RELATIONSHIPS BETWEEN BACTERIA AND PHYTOPLANKTON IN THE BRANSFIELD STRAIT AND SOUTHERN DRAKE PASSAGE

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ABSTRACT. Bacterial biomass (cell numbers) and phytoplankton biomass (particulate chlorophyll *a*) were estimated at 27 and 43 stations respectively (with 22 coincident), as part of the BIOMASS SIBEX programme, in Bransfield Strait and Drake Passage during January–February 1985. Bacterial biomass ranged from 3.159×10^{13} to 6.234×10^{13} cells m^{-2} sea surface whilst phytoplankton biomass ranged from 8.5 to 298 mg chlorophyll *a* m^{-2} (both integrated to 200 m depth). These values are consistent with previously published work. Net phytoplankton species composition, described on the basis of vertical net hauls at 50 stations, also resembled that found previously in this area. The ratio of bacterial- to phytoplankton-carbon increased with depth, with a mean value of 9.32 % (range 0.19–53.03 %) for samples in the top 50 m of the water column but usually representing at least half of the microplankton biomass at depths exceeding 100 m. Correlation between bacterial and phytoplankton biomass was negative but not significant. It is suggested that variation in total chlorophyll *a*, dominated by large-celled diatoms, would not affect bacterial biomass which would be more closely linked to that of picophytoplankton.

INTRODUCTION

Bacterioplankton and phytoplankton are key elements in the pelagic marine ecosystem. Whilst there is now a large body of information on Southern Ocean phytoplankton (e.g. El-Sayed, 1984; Heywood and Whitaker, 1984; Priddle and others, 1986), data on the bacterioplankton are more sparse. In particular, it is unclear how heterotrophic bacteria in the euphotic zone respond to fluctuations in energy supply resulting from changes in phytoplankton abundance.

The results presented here were collected during the SIBEX experiment of BIOMASS, an international programme concerned with the investigation of the Southern Ocean ecosystem and its living resources (El-Sayed, 1977). The study comprised multidisciplinary surveys, involving physical oceanography, microbiology, zooplankton and predator studies, carried out repeatedly in selected research areas over a two year period. The large station grid covered a variety of water masses in the region of the Southern Ocean close to the South Shetland Islands and the Antarctic Peninsula. Data on the horizontal and vertical distribution of bacteria and phytoplankton are compared to assess covariation which might indicate biological relationships.

STUDY AREA

The Bransfield Strait is located between the South Shetland Islands and the Antarctic Peninsula. Its waters are the product of an interaction between two distinctive Surface Waters, and local influences (Heywood, 1985; Heywood and Priddle, in press). Weddell Sea water enters round Joinville and D'Urville Islands to spread northwards across the Strait and southwards along the coast of the Peninsula (Fig. 1). Water from the South East Pacific Basin enters between Low, Smith and Snow

Islands and passes north and south of Deception Island. The southern tongue meets Weddell Sea water and is deflected back to join the tongue passing along the northern side of the strait. The main outflow passes round Elephant and Clarence Islands. Entry of Warm Deep Water is restricted by shallow sills that stretch across the entrances to the Strait. The cold Bottom Water of the deep basins within the Strait is formed *in situ* during the formation of ice from waters lying over shallow coastal shelf areas in winter (Clowes, 1934). The waters of the southern Drake Passage are essentially those of the South East Pacific Basin with slight intrusion by Bellingshausen Sea water at the south-eastern end.

The SIBEX research area comprised two grids of stations, one in the southern Drake Passage and one in the Bransfield Strait. Both grids commenced at a longitude midway between Elephant and Clarence Islands and extended past the South Shetland Islands towards the Bellingshausen Sea (Fig. 1). A total of 53 stations was sampled between 16 January and 6 February, 1985.

