for no more than a few percent of standing stocks, and this is probably of a similar order to the growth rates of krill. Our suggestion that krill growth counteracts biomass removal would explain the discrepancy between the previous suggestions of a long residence time of shelf water and a <1 mo turnover time. If krill are growing at a similar rate to their biomass removal, the ACC does not need to supply a large biomass continually. It needs to replace the individuals lost to predation, and slower rates of exchange would appear to be sufficient to do this. Therefore, local growth may be a significant factor in the mass balance of krill in this region.

Our budget encompasses a time and place where demand for krill by land-based predators is likely to be maximal. The location and timing of such a budget will dictate its outcome. For example, to the northeast of South Georgia krill biomass is substantially higher than in our region to the west (Brierley et al. 1999b), yet the impact from land-based higher predators would be reduced. Conversely, at smaller scales, such as near Bird Island or over the northwestern shelf break, where macaroni penguins often forage, localised predation pressure may at times be intense, especially on the larger krill which are preferentially selected (Reid et al. 1996).

With both advection and growth counteracting krill removal by land-based predators, there could be important but unmeasured loss terms in the krill budget. Our estimates are restricted to land-based predators, and these have been well assessed. However, we need better assessments both of transport processes and of removal rates by fish, squid and whales.

4. INTERANNUAL VARIABILITY

4.1. Introduction

Change, on a variety of temporal scales, must be characterised in order to develop an appreciation of

ecosystem functioning. The seasonal timescale is dominant in the Antarctic (Smetacek et al. 1990, Clarke & Leakey 1996). However, the longer time scales—interannual and longer—have been thrown into focus by current emphasis on climate change. It is ironic that at South Georgia, due to the logistical difficulty of winter surveys, we know more about interannual variability than of the much more profound differences between summer and winter. Seasonal changes have been discussed in Sections 2 and 3, while here we synthesise the available information on change over longer scales.

Since the *Discovery Investigations*, interannual variability has been known to characterise South Georgia (Harmer 1931, Kemp & Bennet 1932, Deacon 1977). A striking manifestation of this is the condition, diet and breeding success of krill-reliant predators (Croxall et al. 1988, Kock et al. 1994, Everson et al. 1997). These have been linked clearly to periodic (once or twice a decade) shortages of krill around the island (Murphy et al. 1998, Brierley et al. 1999b). Interannual variability also occurs in water temperatures, seasonal nutrient deficits, phytoplankton biomass and copepod biomass (Deacon 1977, Whitehouse et al. 1996a, Atkinson et al. 1999). Understanding the causes, effects and implications of this is now an active area of Antarctic marine research (e.g. Palmer LTER Group 1996). The state of knowledge at South Georgia has been covered recently (Whitehouse et al. 1996a for oceanography, nutrients and chl *a*; Murphy et al. 1998 for krill) so we provide only a brief resumé here.

4.2. The environment and lower trophic levels

The earliest observations of interannual variability at South Georgia are from the whaling records. Harmer (1931) and Kemp & Bennett (1932) documented 'fin whale years' and 'blue whale years' associated with oscillations in the catches of these 2 species. These appeared to be related to warm and cold air temperatures respectively, and were suggested to reflect interannual fluctuations in the environment. Deacon (1977) found a direct link between anomalously warm and cold seawater temperatures and coincident air temperatures measured at one of the whaling stations. Whitehouse et al. (1996a) examined interannual variability of temperature, salinity, nutrients and chl *a* using all available data for the period 1926–1990. They found a link between abnormally warm or cold water temperatures around the island and the duration of sea ice in the Southern Scotia Arc in the previous winter. This analysis, together with that of Deacon (1977), suggests that water temperatures around the island reflect wider scale (Scotia Sea or larger) climatic processes rather than local changes (Whitehouse et al. 1996a).

Comparisons of nutrients, chl *a* and the physical environment provide insights into interannual variability in the lower trophic levels (Whitehouse et al. 1996a). Silicate concentrations fell to potentially limiting levels ($<5 \text{ mmol m}^{-3}$) during 3 of the 11 summers where data were available. Using the winter to summer decrease in mixed layer nutrient concentrations as a crude gauge of the summer's total export primary production, Whitehouse et al. (1996a) found that seasons of anomalously low water temperatures (e.g. 1981/1982) tended to have low total export primary production, whereas warmer seasons such as 1985/1986 had higher total export production. The next step would be to examine whether this interannual variability is translated into signals in biogeochemical cycling and higher trophic levels. Although krill have now been monitored for several years (Brierley et al. 1999b), mesozooplankton have only recently been monitored consistently. Early indications are that the large fluctuations in biomass that occur for krill at South Georgia also occur for the copepods. In the first 3 yr of monitoring, copepod biomass varied by nearly an order of magnitude, with the highest biomass in a season of abnormally low krill biomass (Atkinson et al. 1999).

