The South African SIBEX I Cruise to the Prydz Bay region, 1984: X. Biomass and production of bacterioplankton in Prydz Bay, Antarctica, and phytoplankton, detritus and bacterial relationships

S.J. Painting[1], M.I. Lucas[1] and J.M.E. Stenton-Dozey[2]
[1]Benguela Ecology Programme
Sea Fisheries Research Institute
Private Bag X2, Roggebaai 8012
[2]Marine Pollution Monitoring Programme
Department of Zoology,
University of Cape Town, Rondebosch, 7700

This paper reports on an attempt to estimate carbon and nitrogen flow, from phytoplankton through the bacterioplankton, in the SIBEX I survey area. The work was included in the SIBEX I programme as an adjunct to the main thrust of the programme but with a view to identifying processes deserving of further study during SIBEX II. From the data it seems likely that regenerated nitrogen may contribute 50 % or more of phytoplankton requirements, and chemoautotrophic nitrification rates below the euphotic zone are likely to be of importance in sustaining the high values for nitrate normally observed in Antarctic waters.

In hierdie artikel word verslag gedoen oor 'n poging om die vloei van koolstof en stikstof, uit fitoplankton deur die bakterioplankton, in die SIBEX I-waarnemingsgebied te bepaal. Dié werk is by die SIBEX I-program ingesluit as toevoeging tot die hoofrigting met die oog daarop om prosesse te identifiseer wat verdere bestudering tydens SIBEX II sou regverdig. Uit die gegewens kom dit voor asof geregenereerde stikstof in 50 % of meer van die fitoplankton se behoeftes voorsien. Chemoöutotrofiese nitrifisering onderkant die eufotiese sone speel waarskynlik 'n belangrike rol in die handhawing van die hoë nitraatsyfers wat gewoonlik in Antarktiese waters waargeneem word.

Introduction

Bacteria are ubiquitous in the ocean and the significance of their role in carbon flow in the marine environment has recently been the subject of numerous investigations. For example, estimates have been made of the transfer of photosynthetically fixed carbon through the bacterioplankton community in the English Channel (Newell & Linley 1984, Holligan *et al.* 1984), in the Peruvian upwelling system (Sorokin & Mikheev 1979) and in enclosed ecosystems (CEPEX) (Fuhrman & Azam 1980, Laake *et al.* 1983). In each of these studies a large proportion of the total phytoplankton production (20-80 %) was estimated to enter the bacterial consumer food chain. These observations are contrary to the classical view of the herbivore-dominated phytoplankton grazing food chain (Steele 1974). In the Middle Atlantic Bight, however, Falkowski *et al.* (1983) have shown that there is tight coupling between primary production and grazers, with little production available for microheterotrophs.

In a succinct review, Williams (1981) attempted to reconcile the classical view of a herbivore dominated food chain with observations of high net growth yields (50-80 %) for bacteria based on glucose and amino-acid substrates (Williams 1970, Crawford *et al.* 1974, Williams *et al.* 1976) and concluded that at least 50-60 per cent of primary production should pass through planktonic microheterotrophs before it is mineralised. However, Williams (1981) stresses that the calculations on the proportion of primary production entering the bacterioplankton are very sensitive to the estimates of the fraction of primary production exuded as dissolved organic carbon, as it has been shown that the net growth yield of bacteria on labile soluble substrates may be high (up to 85 %), while the net growth yield on particulate matter is much lower (10-15 %) (for review see Linley & Newell, *in press*). Furthermore, the quantification of carbon flow and nutrient cycling by bacteria is very sensitive to accurate measures of bacterial numbers, biomass and production, net growth yield or carbon conversion efficiency, the activity of the cells and the grazing impact of protozoan and zooplankton. (See Riemann *et al.* 1984).

In this study we have attempted to estimate carbon and nitrogen flow, from phytoplankton through the bacterioplankton, in the Prydz Bay region of Antarctica. Our estimates of bacterial biomass and activity are also compared with the findings of others for different regions of the Antarctic (see Hanson *et al.* 1983, Hanson & Lowery, 1985).

Materials and methods

Collection of material

Samples were collected from a grid of 46 stations situated between 65°S and 62°S, and 52°E and 64°E which were visited between 26 March – 2 April, 1984 by *SA Agulhas* in the course of the SIBEX I programme. At each station physical and chemical data were collected from CTD profiles down to about 5000 m. NIO bottle samples were also taken at a number of depths to provide accurate salinity and temperature measurements for sigma-t calculations. At daylight stations, bottle-water samples were sub-sampled for bacteria, particulate CHN and in some cases for flagellate counts. At the 100, 50, 25 and 1 per cent irradiance levels bottle-water samples were taken for chlorophyll *a* analysis and for simulated *in situ* primary production incubations which were carried out by Allanson (this volume).

Analyses of material

Bacterial biomass and number

Samples of water (20 ml) were fixed with 1,25 per cent gluteraldehyde and counted for bacterial numbers using the acridine orange direct counting technique, after filtration onto 0,2 μm Nuclepore filters (Hobbie *et al.* 1977). Differential counts were made for seven categories of bacterial morphs, the sizes of which were determined from both visual estimates on the epifluorescence microscope and from scanning electron micrographs (See Table 1). Bacterial biomass and bacterial carbon were then estimated using mean cell volumes for the size categories, a specific gravity of 1,1 g cm^{-3} (Doetsch & Cook 1973) and a wet biomass to carbon ratio of 0,11 (Linley 1983). Nitrogen equivalents for bacteria were estimated from the C:N ratio of 5 determined for marine bacteria (Fenchel & Blackburn 1979).

Bacterial production

Estimates of bacterial productivity were obtained from ^{3}H-Thymidine incorporation into DNA (Fuhrman & Azam 1980, 1982). Bacterial production estimates were made daily for each depth profile, usually at three depths corresponding to the upper mixed layer (±10 m), the pycnocline (±90 m) and below the pycnocline (±150 m). Samples of water (50 ml) from the NIO bottles were screened through a 60 μm mesh and incubated with 5 nM ^{3}H-Thymidine (46-50 Ci/mmol) in 150 ml flasks at ambient water temperature on an orbital shaker for six hours. Subsamples taken hourly for the first three hours and at the end of the incubation were precipitated with TCA and filtered onto 3,0 μm and 0,2 μm Millipore filters. Incorporated ^{3}H-Thymidine was then estimated on a Hewlett-Packard scintillation counter at the University of Cape Town, converted to moles of thymidine incorporated.h^{-1} and expressed as an increase in the number of cells.h^{-1}. Biomass was calculated using biovolume estimates (Table 1) and the numerical proportion of bacteria in each size category (Table 2). At the end of each incubation 20 ml water samples were preserved with one per cent gluteraldehyde for autoradiographic determinations of the percentage of active bacteria.