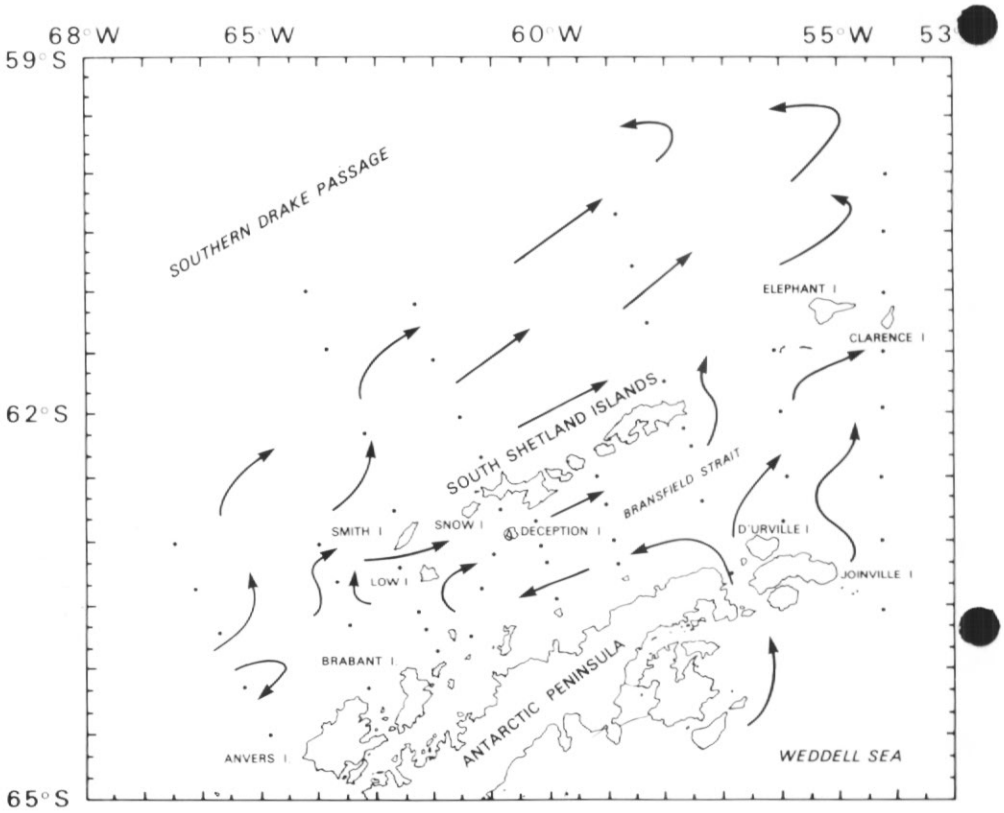

Fig. 1. Map of the Bransfield Strait and southern Drake Passage, showing the main directions of water movement (based on geopotential topography from Heywood and Priddle, in press). Dots indicate the positions of the 53 standard stations comprising the SIBEX sampling grid.

Materials and Methods

Bacteria

Twenty-seven of the 53 stations were sampled for bacteriological analysis, using 2.5 dm^3 Niskin bottles carried on a General Oceanics rosette (Fig. 2a). Samples were taken from six depths, the range of depths being dependent on the bottom depth at each particular site. Subsamples (0.2 dm^3) were withdrawn from the Niskin bottles for total counts of bacteria. These were obtained by epifluorescence microscopy, using a modification of the technique outlined by Hobbie and others (1977). The subsamples were filtered through 47 mm diameter polycarbonate filters (Nuclepore) with a pore size of 0.2 μm. The filters were pre-stained with a solution of Irgalan Black (Ciba-Geigy Ltd; 2 g dissolved in 1 dm^3 2% acetic acid), air dried and sterilized by autoclaving. Prior to filtration, each subsample was fixed by adding glutaraldehyde (2% final concentration) and was then drawn through under gentle vacuum. Counting proved to be impossible on board ship due to excessive vibration and rolling motion. The filters were therefore transferred to sterile 5 cm petri dishes (Sterilin) and stored in sealed plastic bags at 4°C for counting in the UK. Working in a sterile cabinet, filters were stained with Acridine Orange (100 mg dm^{-3}) for 5 minutes, rinsed with filtered de-ionized water and mounted on glass microscope slides under a 1:2 v:v mixture of Citifluor and de-ionized water. Citifluor (Citifluor Ltd, London) can be used to retard photofading of bacterial fluorescence under UV light (Wynn-Williams, 1985). The preparation was examined under oil at 1000 × magnification using a Leitz Laborlux 12 microscope fitted with a Ploemopak 2.5 epifluorescence unit, a 50 W Hg lamp, an I2 filter block (BP 450–490 excitation filter, RKP 510 beam splitter and LP 515 suppression filter) and an NPL Fluotar 100/1.32 oil immersion objective. Twenty fields, with approximately 30 bacteria per field, were counted for each sample to allow for uneven distribution of bacteria on the filter. [NB. When using polycarbonate filter holders (Sartorius), the outer 3 mm of the filter does not come into contact with any bacteria, giving an effective filtration diameter of only 41 mm. This was taken into account when calculating results.]

Phytoplankton

Water samples for phytoplankton biomass estimates were obtained at 43 of the 53 stations, 22 of these coinciding with the stations analysed for bacteria (see Fig. 2a). Subsamples (0.5 dm^3) of water from standard depths were filtered onto Whatman GF/C filters (particle retention ~ 1.5 μm) under light vacuum. Pigments from the phytoplankton retained by the filters were extracted in 90% acetone in the dark at ~ −2°C for 24 h before the estimation of chlorophyll on a Sequoia-Turner 112 filter fluorometer, calibrated against standard chlorophyll *a* (Sigma Chemical).

Phytoplankton taxonomic samples were obtained at all but three stations by slow, vertical hauls, generally made from 100 m depth to the surface with a 50 cm mouth 5:1 net of 10 μm mesh. The samples were examined on board ship to assess the abundance of the major diatom taxa. Hauls were made from only 50 m at ten stations, where phytoplankton were particularly abundant or where bottom depth was limiting.

