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THE DISTRIBUTION AND ABUNDANCE OF CHROOCOCCOID CYANOBACTERIA IN THE SOUTHERN OCEAN

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Abstract: The abundance of phycoerythrin-containing chroococcoid cyanobacteria in the surface waters between Australia and Antarctica were determined by counts of yellow autofluorescing cells on four transects of the Southern Ocean in the 1985/86 austral summer and by analysis of the pigment zeaxanthin. Despite widely differing daylengths on these transects the principal determinant of cyanobacterial abundance appears to be temperature, with cell number being exponentially related to water temperature. Ultrastructural differences found in the cell wall of Southern Ocean cyanobacteria may indicate the presence of different strains.

1. Introduction

The occurrence of chroococcoid cyanobacteria (blue green algae) in the sea has been known since early this century but only recently has it been shown that these organisms, ascribed to the genus *Synechococcus*, occur in high concentrations in the world's oceans (JOHNSON and SIEBURTH, 1979; WATERBURY *et al.*, 1979; LI *et al.*, 1983; PLATT *et al.*, 1983; MURPHY and HAUGEN, 1985; TAKAHASHI and HORI, 1984; TAKAHASHI *et al.*, 1985) and contribute significantly to primary productivity (WATERBURY *et al.*, 1979; JOINT *et al.*, 1986; LI *et al.*, 1983; PLATT *et al.*, 1983). Specific growth rates of marine cyanobacteria have been found to be around 1.6 doublings per day and in the open ocean they constitute a significant component in the food web as a diverse assemblage of microheterotrophs graze 30–40% of the standing crop of these organisms daily (ITURRIAGA and MITCHELL, 1986).

Despite the importance of these picoplanktonic primary producers in pelagic food web dynamics little has been reported on the factors controlling their distribution and abundance. MURPHY and HAUGEN (1985) found that the decrease in cyanobacterial numbers in the North Atlantic correlated with decreasing temperature. Similarly, CARON *et al.* (1985), investigating the vertical and seasonal population dynamics of chroococcoid cyanobacteria in Lake Ontario reported maximum cell numbers to occur at the time of maximum water temperature. They have also been shown to constitute the major part of the phytoplankton standing crop in oligotrophic waters (PLATT *et al.*, 1983) and to contain light-harvesting pigments which absorb in the blue-green region of the spectrum enabling them to photosynthesize deep in the photic zone of the water column (WOOD, 1985).

Cyanobacteria are very often the dominant autotrophs in aquatic habitats on

the Antarctic Continent. These habitats range from soils, endolithic and sublithic environments to lakes and streams of greatly varying salinity, although they do not appear to favour the combination of low temperature and high salinity (WRIGHT and BURTON, 1981). In Antarctica they continue to photosynthesize at sub-zero temperatures and *Nostoc* continues to fix nitrogen at −5°C, albeit at a low rate (BECKER, 1982; DAVEY and MARCHANT, 1983). In the Southern Ocean light levels are low for much of the year due to the low elevation of the sun and attenuation by snow-covered sea-ice (SULLIVAN *et al.*, 1985; TILZER *et al.*, 1985). Here we report studies on the distribution and abundance of cyanobacteria in the surface waters of the Indian Ocean sector of the Southern Ocean.

2. Materials and Methods

Water samples were collected on the southbound (V1 out, V5 out) and northbound (V1 in, V5 in) parts of two cruises between Hobart, Australia and Antarctica in the 1985/86 austral summer. Details of the collecting sites are given in Table 1.

Samples were taken from the surface by bucket or centrifugal pump, the intake of which is 5 m below the surface, near the stern of the ship. Cells were concentrated by filtration through 0.2 μm pore size, 25 mm diameter Nuclepore filters. Cyanobacteria were enumerated by epifluorescence microscopy using a Zeiss WL microscope fitted with a HBO 50 mercury vapour lamp, a BP 540–590 exciter filter, FT 510 dichroic beam splitter and LP 520 barrier filter. The microscope was shock mounted to reduce vibrations produced by the ship's engines (MARCHANT, 1985). Yellow autofluorescing picoplankton were counted as cyanobacteria in at least fourteen random fields on each filter. As the yellow autofluorescence is due to the presence of phycoerythrin, any cyanobacteria lacking this pigment would not be enumerated which may lead to an underestimate of these organisms.