Table 1
Calculation of biovolume

Category		Range in dimensions (μm)	Mean dimensions (μm)	Volume (μm^3)	Mean AODC volume (μm^3)	Mean SEM volume (μm^3)
Small cocci.	S.C	0,2 – 0.3	0,25	0,004 – 0,014	0,009	0,007
Large cocci.	L.C	0.31 – 0.8	0,56	0,015 – 0,268	0,142	0,059
Small rods.	S.R	0,3 × 0,8 0,6 × 1.2	—	0,057 – 0,339	0,198	0,139
Large rods.	L.R	0,6 × 1.21 0,8 × 2,0	—	0,339 – 1,0	0,672	0,656
Small 'u' shaped	S.U	0,3 × 0,8 0,6 × 1,2	—	0,057 – 0,339	0,198	0,139
Large 'u' shaped	L.U	0,6 × 1,21 0,8 × 2,0	—	0,339 – 1,0	0,672	0,656
'S' shaped	'S'	0,3 × 0,8 0,6 × 1.2	—	0,057 – 0,339	0,198	0,139

Table 2
Relative importance (%) of different bacterial morphs

Station 24 Numbers (N) and Biomass (B)

Depth (m)	S.C N	S.C B	L.C N	L.C B	S.R N	S.R B	L.R N	L.R B	S U N	S U B	L.U N	L.U B	'S' N	'S' B	Total Numbers ($\times 10^6 ml^{-1}$)	Total Biomass ($mg.m^{-3}$)
0	27	2	28	30	11	17		—	32	47	—		3	4	,274	39,9
10	24	1	29	29	16	22	1	6	26	36	—		5	7	,356	55,9
30	1*	<,1*	32	26	21	24			39	43			6	7	,209	41,0
50	32	2	27	31	13	21			22	36			3	10	,327	44,0
75	23	1	30	32	14	20			29	42			4	5	,326	49,1
100	23	2	37	39	12	20			24	35			4	6	,270	39,7
150	23	2	32	34	10	18			29	43			4	5	,086	12,9
300	37	3	36	48	15	16			7	13			4	8	,098	11,7
2000	—	—	—	—	—	—			100*	100*			—	—	,008	1,9
Mean	27	2	31	34	14	20			29	40			4	6		

*These data excluded from means.

CHN analyses

Approximately 3,0 ℓ of water was filtered onto pre-ashed Gelman A/E filters (±μm mesh-size) and stored frozen on the ship. These filters were then analysed for particulate carbon and nitrogen by high temperature oxidation in a Hereaus elemental analyser using cyclohexanone (10,14 % N; 51,79 % C) as a standard.

Results

For the purpose of this preliminary report the data presented are those for stations 24, 26, 28 and 44 only. Analyses of the stations to date suggest that all the grid stations were very similar with the possible exception of station 30. However the results given here adequately summarise the microbiological events occurring over the grid at the time of the cruise. Although small changes in data are apparent between stations, the overall description of events and interpretations of the data remain the same.

Bacterial numbers and size classes

The size categories of bacteria counted are summarised in Table 1. The relative importance (percentage) of the different bacterial classes at Station 24 is given in Table 2. It is apparent that small cocci, large cocci and small 'U'-shaped bacteria account for the greatest numerical proportions (=87 %) of the total count. Each of these groups is numerically equally important but in biomass terms, small cocci contribute only two per cent to the total biomass as they are so small (0,3 μm diameter). The 'U'-shaped and 'S'-shaped bacteria are more abundant than in productive coastal waters. Unlike the nearshore coastal system of the Benguela region, or the West English Channel (Holligan *et al.* 1984), large rods do not contribute significantly in numbers or biomass to the total heterotrophic population of the area studied. The bacteria are generally dominated by smaller forms. This tendency to reduced size in oceanic waters is suggestive of a nutritionally poor environment, in keeping with the observations of a psychrophilic strain (Ant – 300) of bacteria from Antarctic surface water which was starved for periods of up to 1 year (Novitsky & Morita 1977). During this time the biovolume of the bacteria decreased and respiration rates dropped to 0,005 per cent of the initial rate, indicating a marked decrease in the activity of the cells although they remained viable.

Table 2 also gives total numbers of bacteria counted in a depth profile down to 5000 m for station 24. The numbers are uniformly low (2,09-3,56 × 10^5 cells $ml.^{-1}$) in the upper mixed layer (UML) above 100 m depth. Similarly, Hanson *et al.* (1983) recorded bacterial numbers of between 1 × 10^4 to 2 × 10^5 cells ml^{-1} for the Drake Passage, Antarctica. Much higher numbers of bacteria have been recorded for the Antarctic region and may commonly reach 10^9 $cells.ml^{-1}$ during phytoplankton bloom conditions. Noticeably, the total numbers of bacteria decline by an order of magnitude below 100 m and in the bathypelagic regions, presumably due to the absence of substrates associated with primary production in the euphotic layer.

Biomass

The biomass profile given for stn. 24 in Table 3 is typical of SIBEX I. The uniform bacterial biomass (39,9 – 55,9 $mg.m^{-3}$) down to 75 m is consistent with constant sigma-t values over that depth indicating a well mixed UML. Bacterial biomass estimates were about an order of magnitude lower than have been reported for the Scotia Sea and productive coastal Antarctic regions (Fuhrman and Azam 1980) but this can be attributed to the low bacterial numbers, phytoplankton biomass and productivity recorded during SIBEX I. Nevertheless, our estimates of bacterial biomass (319 – 430 $mg.C.m^{-2}$; see Table 5) exceed values recorded by Hanson *et al.* (1983) for the Drake Passage in the austral summer. By converting cell counts and ATP concentrations in the <0,4 μm fraction, they estimated bacterial biomass to have a mean of 111,0 $mg.C.m^{-2}$ over 200 m which they estimated to be about 1,5% of the microbial carbon biomass (>0,4 μm; <100 μm). It should be noted however, that ATP estimates of biomass may be subject to error since Stuart (1982) has shown that the C:ATP ratio for bacteria may vary from 250 – 500:1 depending on their growth phase.