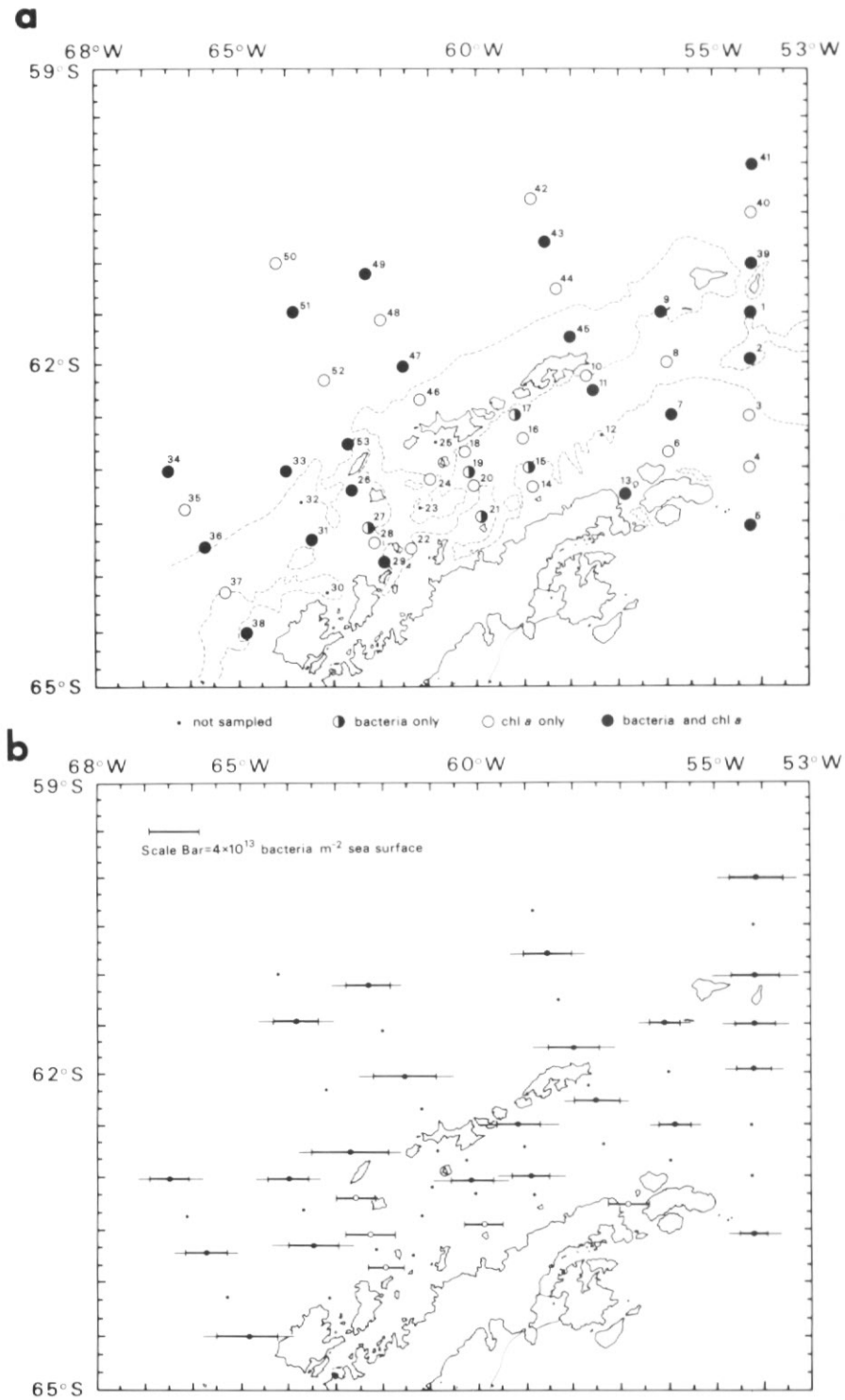

Fig. 2. (a) Distribution of stations sampled for bacteria and/or phytoplankton during the present study. The 500 m depth contour is indicated by a broken line. (b) Abundance of bacteria at selected stations in the survey area. Symbols represent total counts of bacteria, integrated over depth, per m^2 of sea surface. Inner thick bar is the count to 100 m depth, the longer thin bar to 200 m. Those stations where integration only to 100 m was possible are indicated by open circles.

Results

Abundance of bacteria

Values for bacterial numbers sampled at 10 m depth ranged from 1.423×10^8 dm^{-3} (Station 45) to 5.077×10^8 dm^{-3} (Station 53). At each station there was very little variation in numbers with increasing depth within the euphotic zone. Bacterial counts were analysed statistically from a range of sample depths between the surface and 250 m, though not all depths were sampled at each station. To estimate an overall count–depth profile, allowing for the unequal representation of stations, a log-linear model in depth and station was fitted to the data using the statistical package GENSTAT (Alvey and others, 1983; Kassab and others, 1985). Taking all stations together, bacterial numbers were more or less consistent over the top 50 m of the water column (Fig. 3). The mean of all values between 10 and 50 m was 0.95 of the surface value (95% confidence interval of 0.86–1.04). Mean bacterial numbers decreased significantly below 50 m. Bacterial numbers from deep water samples ranged from 3.126×10^7 dm^{-3} (3000 m) to 1.336×10^8 dm^{-3} (553 m). The abundance of bacteria resembled other published values for Southern Ocean sites (Fuhrman and Azam, 1980; Hanson and others, 1983; Painting and others, 1985; Zdanowski, 1985; Kogure and others, 1986).

