

## DISTRIBUTION AND COMMUNITY STRUCTURE OF PICOPHYTO- PLANKTON IN THE SOUTHERN OCEAN DURING THE LATE AUSTRAL SUMMER OF 1992

Tsuneo ODATE<sup>1</sup> and Mitsuo FUKUCHI<sup>2</sup>

<sup>1</sup>*Faculty of Bioresources, Mie University, 1515, Kamihama-cho, Tsu 514*

<sup>2</sup>*National Institute of Polar Research, 9–10, Kaga 1-chome, Itabashi-ku, Tokyo 173*

**Abstract:** Abundance and community structure of picophytoplankton populations were investigated in the Southern Ocean during the late austral summer of 1992. Three major oceanographic fronts, the Antarctic Polar Front, the Subantarctic Front, and the Subtropical Convergence, were recognized based on the degree of latitudinal gradients of surface water temperature and nutrient concentrations. These fronts divide the area into four distinct zones, the Antarctic Zone (ANZ), the Polar Frontal Zone (PFZ), the Subantarctic Zone (SAZ), and the Subtropical Zone (STZ). Chlorophyll *a* concentration retained on a glass fiber filter (bulk CHL) was the most abundant ( $0.93 \pm 0.24 \mu\text{g/l}$ ) in the SAZ. Although the bulk CHLs in the surface waters of the other water masses were almost the same, *ca.*  $0.3 \mu\text{g/l}$ , the percent contribution of the pico fraction (less than  $2 \mu\text{m}$ ) was different,  $74 \pm 5\%$  (STZ),  $43 \pm 11\%$  (PFZ), and  $23 \pm 11\%$  (ANZ). The cell density of cyanobacteria (CY) was greater than that of other picophytoplankton (OP) north of the Subantarctic Front (SAF). The lowest cell densities of CY and OP were found in the surface water of the ANZ ( $0.041 \pm 0.035 \times 10^3$  and  $3.5 \pm 1.8 \times 10^3$  cells/ml, respectively) while the highest ones were noted in the SAZ ( $49 \pm 12 \times 10^3$  and  $15 \pm 1.6 \times 10^3$  cells/ml, respectively). Since these changes evidently occurred around the oceanographic fronts, the fronts are important boundaries for geographical variations of phytoplankton size composition and picophytoplankton community structure in the Southern Ocean.

### 1. Introduction

There are prominent oceanographic fronts in the Southern Ocean, that is, the Subtropical Convergence (STC) which forms a boundary between the Subtropical Zone (STZ) and the Subantarctic Zone (SAZ), the Subantarctic Front (SAF) which divides the SAZ and the Polar Frontal Zone (PFZ), the Antarctic Polar Front (APF) which borders the PFZ and the Antarctic Zone (ANZ), and the Antarctic Divergence (AND) which divides the ANZ and the Antarctic Coastal Zone (ACZ) (LUTJEHARMS *et al.*, 1985; ISHINO, 1989; TOMCZAK and GODFREY, 1994). Discontinuity of the water masses largely affects geographical distribution of many planktonic organisms in the Southern Ocean. For instance, it is well known that community structure of diatoms varies around the fronts (FUKASE, 1962; HASLE, 1969) and that latitudinal zonation of zooplankton communities coincides

with the horizontal distribution of water masses (HEMPEL, 1985).

The Antarctic pelagic ecosystem has been regarded as a simple trophic progression from large-sized diatoms to krill and to whale (HART, 1942). It has been assumed that primary production would have to be high in order to support large biomass at higher trophic levels (HEWES *et al.*, 1985). Extensive studies during the past two decades, however, have indicated that primary production and biomass of phytoplankton in the Southern Ocean are moderate or low as compared to those of other oceanic areas (EL-SAYED, 1970; FUKUCHI, 1980; BRÖKEL, 1981; EL-SAYED and TAGUCHI, 1981; HEWES *et al.*, 1985). Recently, nanophytoplankton has been recognized as the major component of the Antarctic phytoplankton community (BRÖKEL, 1981; HEWES *et al.*, 1985, 1990; KOSAKI *et al.*, 1985; WEBER and EL-SAYED, 1987; SULLIVAN *et al.*, 1990). According to the recent results the simple grazing food chain has been reconsidered and microbial food webs, dominated by small-sized primary producers and heterotrophs have significant roles more than expected before in the Antarctic pelagic ecosystems (HEWES *et al.*, 1985, 1990).