For pigment analysis, water samples taken at the same time as those for cell counts were filtered through Whatman GF/F glass fibre filters until clogged. These filters were stored under liquid nitrogen until analysis by HPLC. The frozen filter was broken into pieces of approximately 5 mm diameter, sonicated in 4 m*l* methanol using a Braun Labsonic 1510 sonicator equipped with a 4 mm diameter needle probe (30 s at 50 W), and filtered using a simple centrifugal system described elsewhere (WRIGHT and SHEARER, 1984). The filter debris was washed with 0.5 m*l* methanol and recentrifuged. The combined extract was filtered through a Millex-SR filter unit (0.5 μm pore-size, Millipore Corp.). Two hundred microlitres of the extract were injected directly into a Waters Associates liquid chromatograph. Two RCM-100 radial compression modules, containing Rad-Pak A cartridges (5 μm particle size, octadecyl silica), were used in series, protected by a precolumn filter and an RCSS Guard-Pak. The pigments were eluted using a linear gradient from 90: 10 acetonitrile: water to ethyl acetate over 20 min at 2 m*l* min^{-1}. They were detected by absorbance at 405 and 436 nm, and integrated using a Waters Data Module. Pigments were identified by co-chromatography with known standards and by absorption spectra taken on-stream using a Hewlett-Packard 8450A spectrophotometer.

Surface water temperature was measured at the sea water intake by thermistor

Table 1. Cyanobacterial cell numbers together with the date, position, water temperature and daylength at the time of sample collection.

Voyage	Date	Lat.	Long	Temp. (°C)	Cells/*l*	S.D.	Daylength (h)
1 OUT	18/9/85	47°27.4′	140°03.52′	9.1	1.6E+07	1.1E+06	11.51
	18/9/85	48 31.8	137 30.61	7.4	1.4E+06	3.3E+05	11.51
	19/9/85	49 36.83	134 45.29	7.7	3.0E+06	1.6E+05	12.00
	19/9/85	50 39.71	131 39.71	5.8	3.8E+06	1.5E+06	12.00
	20/9/85	51 39.70	128 16.31	6.6	1.1E+06	2.6E+05	12.00
	20/9/85	52 25.57	125 39.27	3.6	2.3E+05	4.0E+04	12.00
	21/9/85	53 10.56	122 05.11	3.2	3.8E+05	9.3E+04	12.00
	21/9/85	53 54.97	118 18.82	3.6	8.9E+04	2.3E+04	11.59
	22/9/85	54 24.21	115 30.82	3.3	2.7E+04	8.5E+03	12.12
	22/9/85	55 12.76	113 11.87	2	5.5E+04	1.3E+04	12.12
	23/9/85	56 09.30	110 15.19	0.1	1.0E+04	6.8E+03	12.12
	23/9/85	56 34.38	107 13.28	−1.2	1.5E+04	9.0E+03	12.12
1 IN	16/12/85	62 09.3	53 46.8	−1	5.8E+03	1.7E+04	19.25
	17/12/85	61 11.3	58 50.9	−1	2.4E+03	8.8E+03	18.10
	20/12/85	58 02.2	86 18.3	1.2	1.8E+03	6.9E+03	17.55
	21/12/85	57 11.8	97 09.9	0.8	2.4E+04	9.1E+04	17.37
	22/12/85	56 44.0	105 44.2	1.7	1.5E+04	2.9E+04	17.37
	23/12/85	55 36.8	114 16.3	3.8	2.2E+03	8.3E+03	17.37
	24/12/85	54 49.3	118 27.1	4.4	1.5E+04	1.9E+04	17.37
	24/12/85	54 01.4	122 05.3	5.8	3.0E+04	3.3E+04	17.08
	25/12/85	52 49.8	126 22.9	6.8	4.2E+04	3.1E+04	16.44
	26/12/85	49 24.1	136 00.2	8.4	3.3E+06	2.2E+06	16.22
	27/12/85	47 51.1	139 41.2	11.5	7.9E+06	3.7E+06	16.00
	27/12/85	46 27.8	142 28.0	12	1.0E+07	4.2E+06	15.35
	28/12/85	44 58.6	145 00.2	13.9	3.4E+07	1.4E+07	15.35
5 OUT	6/1/86	48 58.7	140 55.4	10.5	3.6E+06	9.4E+05	17.57
	7/1/86	51 47.7	136 49.3	9	5.9E+05	1.4E+05	16.27
	7/1/86	53 02.0	134 44.0	7.4	7.0E+05	2.8E+05	16.27
	8/1/86	54 21.6	132 14.3	6.2	2.1E+05	1.4E+05	16.49
	8/1/86	55 23.6	130 16.7	5.3	1.5E+05	9.8E+04	16.49
	9/1/86	57 23.0	125 39.0	3.8	3.8E+04	2.6E+04	17.46
	9/1/86	58 16.7	123 12.9	3.1	1.7E+05	5.2E+04	17.46
	10/1/86	59 55.2	118 09.2	2.4	3.6E+04	3.8E+04	18.12
	10/1/86	60 42.9	115 09.1	1.6	1.2E+04	1.9E+04	18.12
5 IN	16/2/86	57 35.5	111 35.9	4.2	4.0E+04	5.8E+04	14.57
	17/2/86	54 46.7	112 28.9	4.8	4.7E+04	2.8E+04	14.33
	17/2/86	54 18.6	112 38.7	5.2	3.7E+04	2.9E+04	14.33
	18/2/86	52 55.6	118 57.6	5	7.5E+04	6.7E+04	14.14
	19/2/86	51 30.2	126 45.8	8.2	4.2E+05	1.3E+05	14.10
	20/2/86	49 23.3	133 57.1	9.4	8.4E+05	2.1E+05	14.01
	21/2/86	46 51.4	140 21.9	11.8	2.1E+06	4.4E+05	13.32
	22/2/86	46 16.1	145 47.3	13.8	8.6E+06	3.3E+06	13.32