Quantitative relationship between phytoplankton and bacteria

Although the bacterial biomass recorded during SIBEX I was low, bacterial carbon nevertheless amounted to between 37% (stns. 24, 26, 28) and 67% (stn. 44) of phytoplankton carbon above the 1% irradiance depth (see Tables 3, 4, 5 and Figure 1). However, chlorophyll carbon was calculated from Chl.*a* × 100 rather than the more commonly used factor of 70 (Platt, 1981). Clearly, bacterial biomass relative to phytoplankton can be equivalent to, or in excess of phytoplankton carbon biomass estimates if more conservative values for phytoplankton cellular carbon are used. For the S. Benguela ecosystem (March 1983) bacterial carbon was 12 – 51% of phytoplankton biomass above the 1% irradiance depth (Lucas *et al.* 1986) and 2 – 10% for surface waters of the W. English Channel (Linley *et al.* 1983). Similar values have been recorded for other temperate coastal ecosystems (see Laake *et al.* 1983). The Prydz Bay region during SIBEX I seems therefore to have been characterised by low bacterial biomass which was nevertheless high relative to phytoplankton biomass.

Figure 1 shows the relationship between bacterial biomass and chlorophyll *a* carbon above the 1% irradiance depth for stations 24, 26, 28 and 44. The poor linear correlation coefficient (r = 0,34; slope 2) can however, be improved if bacterial data from the aphotic zone (300 m) is included, corre-

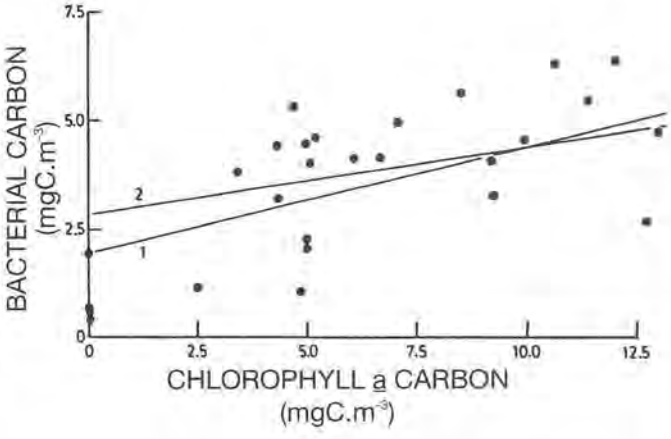

Fig. 1. Relationship between bacterial carbon biomass and chlorophyll *a* carbon for stations 24, 26, 28 and 44. Regression 1 includes bacterial data from 300 m where it is assumed that there is zero phytoplankton biomass (y = 0,248x + 1,88; r = 0,60; n = 28). Regression 2 excludes these points. (y = 0,139x + 2,87; r = 0,34; n = 24).

Table 3

Bacteria and phytoplankton biomass

Station 24

Note: 1. Uniform bacterial biomass down to 75 m
2. Sigma t values and uniform biomass indicate UML mixing

Corrected D (m)	T °C	‰	Sigma t	Bact. B (mg.m^{-3})	Chl. a (mg.m^{-3})	1° Prod. (mg.m^{-3}h^{-1})	Spec 1° Prod. (mg.C.mg.Chla^{-1}h^{-1})	Irrad. (%)
0	,33	33.86	27.17	39,92	,052 0*	0,13	2,92	100
10	,25	33.85	27.16	55,90	,085 14	0,11	1,23	50
30	,27	33.86	27.17	40,99	,067 28	0,06	0,89	25
50	,27	33.85	27.17	43,98	,050 47	0,05	0,96	10
75	−1,20	34.10	27.43	49,11	,071 61	0,03	0,42	5
89	−1,29	34.11	27.44	39,66	,092 94	0,03	0,27	1
137	,88	34.42	27,58	12,88				
292	1,83	34,63	27,69	11,67				
±2000				1,86				
±5000				1,62				

*These numbers indicate depth (m) for phytoplankton samples

Table 4

Bacterial and phytoplankton production

Sigma t	Corrected Depth (m)	Bacterial Biomass (mg.C.m^{-3})	Bacterial Production (mg.C.m^{-3}d^{-1})	Mean	$P/_B$	Chl. *a* (mg.m^{-3})	1° Production (mg.C.m^{-3}d^{-1}) (× 12 h)	
27,16	10	5,59	0,085 – 0,550	0,31	0,05	0,085	1,32	
27,44	89	3,97	0,112 – 0,726	0,84	0,21	0,092	0,36	Station 24
27,58	137	1,29	0,145 – 0,940	1,08	0,84	—		
27,22	10	0,75	(no uptake)			0,050	1,56	
27,53	75	3,22	0,201 – 1,755	0,755	0,23	0,092	0,24	Station 26
27,64	137	2,80	0,187 – 1,215	0,701	0,25	—		
27,73	±4000	(2,40)?	(no uptake)			—		
27,38	10	5,39	0,106 – 0,689	0,397	0,07	0,114	2,16	
27,67	75	2,60	0,09 – 0,59	0,340	0,13	0,127	0,84	
27,72	142	1,44	0,08 – 0,55	0,315	0,22	—		Station 28
>27.77	±3700	0,55	0,022 – 0,143	0,082	0,15	—		

Table 5

Summary of integrated data above 1 % irradiance (±100 m)

Station Number	Bacterial Biomass (mg.C.m^{-2})(B×0.1)	Chl. *a* (mg.m^{-2})	C.equi of Chl. *a* (Chl. *a* × 100) (mg.C.m^{-2})	1° Production (mg.C.m^{-2}h^{-1})	Bacterial Production (mg.C.m^{-2}h^{-1})
24	430,4	6,66	666,0	5,6	2,13
26	318,6	7,51	751,0	7,7	2,40
28	408,8	10,40	1040,0	10,8	1,37
44	391,1	4,45	445,0	7,7	—
S. Benguela ecosystem* (Mar. 1983)	600 – 2600	12 – 240	1200 – 24000	29 – 212	42 – 83

*Data from Newell *et al.* 1985, Lucas *et al.* 1986, Painting *et al.* 1986.