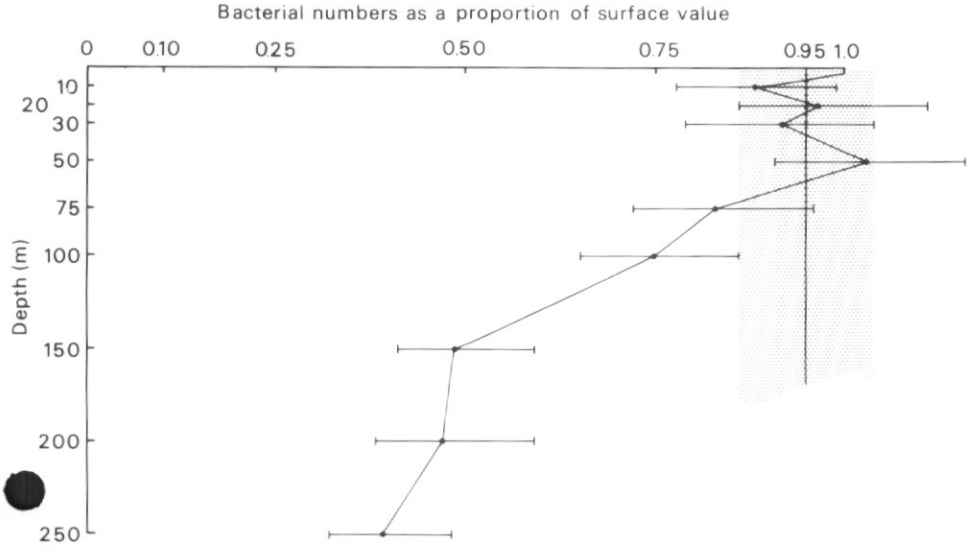

Fig. 3. The relationship between pooled bacterial numbers, averaged for all appropriate stations and expressed as a proportion of the surface value, and depth in the water column. Estimates are based on a log-linear model (see text) and horizontal bars denote 95% confidence intervals. The bars are asymmetric because a log-linear model was used. A mean proportion of the surface count derived from the depth layer 10–50 m is also indicated (shading indicates 95% confidence intervals for this mean of 0.86–1.04) to show the great similarity of counts in shallow depths.

Analysis of variance of bacterial numbers within samples and between stations at particular depths shows that between 40 to 83% of the variability is contributed by within sample (i.e. methodological) variation (Table I). Thus, although not homogeneous, bacterial numbers showed little variation with site throughout the study area (Fig. 2b). Numbers per square metre of sea surface were integrated to 100 m depth,

Table I. Analysis of variance of bacterial counts between and within stations. Counts are log transformed to stabilize within station variability. All F-ratios are statistically significant ($P < 0.01$). The within station variability describes the variation in counts within the polycarbonate membranes used (see methods).

Depth (m)	Between stations		Within stations			
	Mean square	d.f.	Mean square	d.f.	F	Within station variance as a % of total variance
Surface (3 m)	0.830	18	0.045	356	18.5	53
10	1.110	16	0.041	323	26.9	43
20	0.903	12	0.047	247	19.1	52
30	0.317	13	0.037	261	8.6	73
50	1.350	16	0.044	323	30.6	40
75	0.670	12	0.037	242	18.1	54
100	0.410	14	0.053	285	7.7	75
150	0.125	8	0.024	166	5.2	83
200	0.290	5	0.038	114	7.8	75
250	0.206	9	0.031	190	6.7	78

Table II. Statistical comparisons (Mann-Whitney U Test MINITAB, Ryan and others, 1985) of data from groups of stations for both bacterial abundance (number $\times 10^{13}$ m^{-2} sea surface) and chlorophyll *a* concentrations (mg m^{-2}), integrated to 100 m depth. Comparisons 1–4 were made using all available data for each category. Comparisons 5–8 used only data from stations where both bacteria and chlorophyll *a* were sampled (see Fig. 2a). The station grouping with the higher mean value is shown in column *A* for each comparison. (n) = number of stations and SE. = standard error.

Data	Comparison		
	A(n) Mean ± SE.	*B*(n) Mean ± SE.	Probability
All possible stations			
Bacterial numbers	1. Drake Passage (8) 3.271 ± 0.244	Bransfield Strait (11) 2.412 ± 0.098	*0.0011*
	2. Offshore* (15) 2.774 ± 0.123	Inshore (12) 2.599 ± 0.236	0.2134
Chlorophyll *a*	3. Bransfield Strait (16) 76.68 ± 15.63	Drake Passage (15) 22.24 ± 6.13	*0.0002*
	4. Inshore (19) 63.46 ± 14.08	Offshore (24) 32.13 ± 5.37	*0.0106*
Stations where bacterial and chlorophyll samples coincided			
Bacterial numbers	5. Drake Passage (8) 3.271 ± 0.244	Bransfield Strait (6) 2.307 ± 0.140	*0.0024*
	6. Offshore (12) 2.846 ± 0.146	Inshore (10) 2.596 ± 0.281	0.1563
Chlorophyll *a*	7. Bransfield Strait (6) 87.51 ± 42.29	Drake Passage (8) 24.31 ± 6.32	*0.0239*
	8. Inshore (10) 66.80 + 26.19	Offshore (12) 29.37 ± 5.09	0.1379

* Offshore stations were those where depth to seabed was > 500 m.

and to 200 m where possible. Figures for 200 m water column varied from 3.159×10^{13} m^{-2} in the Weddell Sea water of the Bransfield Strait (Station 7) to 6.234×10^{13} m^{-2} in South East Pacific Basin water near Smith Island (Station 53). In general bacterial numbers were significantly higher in Drake Passage than in Bransfield Strait (Table II). There was no significant difference in numbers of bacteria, integrated over depth, when comparing inshore (bottom depth < 500 m) and offshore stations.