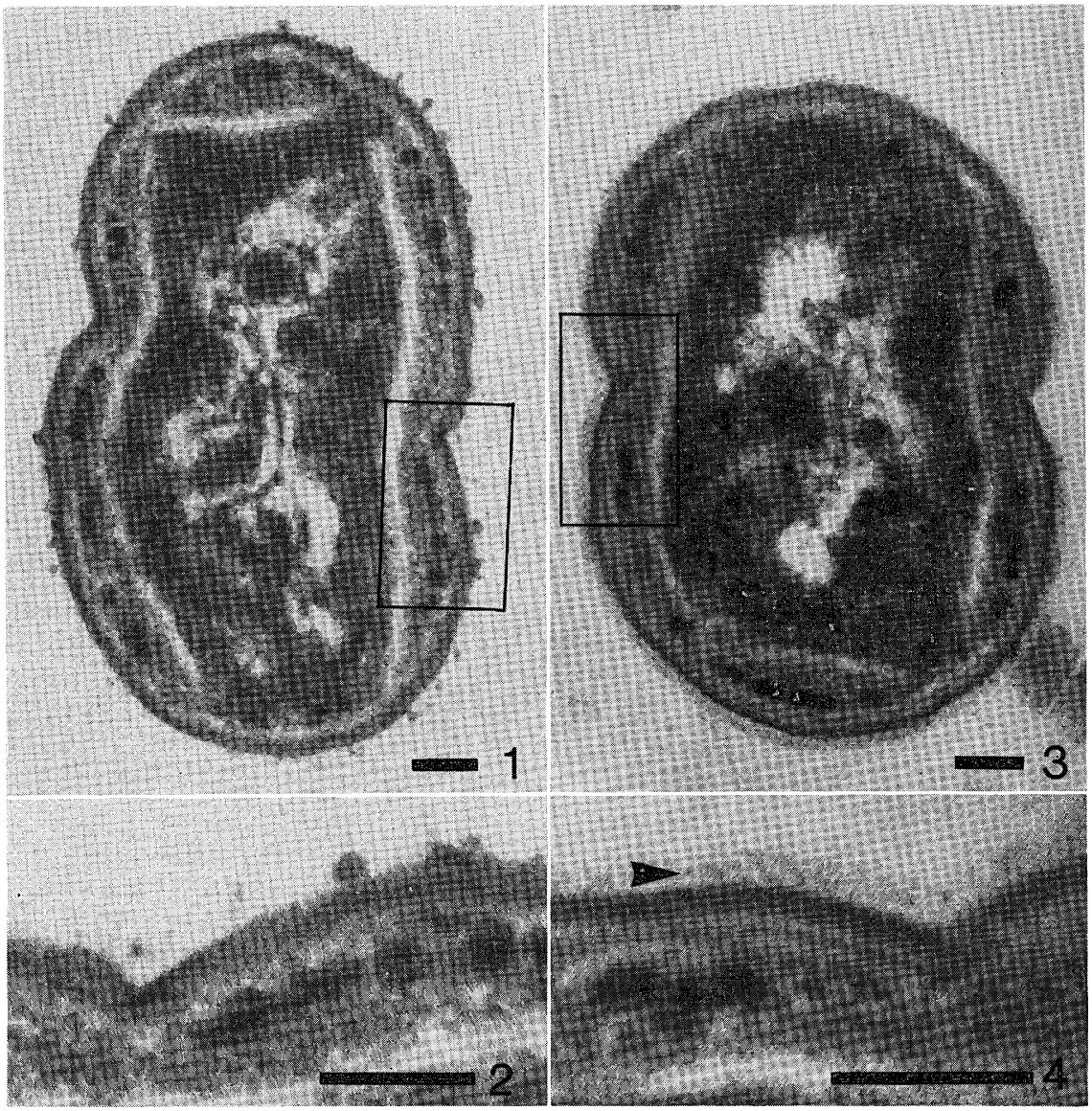
or by a calibrated mercury-in-glass thermometer. Daylength was determined from the Nautical Almanac 1985, 1986 (SECRETARY OF STATE FOR DEFENCE, 1983, 1984).