sponding with zero chlorophyll *a* carbon (r = 0,60; slope 1). If this relationship is transformed to correlate numbers of bacteria (ordinate) relative to chlorophyll *a* (abscissa): the linear regression is y = 0,179 + 0,732 × (r = 0,32; n = 28). Although again a poor correlation, the relationship seems reasonable since the slope relating bacterial numbers to chlorophyll *a* concentration is very similar to that given (Y = 2,348 + 0,822 X) by Linley *et al.* (1983) and if chlorophyll *a* data from Linley *et al.* (1983) is incorporated into our equation, the predicted bacterial numbers are within 5% of the numbers that they recorded. Several authors have since noted a consistent relationship between bacterial numbers and chlorophyll *a* in both fresh and marine waters and almost without exception the relationship is good although it is better expressed as a power curve where b<1, indicating that algal biomass increases more rapidly than bacterial numbers (see Bird & Kalff 1984; Verheye-Dua *et al.* 1986). This can probably be attributed to grazing pressure on bacteria by flagellates and other protozoans which will limit bacterial biomass development (see Azam *et al.* 1983).

Estimates of bacterial and phytoplankton production are given in Tables 4 & 5. Three points are noteworthy. Firstly, it is clear that estimates of bacterial procution by ^{3}H-Thymidine incorporation into DNA give a wide range of values, depending as the method does, on the numerous factors required to convert incorporated thymidine into cellular carbon (see Fuhrman & Azam 1982 and for a critical review, Pollard & Moriarty, 1984). In this study we have used the mean value of the ranges given although in subsequent studies (Painting *et al.* 1986, Lucas *et al.* 1986) we have shown that the more conservative lower estimate of bacterial production may be the more realistic. The second point to note is that in general, bacterial production increases with depth and is maximal at the pycnocline (±150 m) although primary production decreases down to this depth with diminishing percentage irradiance. Lastly, it appears that bacterial P/B ratios also increase towards the pycnocline, reflecting a greater proportion of active bacteria. Increased bacterial activity and production associated with fronts and pycnocline boundary layers is a common observation and may be due to elevated levels of biological activity or accumulations of detritus which stimulate microbial activity (see Floodgate *et al.* 1981, Holligan *et al.* 1984 a & b, Legendre & Demers 1984, Newell *et al.* 1985, Lochte & Turley 1985, Hanson & Lowery 1985).

In this study, integrated bacterial production varied from 13 – 38% of the net integrated primary production down to the 1% irradiance depth. Similar relative proportions have been reported for a number of other ecosystems (Laake *et al.* 1983, Rheinheimer 1984, Lucas *et al.* 1986). However, the absolute levels of production are very low compared to productive coastal and upwelling systems (Holligan *et al.* 1984 a & b, Brown 1984, Painting *et al.* 1986) although our data are in keeping with those recorded for the Antarctic system (see Table 8).

As there is considerable evidence that phytoplankton excrete soluble organic carbon (PDOC) during photosynthesis (Ignatiades & Fogg 1973, Williams 1981, Lancelot 1984), and that bacteria may rapidly and efficiently use the PDOC fraction (Cole *et al.* 1982, Larsson & Hagstrom 1982, Joint & Morris 1982, Lancelot & Billen 1984), it might be expected that bacterial production should be positively correlated with phytoplankton production. Data from stations 24, 26 and 28 do not, however, support this as maximal primary production occurs in the surface water while maximal bacterial production occurs at the pycnocline (±100 m). Figure 2 shows the negative relationship clearly.

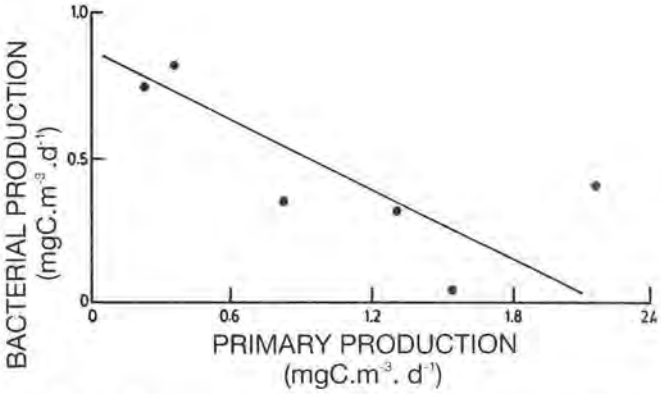

Fig. 2. The relationship between bacterial production and phytoplankton production for stations 24, 26 and 28. (Regression is y = 0,763 – 0,299x; r = −0,712; n = 6)

This apparent anomaly can however, be explained from data in Table 6. Table 6 shows the relationship between total particulate carbon analyses and chlorophyll *a* in the water column down to 100 m at station 44. It is clear that if chlorophyll *a* values are converted to carbon (chl.*a* × 100), phytoplankton carbon amounts to no more than 10 per cent of the total particulate carbon measured. More than 90 per cent of the particulate carbon in the water column is therefore detritus. This is also made clear when the mean P.C.:Chl.*a* ratio (1371:1) for station 44 is compared with an approximate P.C.:Chl.*a* ratio (104 – 199) for an active phytoplankton bloom in the Southern Benguela region (Lucas *et al.* 1986). In the latter case, almost all of the particulate carbon in the water column can be accounted for by phytoplankton.

Figure 3 shows a positive relationship between particulate organic carbon (POC) and bacteria in the water column, suggesting a dependence of bacteria on this substrate, which is dominated by detrital carbon (see Table 7).