Abundance and character of the phytoplankton

Phytoplankton biomass, estimated by concentration of particulate chlorophyll *a*, varied substantially over the research area (Fig. 4a). The chlorophyll amount integrated to 200 m depth (or to maximum water bottle depth if shallower) varied from 8.5 mg m^{-2} sea surface at a station over deep water in Drake Passage (Station 42) to 298 mg m^{-2} at a shallow station near Brabant Island (Station 29). In general, phytoplankton biomass was significantly higher in Bransfield Strait than in Drake Passage which is the reverse of the findings for bacteria (Table II). There was no significant difference between mean biomass for stations loosely characterized as inshore (bottom depth < 500 m) and those offshore, when only those stations with both bacterial and chlorophyll *a* data were compared. However, the difference was significant when all available data were used in the comparison. Much of the generation of high phytoplankton biomass appeared to be initated in sheltered areas nearshore such as the station near Brabant Island, and (based on surface observations only) in some coastal embayments and channels (e.g. Arthur Harbour, Anvers Island).

Depth distribution of chlorophyll *a* varied with total biomass. At stations with low and moderate biomass, chlorophyll was more or less uniformly distributed over the top 100–150 m (Fig. 4b). With increasing biomass, the maximum was in the top 30 m of the water column, with comparatively rapid fall-off with depth (e.g. Stations 20 and 29). No deep chlorophyll maximum was seen in any of the depth profiles.

The large-celled phytoplankton was dominated by diatoms at all stations but community composition varied. No formal analysis of community composition has been carried out but certain taxa can be identified which characterize areas or water masses. Stations in the southern Bransfield Strait were characterized by high abundance of *Chaetoceros socialis* Lauder (Fig. 5a), *C. neglectum* Karsten and *Porosira glacialis* (Grunow) Jørgensen. Those stations on the northern side of the Strait, close to the South Shetland Islands and with less Weddell Sea influence, were dominated by *Rhizosolenia antennata* f. *semispina* Sundström (Fig. 5b) and *Proboscia alata* (Brightwell) Sundström (Fig. 5c), both species often occurring as long chains of cells and as 'rafts'. Nomenclature for *Rhizosolenia* and related taxa follows Sundström (1986) – these two species would previously have been called *Rhizosolenia hebetata* f. *semispina* and *R. alata* respectively. These species also dominated the community in the Pacific/Bellingshausen water at the western end of the Bransfield Strait close to Anvers and Brabant Islands. *Corethron criophilum* Castracane was a characteristic species of the eastern Bransfield Strait (Fig. 5d). The high biomass at Brabant Island was composed of a number of taxa rather than being dominated by one or a few taxa. appeared to contain an admixture of the two communities mentioned above, together with large amounts of *Odontella weissflogii* (Janisch) Grunow and *Eucampia antarctica* (Castracane) Manguin.

Those stations in the Drake Passage, especially in deep water away from the influence of the South Shetlands shelf, were characterized by *Asteromphalus parvulus* Karsten (Fig. 5e), by small *Nitzschia* species such as *N. curta* (Van Heurck) Hasle, *N. angulata* (O'Meara) Hasle, and small specimens of *N. kerguelensis* (O'Meara) Hasle and *N. prolongatoides* Hasle, and by large *Chaetoceros* species such as *C. dichaeta* Ehr and *C. bulbosum* (Ehr) Heiden '*atlanticum*' phase (see Priddle and Fryxell, 1985, p. 24). Large amounts of zooplankton faecal material were found in net samples from several of these stations (Fig. 5f), especially those near the shelf, and these contained predominantly valves of small *Nitzschia* species. The abundance and character of the phytoplankton in the study area resembled closely those recorded earlier (e.g. Hart, 1934; Mandelli and Burkholder, 1966; Kopczyńska and Ligowski, 1982, 1985; Uribe, 1982, 1985; Priddle, 1985).