Cells were prepared for transmission electron microscopy either by using glutaraldehyde fixation of bulk water samples (JOHNSON and SIEBURTH, 1982) or by fixing concentrated phytoplankton with 1% glutaraldehyde made up in sea water for 15 min.

Following initial preservation, both were post-fixed in 1% OsO_4 for 15 min, dehydrated through a graded series of acetone and embedded in SPURR's (1969) low viscosity resin. Thin sections were stained with lead citrate and uranyl acetate and examined with a JEOL 1200EX transmission electron microscope.

3. Results and Discussion

Picoplanktonic cyanobacteria from the Southern Ocean resemble these organisms



Figs. 1–4. Transmission electron micrographs of Southern Ocean cyanobacteria. Scale markers = 100 nm.

Fig. 1. Ultrastructure of a dividing cell. The box indicates the area shown in Fig. 2.

Fig. 2. Detail of the wall of the cell shown in Fig. 1.

Fig. 3. A dividing cell, the outer wall layer of which exhibits regular patterning. The box indicates the area shown in Fig. 4.

Fig. 4. Detail of the patterned structure of the cell wall shown in Fig. 3. The patterned outer layer is indicated by the arrow.

reported from elsewhere in the world's oceans. The cells are 0.8–1.4 μm in diameter and divide by binary fission indicating that they are likely to be *Synechococcus*.

Two different ultrastructural types of cyanobacteria have been seen so far in the Southern Ocean (Figs. 1 and 3). Some cells were found to have a patterned outer layer of cell wall although their cytoplasmic structure appeared to be similar (Fig. 4 *cf.* Fig. 2). Considerable variation in the ultrastructure of the cytoplasm, particularly thylakoid arrangement, and the cell wall of chroococcoid cyanobacteria has been illustrated by other authors (*e.g.* JOHNSON and SIEBURTH, 1979, 1982; JOINT and PIPE, 1984; TAKAHASHI *et al.*, 1985). Spinae have been found on the outer cell walls of clones isolated from the eastern seaboard of the USA (PERKINS *et al.*, 1981; SAROKIN and CARPENTER, 1981). We have not been able to ascertain whether the presence or absence of the patterned wall layer signifies different strains of cyanobacteria or whether it reflects a developmental stage of one strain. However, that both developing daughter cells have this patterning indicates the likelihood of different strains.

As WOOD *et al.* (1985) point out, most authors treat the marine coccoid cyanobacteria as a single ecological and taxonomic unit. However these authors and ONG *et al.* (1984) have demonstrated differences in pigmentation between strains of *Synechococcus* and CAMPBELL *et al.* (1983) found differences in serological affinity indicating the presence of genetically distinct populations of cyanobacteria. The antisera used to demonstrate serologically different strains were produced in rabbits following the injection of fixed whole cells (CAMPBELL *et al.*, 1983). The rabbit antibodies would therefore be developed principally against cell wall components. Thus, these observations of ultrastructural differences in the cell wall, coupled with the recognition of serologically distinct strains suggest that different strains may be distinguished on the basis of the ultrastructure of their cell walls.

Counts of phycoerythrin containing cyanobacteria were made on four transects of the Southern Ocean between Tasmania and Prydz Bay at different times in the 1985/86 austral summer (Table 1). The daylength on the four transects was 11.50–12.12 h, 19.25–15.20 h, 16.25–18.12 h and 14.57–13.23 h respectively.