4.3. Krill

During the last few decades there have been summer seasons (1977/1978, 1983/1984, 1990/1991, 1993/1994, 1998/1999) when krill biomass was only ~5 to 10% of the mean values in other years (Fedoulov et al. 1996, Murphy et al. 1998, Brierley & Goss 1999, Brierley et al. 1999b). We stress, however, that krill biomass varies widely between years, and one cannot easily designate 'normal' or 'poor' krill years. It is uncertain how long these periods of low biomass last, although poor krill years do not appear to be concurrent; several months of low biomass seems more likely. In the poor krill year of 1993/94, surveys in January found low biomass (Brierley et al. 1997) but by March, krill had returned, and by April they supported a fishery (Pakhomov et al. 1997a). However, if the timing of the low krill abundance coincides with the breeding cycle of land-based higher predators, the effects are dramatic, with widespread breeding failures, particularly of gentoo penguins *Pygoscelis papua* and Antarctic fur seals (Croxall et al. 1985, 1999). Icefish condition and possibly their survival and breeding success also appear to be impaired in poor krill years (Kock et al. 1994, Everson et al. 1997, 1999). Other krill predators such as macaroni penguins, however, appear to be able to switch to alternative prey such as the amphipod, *Themisto gaudichaudii*, and do not suffer such a breeding failure (Croxall et al. 1999).

Although these effects are well documented, their causes are still unclear. Cyclical variations in the environment of approximately the correct period have been found in Antarctica, e.g. the 7–9 yearly circumpolar precession of sea ice (Murphy et al. 1995, White & Peterson 1996), and El-Niño Southern Oscillation events. However, after summarising the observations to date, Murphy et al. (1998) concluded that none of the environmental factors that have been measured so far show any clear or direct link to the 'poor' krill years.

Several explanations have been forwarded. All, however, invoke large-scale (Scotia Sea or larger) processes rather than local changes at South Georgia. An early suggestion was of large-scale southwards movements of the PF (Heywood et al. 1985, Atkinson & Peck 1988), but recent oceanographic findings make this unlikely (see Section 2.1.2). Later ideas have implicated the position of the Weddell-Scotia Confluence relative to the island (Maslennikov & Solyanin 1988) or periods of anomalous southerly airflow, which broke down the retention mechanisms of krill in the Scotia Sea, causing large scale demographic changes (Priddle et al. 1988). The latter authors ruled out the possibility that the failure of a single year class in the region supplying South Georgia's krill could result in biomasses ~5 to 10% of more typical values. However, this explanation has been revisited recently (Murphy et al. 1998, Reid et al. 1999). Based on data from krill predators, net catches and population models, these authors invoked the interaction of both biological and physical factors for the irregularly occurring low krill biomass, and suggested how failure of a year class in the source region would be seen at South Georgia. However, Murphy et al. (1998) pointed out that there is no direct link; not all recruitment failures upstream, in the Antarctic Peninsula area, precede low krill biomass years at South Georgia.

For an animal which can live for 5 to 7 yr (Siegel 1987), the idea that the failure of a single year class could cause such a reduction would seem implausible. However, the scarcity of very large krill around South Georgia (Reid et al. 1999, Watkins et al. 1999), would make the scenario possible if mortality rates, particularly of the larger krill, are high (Murphy et al. 1998). This may be the case close to Bird Island, but in the wider South Georgia system we do not know the mortality of krill relative to that at the Antarctic Peninsula for instance.

Indeed, if South Georgia is an area of expatriation from more than one source region, gaining a full understanding of krill population dynamics here will be challenging. Population dynamics in the Weddell Sea and Antarctic Peninsula area may differ (e.g. Siegel et al. 1990, Quetin et al. 1994, Siegel & Loeb 1995), so mixing from these potential sources would

complicate the patterns observed. Watkins et al. (1999) suggested that variations in age structure of krill seen at South Georgia could also reflect variable growth and mortality, both during their transit to the island and their residence there.

Clearly then, there is much to be learnt before we can understand, and successfully predict, the variation in stock sizes of krill at South Georgia. A broadening of approach is now required, although continued monitoring of biomass and population structure is still needed, combining data from predators (Reid et al. 1996, 1999), acoustics (Brierley et al. 1997) and nets (Watkins et al. 1999). It would, for example, be advantageous to study krill growth and mortality rates. South Georgia is an atypical habitat for this adaptable species; there is no reason to suppose that the processes governing local population structure are the same as those elsewhere.

5. CONCLUDING DISCUSSION: ENERGY FLOW IN THE SOUTH GEORGIA FOOD WEB

The seas around South Georgia are characterised not only by high biomass at every trophic level, but also by high rates of growth and transfer between trophic levels. Recent interpretations of its food web have stressed the role of advection. This transports energy, in the form of krill biomass, from higher latitudes to South Georgia, where it is made available to land-breeding predators (Croxall et al. 1984, 1985, Priddle et al. 1988, Murphy 1995, Trathan et al. 1995, Boyd & Croxall 1996, Murphy et al. 1998). Our review has emphasised that enhanced fluxes within the food web also generate high biomass. This is available either for consumption by higher predators, transfer downstream, or sedimentation.