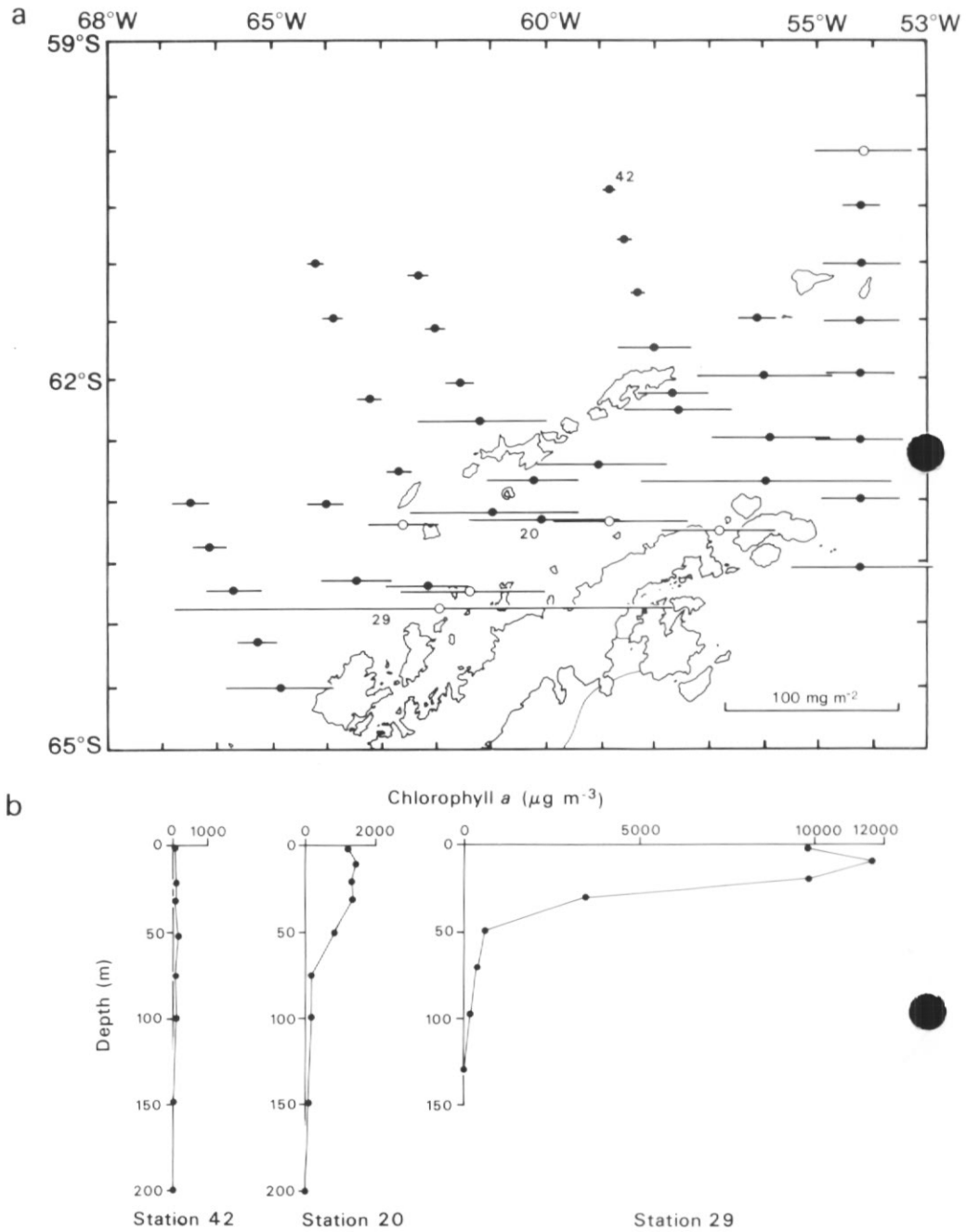

Fig. 4. Variation in the distribution of phytoplankton biomass in Drake Passage and Bransfield Strait during the SIBEX survey, January–February, 1985. (a) Particulate chlorophyll *a* amount integrated to 200 m (●) where possible, or shallower (○), at 43 stations. (b) Vertical distribution of phytoplankton, as chlorophyll *a*, at the stations with highest and lowest integrated biomass, and an intermediate station. Positions of these stations are indicated by their numbers in (a).