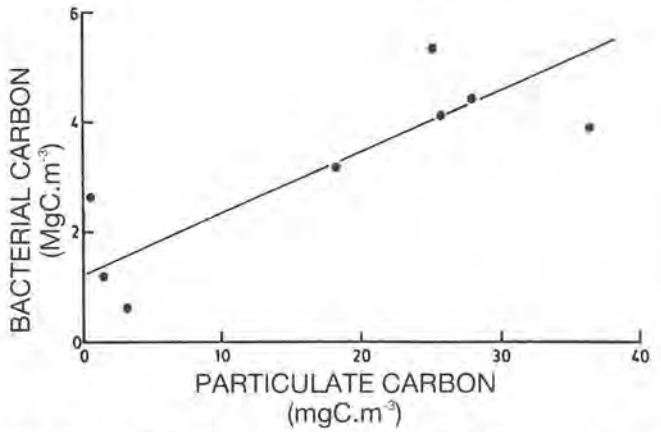

Fig. 3. Relationship between bacterial carbon and particulate carbon in the water column to 5000 m for station 44. (Regression is y = 0,0966x + 1,4535; r = 0,83; n = 8)

A similar strong correlation between bacterial carbon (ordinate) and particulate carbon (abscissa) in the water column has been shown for the S. Benguela region (Y = 0,060 X + 1,96; r = 0,77, n = 85; see Lucas *et al.* 1986) where it was apparent that bacterial carbon was closely correlated with total POC in the water column rather than chlorophyll

Table 6
Particulate carbon : chlorophyll *a*

Station 44

Depth (m)	Chl. *a* ($mg.m^{-3}$)	P.C. ($mg.m^{-3}$)	P.C./Chl. *a*	Notes
0	,043	52,0	1209	At this time, the system appears to be dominated by
15	,043	70,0	2059	detritus; Potential substrate for bacteria
30	,047	59,3	1261	
50	,047	61,7	1313	Other stations analysed also show the dominance of
75	,061	59,3	972	detrital carbon
100	,025	35,3	1412	
S. Benguela ecosystem (17.03.83)	2,2 – 5,5	437 – 570	104 – 199	Data from Lucas *et al.* 1986

a since the latter relationship can vary significantly depending on the phase of the phytoplankton bloom (Lucas *et al.* 1986).

Bacteria, phytoplankton and detritus as a potential food resource

Table 7 shows the relative abundance of particulate carbon and nitrogen as supplied by bacteria, phytoplankton and detritus in the UML at station 44.

Table 7
Potential food resources

Bacteria, Phytoplankton and Detritus expressed as a % of the total POM between Om and 100 m

Station 44

(C:N 5) Bacteria		(C:N 6,00 Phytoplankton		Detritus	
C	N	C	N	C	N
3 — 17	13 – 26	5 – 20	12 – 25	83 – 94	85 – 96

Note: These ranges depend on –
Chl. *a* : C conversion Factors (used 30, 60, 100)
Correction for C:N results and depth

It is immediately clear that detritus is the dominant potential source of particulate organic carbon (83 – 94 %) and particulate organic nitrogen (85 – 96 %) to the consumer organisms. Bacteria and phytoplankton appear to be comparable sources of carbon (3 – 20 %) but bacteria may be a richer source of N due to their relatively low C:N ratio (3,5 – 5,0) compared to that of phytoplankton (C:N = 6,0). However, apart from bacteria, nothing is known of the size spectra of the phytoplankton and detritus during this cruise. It has previously been emphasised that a mean of 70 per cent of phytoplankton carbon could be recorded in the nanoplankton (< 20μm) while this fraction also contributed a mean of 90 per cent of the photosynthetic primary production in the Bellingshausen Sea and South Georgia regions of the Antarctic during the austral summer of 1978 (Brockel 1981).

Although our data show that bacteria and phytoplankton appear to be comparable sources of C and N, the majority of the bacteria (86 %) are ±0,5 μm in diameter, and therefore likely to be unavailable to most meso- and macrozooplankton although they are of considerable trophic importance to heterotrophic flagellates (Fenchel 1982) and presumably to the microzooplankton. Bactivory by these groups may be of considerable importance in nutrient recycling (Azam *et al.* 1983).

The Antarctic krill *Euphausia superba* is able to filter particles of 10 μm with 80 per cent efficiency whilst bacterial-sized particles (0,2 – 0,8 μm diameter) are probably unavailable to adult krill (Boyd *et al.* 1984). It therefore seems that krill may be readily able to filter nanoplankton and detrital particles (normally in the range of 20 – 100 μm) with ease and are likely only to ingest bacteria where these are attached to detrital material.

Discussion

Bacterial production and growth in Antarctic waters

Although the bacterial production rates we recorded (Table 4) are very low, they are well within the range for the Antarctic region (Table 8). Nevertheless, bacterial production in the Antarctic is two to three orders of magnitude less than in other temperate waters. This is borne out by the very long generation times and slow instantaneous growth rates we recorded for Antarctic bacteria during SIBEX I. For station 24 at 10 m the bacterial biomass was 5,59 $mg.C.m^{-3}$ and the mean production was 0,31 $mg.C.m^{-3}d^{-1}$ giving a daily P/B ratio of 0,055 which approximates to a generation time of 433 hrs or 18 days at 0,25 °C. A doubling time of 0,8 – 1,4 per day for bacteria in an enclosed mesocosm (CEPEX) in Norway has been recorded (Laake *et al.* 1983) and in temperate waters Newell & Linley (1984) and Linley & Newell (1984) recorded generation times of 15 – 33 h with a mean of mean of 20,18 – 18,6 h over the temperature range 12 – 30 °C.

Bacterial production in the euphotic zone at station 24 amounted to 38 per cent of photosynthetic production while this value was 31 per cent and 13 per cent at station 26 and 28 respectively. These values compare with a similar value of 12 per cent recorded for the CEPEX enclosure in Norway (Laake *et al.* 1983) and with values recorded in reviews by Azam *et al.* (1983) and Rheinheimer (1984).

SIBEX I samples have not yet been analysed to determine what fraction of the bacterial population was metabolically active. However, this proportion may vary considerably from 90 per cent to only 40 per cent of the population (Es and Meyer-Reil 1982). Our low results for bacterial production relative to their biomass suggests that the major fraction of the population was metabolically inactive but viable at this time. Novitsky & Morita (1977) have shown that bacteria in the Antarctic may remain viable for up to a year even when starved.