Samples for pigment analysis were collected from a few stations on the second voyage (V5), allowing HPLC analysis of zeaxanthin, which has been proposed as a marker for marine cyanobacteria in waters where chlorophyll b-containing phytoplankton are absent (GIESKES and KRAAY, 1983a; GUILLARD *et al.*, 1985). Zeaxanthin concentration decreased with increasing latitude and decreasing temperature but no statistically meaningful results could be deduced from the few samples taken (Fig. 5). Zeaxanthin concentrations in the Prydz Bay area of the Southern Ocean lie in the range 0 to 0.032 $\mu g\, l^{-1}$ (MARCHANT and WRIGHT, 1987), considerably lower than the concentration of this pigment in temperate and tropical waters (0.01 to 0.23 $\mu g\, l^{-1}$, GIESKES and KRAAY, 1983b).

Similar to the results from the North Atlantic and Lake Ontario (MURPHY and HAUGEN, 1985; CARON *et al.*, 1985), a strong correlation was found between surface water temperature and the logarithm of cell number with regressions significant at the 0.1% level and regression slopes significantly different from 0 at the 0.5% level (Fig. 6). This implicated temperature as the principal determinant of cyanobacterial numbers in the Southern Ocean. No significant difference was found to exist between

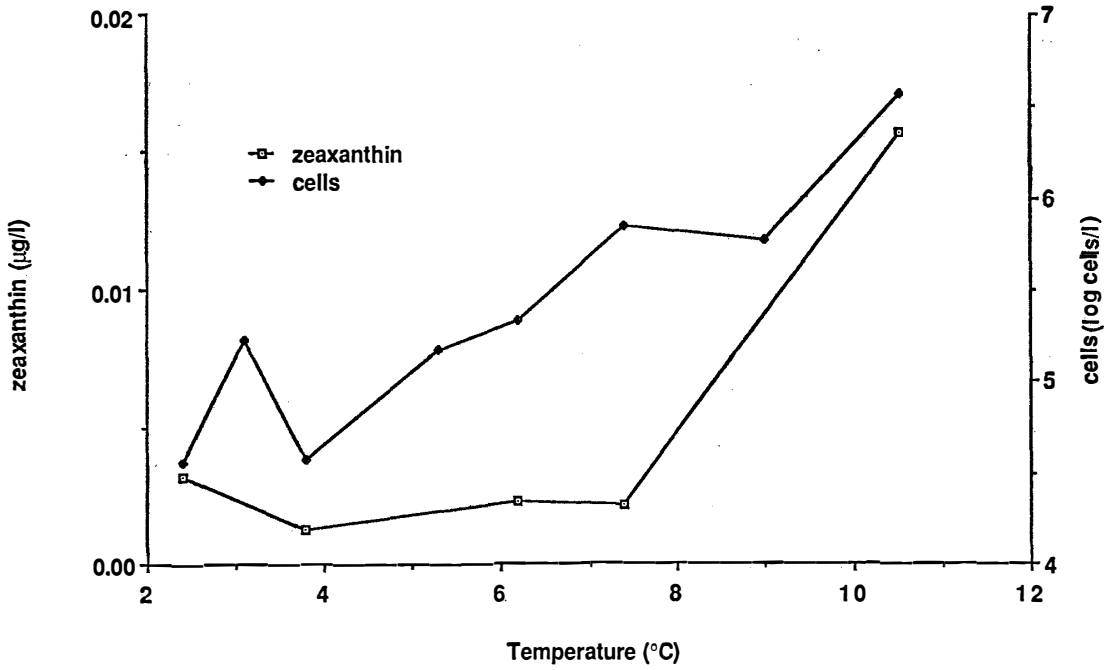


Fig. 5. Concentration of cyanobacteria and zeaxanthin plotted against temperature.