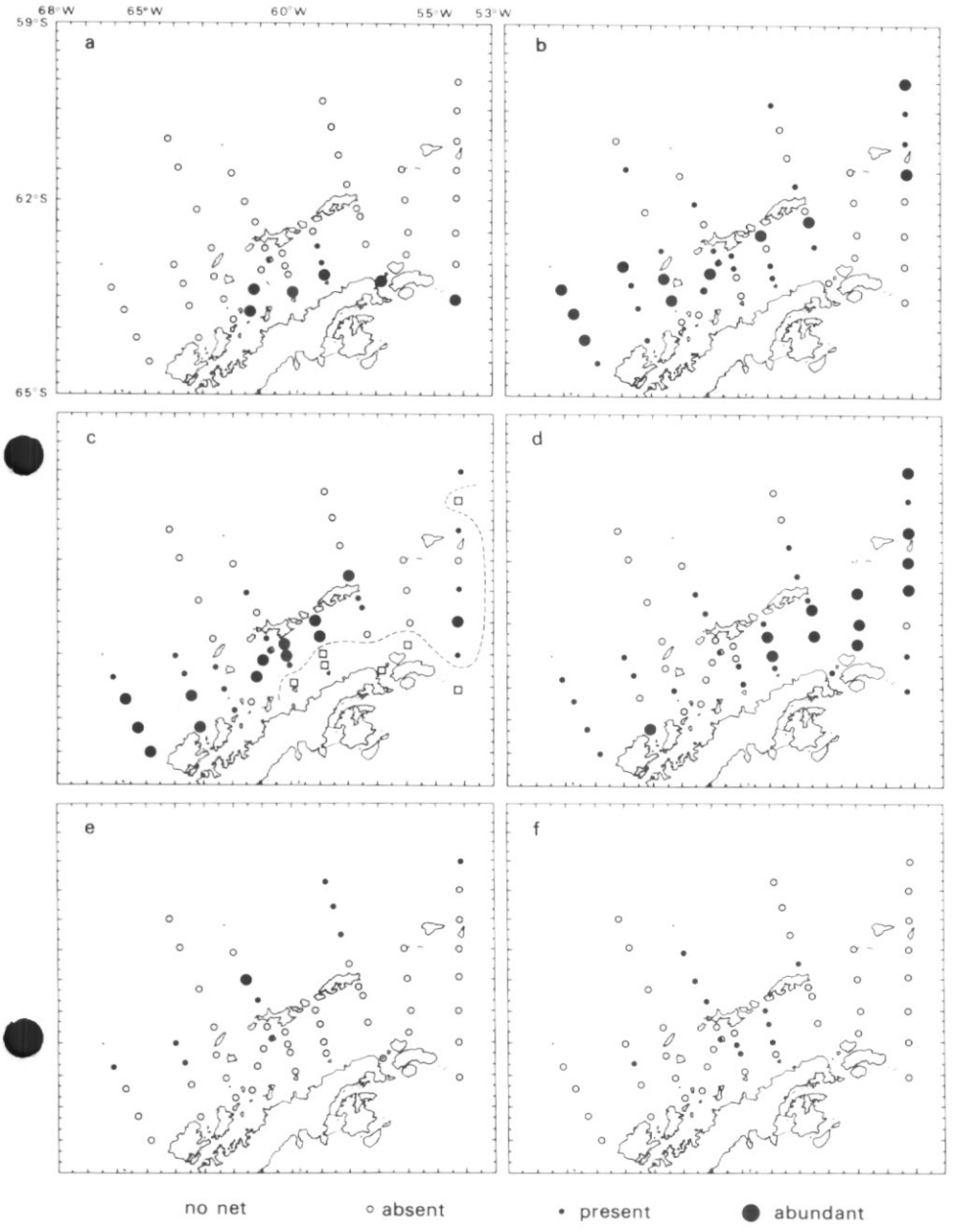

Fig. 5. Distribution of diatom species and of high amounts of zooplankton faecal material at fifty stations in Bransfield Strait and southern Drake Passage, based on vertical phytoplankton net hauls. (a) *Chaetoceros socialis*. (b) *Rhizosolenia antennata*. (c) *Proboscia* '*alata*' (see Sundström, 1986) – squares indicate predominance of the '*inermis*' form, in the area bounded by the broken line. (d) *Corethron criophilum*. (e) *Asteromphalus parvulus*. (f) Presence of abundant zooplankton faecal material.

Ratio of bacterial and phytoplankton biomass

The data from stations sampled for both bacteria and phytoplankton were analysed to look for a relationship between the two. A plot of integrated bacterial numbers versus integrated chlorophyll *a* values (Fig. 6) shows that there was no overall correlation between bacterial and phytoplankton standing stocks (Spearman rank correlation coefficient, $r_s = -0.313$; $P > 0.10$). A similar analysis performed on data from seven discrete depths between 3 and 100 m also showed no correlation at five of these depths. There was a negative correlation at 20 m ($r_s = -0.645$; $0.025 > P > 0.01$) and a positive correlation at 100 m ($r_s = 0.566$; $0.025 > P > 0.01$).

Bacterial and phytoplankton biomass were calculated to compare their relative

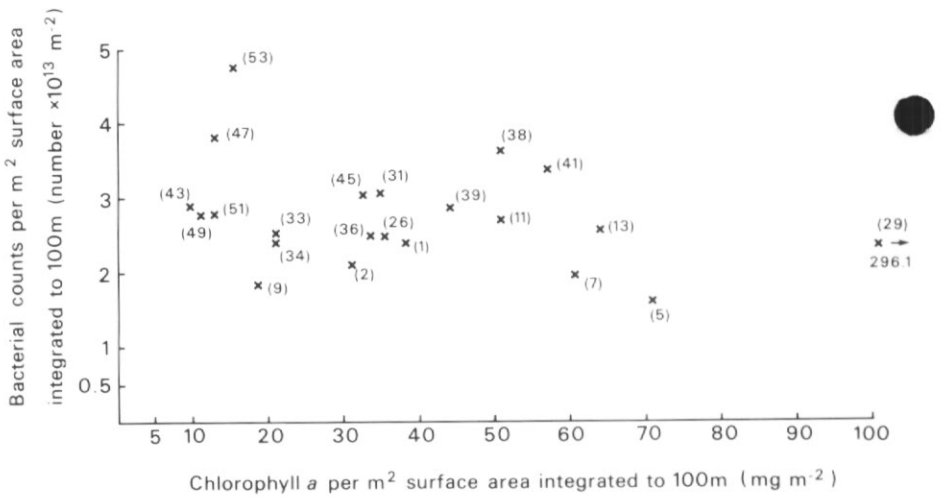

Fig. 6. The relationship between bacterial counts and phytoplankton biomass (as particulate chlorophyll *a*), both being integrated to 100 m depth. Figure in parentheses near each point is the station number. No significant trend can be identified (Spearman rank correlation coefficient, $r_s = -0.313$, $P > 0.10$).

Table III. Bacterial biomass expressed as a percentage of phytoplankton biomass at various depths (see text for conversion factors used). n = number of stations sampled at each depth.