Carbon and nitrogen flow through the microheterotrophic food chain

Carbon and nitrogen flow through the microheterotrophic community based on primary production may be readily calculated on the basis of the familiar energy budget equation of Winberg (1956); (see Petrusewicz & McFadyen 1970):

$$C = P + R + F + U$$

Where
C = amount of energy consumed
P = assimilated energy incorporated as production
R = assimilated energy lost as respiration
F = ingested energy lost as faeces
U = ingested as assimilated energy lost in soluble form

Table 8
Comparisons of bacterial production

Location	Production ($mg.C.m^{-3}d^{-1}$)	Method	Source
Antarctica (Prydz Bay)	0,022 – 1,309	^{3}H-Thymidine	SIBEX I
Antarctica	0,0004 – 2,0	^{3}H-Thymidine	Fuhrman & Azam (1980)
Benguela (1983)	42 – 83	^{3}H-Thymidine	Lucas *et al.* 1986
Plymouth (UK)	10 – 149	Biovolume estimates	Newell *et al* (1981)
York River estuary	0,96 – 132	^{3}H-Thymidine	
Nearshore Georgia	17 – 422	FDC	Newell & Christian (1981)
Sapelo Island	41 – 130	FDC	Newell & Fallon (1982)
Antarctica (Drake Passage)	0,002 – 0,009	^{3}H-Thymidine	Hanson *et al.* (1983)

Carbon flow to bacteria at station 24

To sustain production, heterotrophic bacterioplankton consume photosynthetically derived dissolved organic carbon (PDOC), other dissolved organics, and particulate material which may be derived from a number of sources including phytoplankton exudates, senescent phytoplankton cells, particulate C and N detritus, zooplankton excretion and so-called "messy feeding". (Williams 1981, Cole *et al.* 1982). For the purpose of this study we shall calculate bacterial nutrition in terms of PDOC and detrital material only; the significance of dissolved organic nitrogen and inorganic nitrogen pools to bacteria will be reviewed.

It should be noted that estimates of carbon and nitrogen flow through bacteria are very sensitive to estimates of bacterial production, net growth yield and activity of the bacteria. Since the measure of bacterial production (Fuhrman & Azam 1980) results in a wide range (×7) in our estimate using the ^{3}H-Thymidine incorporation into DNA technique, the following calculations should be interpreted in terms of their broad conclusions rather than in terms of specific results.

Bacterial consumption of carbon (Cc) can be estimated from the carbon incorporated into bacterial carbon biomass (ie: net growth yield) and expressed as a percentage of the substrate carbon utilised. An estimate of the carbon conversion efficiency is thus obtained. Experimental evidence has shown that incorporation of refractory particulate material results in a low net growth yield (10 – 15 %) for bacteria (Newell & Lucas 1981, Newell *et al.* 1981), while bacteria exhibit very high net growth yields (60 – 90 %) when utilising soluble labile components such as glucose and amino-acids (see Williams 1981, Joint & Morris 1982). In the course of primary production, it has been shown that up to 30 per cent of the fixed carbon may be lost as PDOC exudates while 70 per cent of the carbon remains fixed as particulate material (see Ignatiades & Fogg 1973, Williams 1981, Larsson & Hagstrom 1982). To estimate carbon flow through bacterioplankton, based on primary production, it is necessary therefore to estimate bacterial carbon consumption on the basis of the differing net growth yields (or conversion efficiences) observed for the particulate and PDOC fractions of primary production. For a natural phytoplankton assemblage, a net growth efficiency of 31 per cent was estimated for bacteria utilising both PDOC and POC components of a decaying phytoplankton bloom, (Newell *et al.* 1981, Painting unpubl. data). Bacterial consumption of carbon (Cc) required to sustain measured bacterial carbon production (pc) rates may therefore be calculated from:

$$Cc = Pc/0,31$$

The remaining components of the energy balance equation (R, F & U) may be taken to be carbon respired as carbon dioxide. If thymidine is used as a substrate to measure bacterial production these variables may be disregarded. Our estimates of bacterial carbon production (Pc) agree with previous estimates obtained by Fuhrman & Azam (1980) (see Table 8) and may therefore be used with some confidence to estimate carbon flow through this community.

Estimates of carbon flow to bacteria at station 24 based on primary production (PDOC) and detritus are given in Table 9. Bacterial production and phytoplankton production were measured at three depths, 10 m, 89 m and 137 m. Note that at 137 m there was assumed to be zero primary production as this was well below the one per cent irradiance level (89 m) and also below the pycnocline (Table 3). The 10 m depth was firmly within the UML while the 89 m depth corresponded to the pycnocline (Table 3). As can be seen in Table 9, primary production decreased with depth whilst mean bacterial production increased from 0,315 to 1,08 $mg.C.m^{-3}.d^{-1}$ between 10 m and 137 m. Since bacterial production increases with depth, so too do the carbon consumption requirements in order to meet bacterial carbon production.

At 10 m depth bacterial production (0,315 $mg.C.m^{-3}.d^{-1}$) is some 22 per cent of phytoplankton production (1,440 $mg.C.m^{-3}.d^{-1}$). At this depth bacterial carbon consumption requirements are therefore Cc = 0,315/0,31 = 1,02 $mg.C.m^{-3}.d^{-1}$ if we assume the net growth yield of bacteria to be 31 ‰. It is likely that some 30 per cent of the primary production may be excreted as PDOC, amounting to 0,4732 $mg.C.m^{-3}.d^{-1}$. Production of this soluble carbon pool would however meet only 42 per cent of the bacterial carbon requirements based on a net growth yield of 31 ‰. However, if the bacterial net growth yield were 75 per cent as may be expected for the utilisation of soluble photosynthetic products (Williams 1981) then bacterial carbon requirements to meet bacterial production would amount to Cc = 0,315/0,75 = 0,420 $mg.C.m^{-3}.d^{-1}$, which could be met entirely by PDOC exudation at 30 per cent of measured primary production (0,432 $mg.C.m^{-3}.d^{-1}$). This suggests that bacterial production in the euphotic zone may be closely coupled to PDOC exudation. Note that in this scenario fixed particulate primary production is not utilised by bacteria and may be available for macrozooplankton herbivores. Furthermore, the pool of detrital POC may be continually replaced by particulate primary production decay so that the detrital resource may in fact be in steady state with bacterial carbon consumption requirements, even allowing for daily settlement of a large fraction (30 to 60 %) of the detrital POC pool into deeper water.