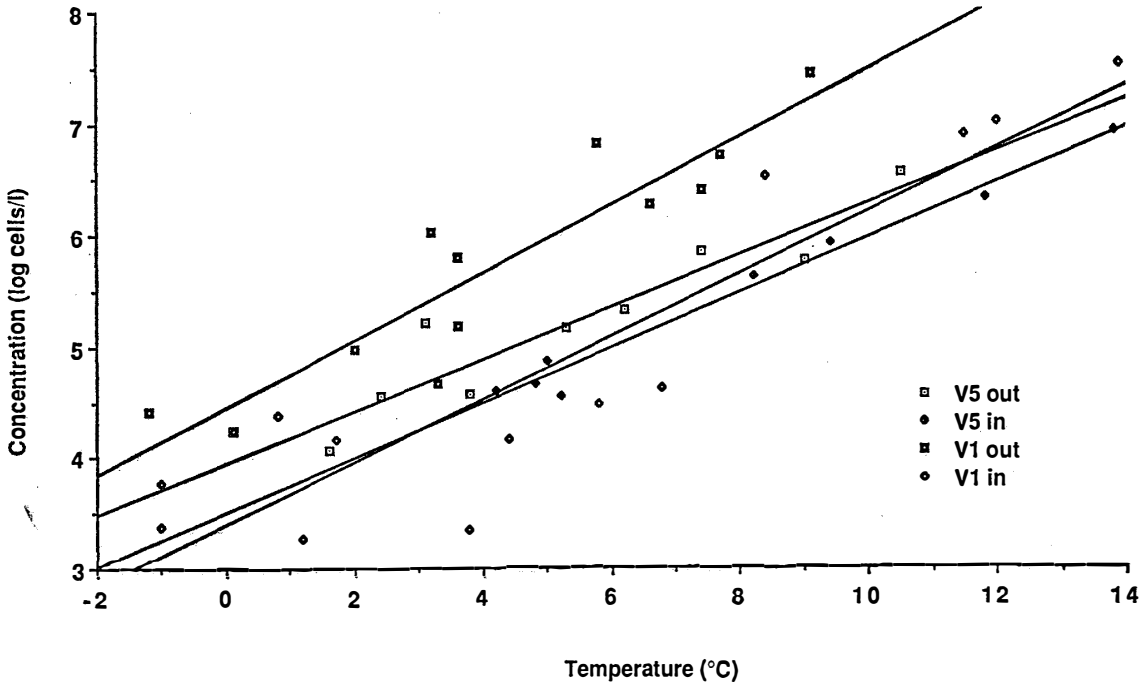


Fig. 6. The concentration of cyanobacteria (log cell number per litre) plotted against surface temperature. Correlation coefficients for the four sets of data are V1 out, 0.92; V1 in, 0.92; V5 out, 0.94 and V5 in, 0.99.

three of the paired transect combinations ($p\{F<0.05\}$), namely, voyage 1 southbound (V1 out) and voyage 1 northbound (V1 in), voyage 5 northbound (V5 in), voyage 5 southbound (V5 out) and voyage 1 southbound (V1 out). The significant similarity of these regressions is despite differences in the light climate between transects. Thus,

in contrast to the widely accepted view that light availability determines the standing crop of phytoplankton, these data indicate the likelihood of temperature as a principal determinant of cyanobacterial numbers in the Southern Ocean.

In this investigation we have not considered the role that nutrients and other environmental factors may play in the control of cyanobacterial abundance. Nitrate concentrations increase with increasing latitude and decreasing temperature in the Southern Ocean (HIGGINS, personal communication). Elucidation of the relative importance of temperature and nutrients, particularly nitrate, requires further investigation, including studies of cultured material.

Recently, WALKER and MARCHANT observed the occurrence of abundant picoplanktonic coccoid cyanobacteria in the water column at a 30-m deep coastal site near the Australian Antarctic station of Davis. Cyanobacterial numbers were greatest during August at the time of maximum increase in the thickening of the sea ice and a lesser peak of abundance at the time of the break up of the sea ice. These cells were found to be associated with the appearance of diatom frustules and sediment particles and it is suggested that the presence of cyanobacteria may be due to benthic material being incorporated into ice platelets forming in the supercooled water. Ice crystals have been implicated in the incorporation of algae into the sea ice (GARRISON *et al.*, 1983). Their reappearance in the summer has been ascribed to their liberation on the melting of the sea ice. It has not been established whether these cyanobacteria are photosynthetically competent. However they may contribute to the increased proportion of phytoplankton as nanoplanktonic sized cells (measured by chlorophyll concentration) during the winter.

Data presented here on both cell counts and pigment analysis indicate that cyanobacteria are a minor component of the phytoplankton of Antarctic seas. Their low concentration is markedly different to the high numbers that are found in tropical and temperate oceans where concentrations are in the order of 10^7–10^8 cells l^{-1}.

Laboratory studies indicate that at least 30–40% of cyanobacteria in the North Pacific Ocean are consumed by microheterotrophs daily (ITURRIAGA and MITCHELL, 1986). Their very low numbers in Antarctic waters provoke questions about differences in the organisms present and the nature of the interactions between those organisms at the lower end of the food chain in polar waters compared with what has been found in warmer waters.

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