	Ratio of bacterial C to phytoplankton C		
Depth (*m*)	*n*	*Range of values* (%)	*Mean* ± *SE* (%)
Surface (3 m)	14	0.19–15.52	5.11 ± 1.02
10	16	0.19–53.03	10.17 ± 3.39
20	11	1.69–41.65	13.13 ± 4.45
30	11	0.51–27.94	8.00 ± 2.63
50	14	2.11–36.23	10.17 ± 2.52
75	10	3.05–30.86	14.38 ± 3.25
100	13	2.82–31.51	15.09 ± 2.06
150	8	14.98–100	54.07 ± 13.85
200	5	19.35–100	83.87 ± 16.13
250	10	7.09–100	75.24 ± 12.73

levels in the water column. In the absence of direct information, we have followed Painting and others (1985) in using a carbon: chlorophyll *a* ratio of 100. Similarly, bacterial biomass has been calculated from cell counts on the basis of an average value for Antarctic marine bacteria of 8.3×10^{-15} g C per cell (Fuhrman and Azam, 1980). Obviously, absolute magnitude of the ratio of bacterial and algal biomass is dependent on the reality and consistency of these estimates. Carbon:chlorophyll ratios are highly variable and published data for the Antarctic show some very high values, probably associated with dark adapted cells containing high levels of storage compounds (e.g. Smith and Morris, 1980; El-Sayed and Taguchi, 1981). Using these conversion factors, phytoplankton biomass (integrated to 200 m depth) ranged from 0.85 g C m^{-2} sea surface to 29.8 g C m^{-2}, whereas bacterial biomass varied from only 0.26 g C m^{-2} to 0.52 g C m^{-2}. Table III shows the ratio of bacterial carbon to phytoplankton carbon found at various depths during this study. Phytoplankton biomass was generally much higher than bacterial biomass within the euphotic zone. However, the relative importance of the latter increased with increasing depth and below 100 m bacterial biomass became much more important. The wide range of ratios recorded was due mainly to fluctuations in algal numbers, bacterial numbers being relatively constant.

Discussion

Since bacteria in the euphotic zone are largely reliant on phytoplankton for energy supply, either through excretion by the algae of dissolved organic material (Lancelot, 1979; Lancelot and Billen, 1984; Jones and Cannon, 1986) or by decomposition of dead phytoplankton cells (Riemann and Sondergaard, 1986), it is logical to expect bacteria to respond to variation in phytoplankton growth and abundance. The samples in this study covered a range of scales of variation. Large-scale variability of phytoplankton biomass in the study area was linked to differences in water mass characteristics, e.g. the contrast between Drake Passage and Bransfield Strait stations. This variation would have been well-established over long time scales corresponding to the growth season of the algae. Superimposed upon this pattern was shorter-time-scale variation associated with local phytoplankton population maxima, such as that found near Brabant Island in the present study and a high phytoplankton biomass formed later in an eddy off King George Island, South Shetland Islands (Heywood and Priddle, in press).

Bacterial response to variation in the environment may not be consistent over different time scales. Three types of response can be envisaged:

1. Changes in metabolic activity. These probably provide the usual response to short-term changes in the environment. No data are available on this aspect for the present study, so we would not expect to recognize responses to local changes in phytoplankton biomass.

2. Increase in biomass, manifested by change in mean cell size but without increase in cell numbers. Morita (1985) has presented evidence that the majority of oceanic bacteria may comprise inactive, small cells ('ultramicrocells') which respond to increase in food availability by increasing cell size and metabolic activity. Change in biomass implies longer-term response to the environment and is thus linked to longer-term variation acting on larger spatial scales. Since only differences in bacterial cell numbers were measured, this response would also not have been recognized in this study.

3. Increase in biomass through cell division, leading to an increase in the number of bacterial cells (the variable measured in this study). Generation- or doubling-times

for Southern Ocean pelagic bacteria are apparently long (several days to a few weeks, as determined by the uptake of [^{3}H]thymidine — Furhman and Azam, 1980; Hanson and others, 1983; Kogure and others, 1986) and this suggests that only well-established long-term changes in phytoplankton abundance might be likely to induce corresponding changes in bacterial numbers. Such long-term changes would include features such as fronts and seasonal stratification (Fogg and others, 1985). It is therefore not wholly unexpected that the overall relationship between bacterial and phytoplankton biomass shows no trend (Fig. 6), since phytoplankton maxima were local events superimposed upon more subtle larger-scale differences (Fig. 4). As noted above, bacterial response to these blooms is more likely to be manifested at the metabolic level.

There remains the larger-scale pattern within the study area. Phytoplankton biomass, as indicated by particulate chlorophyll *a*, showed substantially higher levels in Bransfield Strait than in Drake Passage (Table II; Fig. 4) and this pattern is typical for all observations in this area (e.g. Hart, 1934; Lipski, 1982; Uribe, 1982). However, bacterial numbers showed a slight trend to be higher in Drake Passage, the reverse of the pattern of phytoplankton biomass distribution. It seems likely that an important factor in determining this behaviour is the artefact of measuring phytoplankton biomass by chlorophyll *a* concentrations without reference to size composition. As with other oceans, the phytoplankton of the Southern Ocean comprises a relatively constant population of small-celled phytoplankton (Bröckel, 1981; Sasaki, 1984) together with a variable amount of large-celled algae – in the Southern Ocean these are predominantly diatoms. Bacteria participate mainly in the trophic structure associated with picophytoplankton and protozoan micrograzers. In this context, the local high biomass contributed by diatoms may be of little significance, being lost to the microplankton through sedimentation and by zooplankton grazing.

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