Table 9
Carbon flow at station 24

Depth (m)	Upper mixed layer		± 100 m pycnocline		Deep mixed layer	
	10 m		89 m		137 m	
	C. flux ($mg.C.m^{-3}d^{-1}$)	*C. biomass* ($mg.C.m^{-3}$)	*C. flux*	*C. biomass*	*C. flux*	*C. biomass*
Phyto.Pc(^{14}C uptake)	1,440		0,360		Zero	
Phyto.PDOC Ca 30 % Pc	0,432		0,108		Zero	
POC biomass (CHN-C analysis)		25 – 60		25 – 60		25 – 60
Bact.Pc (^{3}H Thymidine uptake)	0,315		0,840		1,08	
Bact.Cc(Pc/0.31)	1,02		2,71		3,48	
Bact.Rc(Cc – Pc)	0,705		1,87		2,40	
Bact.Rc/Bact.Cc (%)	69,0		69,0		69,0	
Bact.Pc/Phyto. Pc (%)	21,9		233,0		—	
Phyto. PDOC/Bact.Cc (%)	42,3		5,3		—	
Bact.Cc/POC biomass ($\%d^{-1}$)		4,1 – 1,7		10,8 – 4,5		13,9 – 5,8
No of days that POC biomass will last		24 – 59		9 – 22		7 – 17

Note:
Phyto. Pc = fixed phytoplankton carbon production; Phyto. PDOC = photosynthetically fixed carbon as soluble exudates.
POC biomass = particulate carbon
Bact = bacteria; Pc = carbon production; Cc = carbon consumption; Rc = carbon respired.

At 89 m depth the situation is different. Bacterial consumption requirements (2,71 $mg.C.m^{-3}.d^{-1}$ at 31 % efficiency, or 1,12 $mg.C.m^{-3}.d^{-1}$ at 75 per cent efficiency) considerably exceed phytoplankton PDOC production (0,108 $mg.C.m^{-3}.d^{-1}$), which could satisfy only four per cent of bacterial carbon requirements and at most 13 per cent even if bacterial net growth yield was 100 per cent efficient. Clearly, for the bacterial population to sustain the observed rates of production at this depth, detrital POC (25 – 60 $mg.C.m^{-3}$ estimated) must be utilised. This would be able to sustain bacterial production for 9 – 22 days. Thereafter, unless primary production contributed further to the detrital POC pool, the bacterial population would either have to increase its net growth efficiency or reduce its respiration rate and become dormant or inactive.

At 137 m depth, below the pycnocline, no primary production was recorded. At this depth, therefore, bacterial production requirements would have to be met entirely by consumption of detrital POC. As bacterial production is highest at this depth (Bact.Pc = 1,08 $mg.C.m^{-3}.d^{-1}$) bacterial consumption requirements are also highest (Bact.Cc = 3,48 $mg.C.m^{-3}.d^{-1}$) so that in this case the detrital POC biomass will sustain production for a somewhat shorter period of 7 – 17 days.

It should, however, be stressed that these calculations of bacterial consumption requirements are based on primary production (PDOC) or POC and ignore the considerable pool of dissolved organic carbon (DOC) in the water column which is frequently of the order 1,0 $mg.C.l^{-1}$ (Durrsma & Dawson 1981). However this pool is likely to consist of non-utilisable and strongly refractory high molecular weight substances (Ogura 1975), whereas utilisable DOC excreted by phytoplankton is likely to be in equilibrium with its uptake by heterotrophic bacteria.

Nitrogen flow to bacteria at station 24

Where sediment sources of nutrients, particularly nitrogen, are remote (>200 m), nitrogen cycling and conservation within the euphotic zone is of key importance in sustaining primary production. Nitrate concentrations are usually high in Antarctic waters (30 – 40 $ug.at.l^{-1}$) and are thought to be derived from nitrification of ammonia released from decomposition and excretion by chemoautotrophic nitrifying bacteria (Olson 1981). Heterotrophic bacteria may utilise PON and DON sources of nitrogen for protein systhesis but although the direct incorporation of low molecular weight DON (eg. aminoacids) may be rapid and efficient (60 – 85 %) (see Palumbo *et al.* 1983), the major portion of the DON pool is considered to be biologically highly refractory (McCarthy 1980, Rheinheimer 1984).

For detrital material containing both particulate carbon and nitrogen, carbon may be incorporated for growth and respiration while the nitrogen element may be incorporated or remineralised as ammonia-N. Fenchel & Blackburn (1979) have considered the C:N ratio of bacteria (taken to be 5) relative to that of the substrate being utilised to determine remineralisation rates. They have assumed that particulate nitrogen incorporation by bacteria is related quantitatively to carbon uptake and the C:N ratio of the substrate. Thus, for the nitrogen requirements of bacteria to be satisfied, the C:N ratio of the substrate should equal the C:N ratio of bacterial cytoplasm (5) divided by the carbon net growth yield (ie: Cb:Nb/NYg). Therefore if the substrate has a higher C:N ratio than this, net immobilisation of DON pools will be required to satisfy bacterial nitrogen requirements. Conversely, if the C:N ratio of the substrate is lower than Cb:Nb/NYg, net mineralisation will occur. Linley & Newell (1984) have used this relationship to demonstrate theoretically that the net growth yield of bacteria is improved when low C:N substrates are utilised or if sources of inorganic nitrogen are available. This has also been shown experimentally by Newell *et al.* (1983).

Recently, attempts have been made to estimate organic nitrogen flux through heterotrophic bacteria based on carbon flux measurements and the appropriate C:N ratio of the substrate (see Fenchel & Blackburn 1979, Newell & Linley

Table 10
Nitrogen flow at station 24

Depth (m)	Upper mixed layer		± 100 m pycnocline		Deep mixed layer	
	10 m		89 m		137 m	
	N. flux ($mg.N.m^{-3}d^{-1}$)	*N. biomass* ($mg.N.m^{-3}$)	*N. flux*	*N. biomass*	*N. flux*	*N. biomass*
Phyto.PN (C:N=6,0)	0,24		0,06		Zero	
PON biomass ($\bar{x}$ C:N=8,7; 10-89 m $\bar{x}$ C:N=12,0; 137 m)		2,9 – 6,9		2,9 – 6,9		2,1 – 5,0
Bact.PN(PC/C:N=5)	0,063		0,168		0,216	
Bact.CN((PC/0,31)/C:N substrate)	0,117		0,311		0,290	
Bact.CN-PN	0,054		0,143		0,074	
Bact.PN/Phyto PN (%)	26,25		280,0		—	
Bact.CN/PON biomass ($\%d^{-1}$)		4,0 – 1,7		10,7 – 4,5		13,9 – 5,8
No of days that PON biomass will last		24 – 59		9 – 22		7 – 17

1984, Linley & Newell, 1984). Using this approach we have have also been able to estimate nitrogen immobilisation and remineralisation by bacteria at station 24 (see Table 10). We have assumed that the C:N ratio of bacteria to be 5 (Fenchel & Blackburn 1979) and that the C:N ratio of phytoplankton is 6,0. In our calculation of nitrogen flux we have considered only the flux of particulate nitrogen based on consumption of particulate carbon given in Table 9 for the appropriate depth.