However, if continued high rates of energy flow are needed to support the large stocks of grazers, it would be latently unstable without some kind of feedback preventing overgrazing. High energy flow from the base of the food web requires substantial plant biomass, as well as high individual growth rates (Banse 1985). Continued herbivory and overgrazing, for example by a krill aggregation, would mean diminishing returns for the krill, as the phytoplankton would take weeks to recover from such a low biomass. A simple comparison of zooplankton plus krill biomass (~10 g C m⁻²) and a representative primary production rate of ~1 g C m⁻² d⁻¹ (Table 1) would imply that grazing impact should be great. However, actual measurements of mean grazing impact do not exceed 50% of daily primary production (Table 4). This, plus the fact that summer chl *a* concentrations rarely fall below 1 mg m⁻³, suggest that some kind of a feedback prevents overgrazing and maintains the high energy flow.

To examine this we return to krill, which appear to have a pivotal role in this system, and try to look at food shortage from the perspective of a school. Foraging and search strategies within aggregated and dispersed krill schools are clearly important (Hamner et al. 1983, and see Miller & Hampton 1989), but these are poorly understood. Further to these, we speculate that feedbacks operate at larger time and space scales, reducing overgrazing and maintaining energy flow (Fig. 7). One possible feedback is through excretion and nitrogen regeneration (Section 3.1.1), but this must remain speculative until we know more about the dynamics of nitrogen preference in a cold water, nitrate-replete system. The other possible feedback is through direct and indirect grazing interactions. The overall biomasses of krill and copepods at South Georgia are roughly similar, and when feeding herbivorously they would compete (Schnack 1985). There was a negative relationship between krill and copepod abundances at a fine scale, mesoscale and possibly at an interannual scale. This appeared to be a direct effect of the krill, but however it came about, it would reduce the competition from copepods. Evidence that copepods were displaced downwards by krill schools (Atkinson et al. 1999) suggests competitive exclusion. Krill swim faster than copepods, and could leave locally overgrazed areas to feed elsewhere.

However, where krill are abundant, low algal biomass, probably due to grazing, has been found (Hardy & Gunther 1935, Antezana & Ray 1984). We speculate that when this occurs at South Georgia, krill switch to protozoans or copepods. This would alleviate their impact on phytoplankton, and by removing other herbivores it would reduce their impact also. We probably observed this during the summer of 1996, when krill biomass was fairly high yet phytoplankton biomass was not exceptionally low, averaging $\sim 1 \text{ mg chl a m}^{-3}$. Analysis of gut fluorescence, biomarkers, and feeding experiments suggested that the krill ingested few algae and had little impact on stocks (Atkinson &

Snýder 1997, Cripps et al. 1999). Instead their clearance rates on protozoans and copepods were high, and this may have been a significant cause of copepod mortality. We suggest that food switching between trophic levels according to availability could mean that krill, and possibly copepods, have a stabilising effect on population sizes within the lower trophic levels. Moreover, this stabilising effect maintains high rates of energy flow up the food chain, which at South Georgia results in greater food availability for higher predators. The identification of factors such as these is a prerequisite to a better understanding of the South Georgia pelagic ecosystem.

Acknowledgements. We first thank all the scientists who have contributed data and insights on the South Georgia pelagic ecosystem, and in particular to our colleagues at the British Antarctic Survey. We are indebted to NASA for permission to use the SeaWiFS images and to Dr Phil Trathan for providing us with Fig. 2. Constructive comments on the manuscript were provided by Drs Ian Boyd, Eugene Murphy, Andrew Brierley, John Croxall, Paul Rodhouse, Phil Trathan and 3 anonymous referees.

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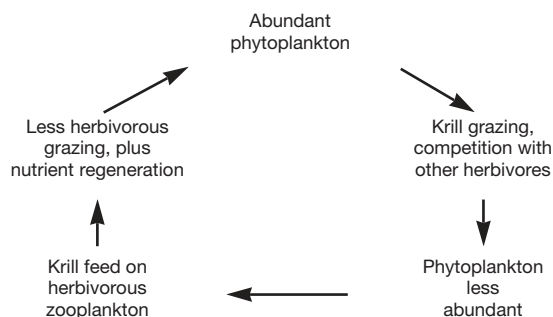


Fig. 7. Hypothetical feedbacks that potentially help to prevent overgrazing of phytoplankton in localised regions of abundant krill at South Georgia

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Editorial responsibility: Otto Kinne (Editor),
Oldendorf/Luhe, Germany

Submitted: June 6, 2000; Accepted: November 30, 2000
Proofs received from author(s): June 8, 2001