At 10 m depth, bacterial nitrogen incorporation associated with particulate detrital consumption is 0,17 $mg.N.m^{-3}.d^{-1}$ and is calculated from Bact. Cn = ((Pc/0,31) C/N substrate = 8,7) = 0,117 $mg.N.m^{-3}.d^{-1}$, where (Pc/0,31) is the estimate of bacterial carbon production divided by the net growth yield (see Table 9) and the C:N ratio of the substrate is derived from direct measurements of particulate C and N. Bacterial nitrogen production is given by Bact.Pn = (Pc/C:N = 5) = 0,063 $mg.N.m^{-3}.d^{-1}$. where Pc is bacterial carbon production (see Table 9). Thus, incorporated nitrogen (0,117 $mg.N.m^{-3}.d^{-1}$) thereby resulting in remineralisation of approximately 0,054 $mg.N.m^{-3}.d^{-1}$ or $3,8 \times 10^{-3}\mu g.at.N.l^{-1}.d^{-1}$. By a similar calculation, bacterial remineralised nitrogen at 89 m depth was 0,143 $mg.N.m^{-3}.d^{-1}$ or $10,2 \times 10^{-3}\mu g.at.N.l^{-1}.d^{-1}$. where the mean C:N of the substrate was also 8,7. Similarly, at 137 m depth, below the pycnocline, bacterial nitrogen production ($0,216 \times 10^{-3}\mu g.at.N.l^{-1}.d^{-1}$) could be met by our estimate of particulate nitrogen incorporation ($0,290 \times 10^{-3}\mu g.at.N.l^{-1}.d^{-1}$) associated with particulate nitrogen incorporation ($0,290\ 10^{-3}\mu g.at.N.l^{-1}.d^{-1}$) associated with particulate carbon uptake where the C:N of the substrate had risen to 12,0. At this depth net nitrogen remineralisation therefore amounted to $0,074 \times 10^{-3}\mu g.at.N.l^{-1}.d^{-1}$ or $5 \times 10^{-3}\mu g.at.N.l^{-1}.d^{-1}$.

As the sediments are remote (±5 km) nutrient remineralisation processes above the pycnocline are likely to be of considerable importance in sustaining primary production. Table 11 summarises our estimates of bacterial nitrogen remineralisation for station 24.

The integral of primary production at station 24 was 5,56 $mg.C.m^{-2}.h^{-1}$ (Allanson, *pers. comm.*) which approximates to 66,7 $mg.C.m^{-2}.d^{-1}$ on a 12 h daily basis. A very approximate integral for bacterial regenerated nitrogen can be calculated for the upper mixed layer (above ±100 m), which amounts to 5,4 $mg.N.m^{-2}.d^{-1}$, based on our most conservative estimate of bacterial regenerated nitrogen at 10 m (0,054 $mg.N.m^{-3}.d^{-1}$). Since phytoplankton nitrogen production can be calculated as 11,1 $mg.N.m^{-2}.d^{-1}$ (C:N = 6) our estimate of bacterial regenerated nitrogen could account for approximately 50 per cent of primary production requirements at this station.

Table 11
The significance of bacterial regenerated nitrogen

Station 24

10 m depth	Primary production	≅ 1,44 $mg.C.m^{-3}d^{-1}$
	From C:N = 6,0;	≅ 0,24 $mg.N.m^{-3}d^{-1}$
	Bacterial regenerated N	= 0,054 $mg.N.m^{-3}d^{-1}$
		= *22,5 % of 1° Prod. Requirements*
89 m depth	Primary production	≅ 0,36 $mg.C.m^{-3}d^{-1}$
	From C:N = 6,0;	≅ 0,06 $mg.N.m^{-3}d^{-1}$
	Bacterial regenerated N	= 0,143 $mg.N.m^{-3}d^{-1}$
		= *238,3 % of 1° Prod. Requirements*
137 m depth	Primary production	= zero
	Bacterial regenerated N	= 0,074 $mg.N.m^{-3}d^{-1}$

Note: At and below the pycnocline (89 m) net nitrogen regeneration exceeds primary production requirements and may therefore sustain or promote further phytoplankton production in the UML given a suitable mixing process.

Conclusions

During SIBEX I independent estimates of nitrogen uptake were made in surface waters (±1 m) using ^{15}N tracer experiments. Results from this work indicate that in surface waters of the Prydz Bay region, the mean ammonia-N uptake rate for five stations was 0,0013 ± 0,0006 $\mu g.at.N.l^{-1}.h^{-1}$, which is equivalent to 0,22 $mg.N.m^{-3}.d^{-1}$ for a 12 h day (Probyn, *in prep.*). Since such ammonia-N uptake rates may be considered equivalent to regeneration rates for a steady state system (Harrison *et al.* 1983), it is interesting to note that our estimates of bacterial nitrogen regeneration (0,054 $mg.N.m^{-3}.d^{-1}$) in the surface waters (10 m) at station 24 are approximately four times lower than estimates derived from

^{15}N uptake data. This, however, is to be expected since ammonia-N uptake rates were experimentally derived for the whole planktonic community and therefore reflect regenerated nitrogen from all sources. Gray *et al.* (1984) have stressed that protozoan bactivory is likely to be the major source of regenerated nitrogen rather than bacterial remineralisation (for review see Rheinheimer 1984) while zooplankton excretion may provide the major proportion of regenerated nitrogen in some systems (Whitledge 1981).

From our data and that of Probyn *(in prep.)* it seems likely that regenerated nitrogen may contribute upwards of 50 per cent of phytoplankton nitrogen requirements. However further analysis of Probyn's data is required before we can confirm the significance of regenerated nitrogen to primary production. Furthermore, future ^{15}N and other tracer studies are required to confirm accurately the relative roles of heterotrophic bacteria, nitrifier chemoautotrophs, protozoan bactivores and zooplankton in the cycling of nitrogen in Antarctic waters. Chemoautotrophic nitrification rates below the euphotic zone are likely to be of particular importance in sustaining the high values for nitrate (30 – 40 $\mu g.at.l^{-1}$) normally observed in Antarctic waters (see Olson 1981).

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