Although the concentration of chlorophyll *a* has been estimated during the cruise of the Japanese Antarctic Research Expedition (JARE) since 1965 (HOSHIAI, 1968), the regional variation of the dominant size class could not be documented since most JARE data were determined with a single filter filtration technique. Moreover, distributions of picophytoplankton populations, such as cyanobacteria, are poorly understood since the former studies on aquatic flora in the Southern Ocean focused only on chemically preservable or relatively large-sized phytoplankton (*i.e.*, diatoms and dinoflagellates) (FUKASE, 1962; HASLE, 1969). The present study aims to reveal prominent features of distribution and community structure of picophytoplankton in different water masses of the Southern Ocean. The present results will provide primary information for understanding the trophodynamics in the Antarctic pelagic ecosystems in comparison with neighboring sea areas.

## 2. Materials and Methods

Sampling of seawater was conducted during the northward cruise (65–35°S along *ca.* 150°E longitude) of the icebreaker SHIRASE from March 12 to 18, 1992 (JARE-33) (Fig. 1). Twenty-eight surface water samples (Stations 1–28) were taken from the outlet of the Surface Water Monitoring System (FUKUCHI and HATTORI, 1987), which continuously recorded surface water temperature and nutrient concentrations (nitrate plus nitrite and silicate). In addition, water samples were collected from ten different layers between 10 and 200 m using Nansen bottles, and surface water was taken with a plastic bucket at five stations: Stations I and II in the ANZ, Stations III and IV in the PFZ, and Station V in the SAZ. The positions of the oceanographic fronts were determined based on the meridional gradients of the variables.

An aliquot (100–200 ml) from the water sample was directly filtered through a Whatman GF/F glass fiber filter with vacuum pressure of less than 100 mmHg (bulk

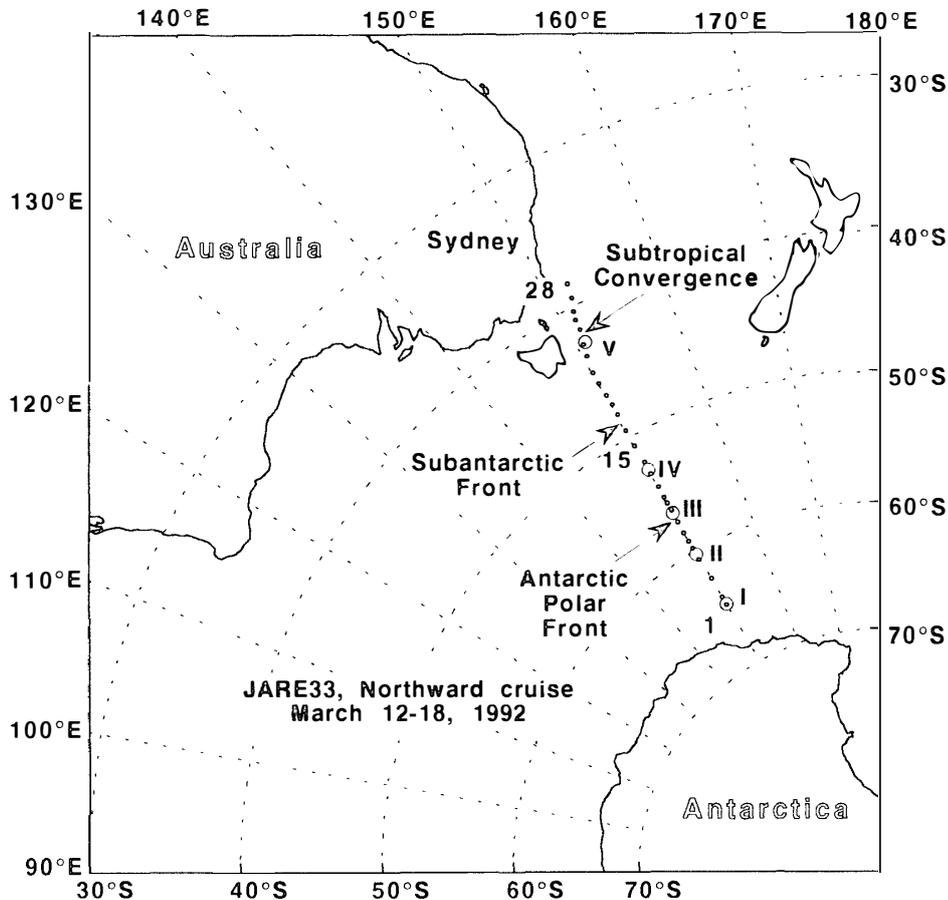


Fig. 1. Location of sampling stations during the northward cruise of JARE-33. Surface water samples were collected at Stations 1–28 (closed circles) while samplings were conducted vertically at Stations I–V (open circles). Three fronts, the Antarctic Polar Front, the Subantarctic Front, and the Subtropical Convergence, were recognized by the changes in the surface water temperature and nutrient concentrations along the cruise track (see Fig. 2).

fraction). Another aliquot (250–500 ml) was also filtered through a Nuclepore filter, of which pore size was  $2\ \mu\text{m}$  ( $< 50\ \text{mmHg}$ ) (micro-nano fraction). A part of the filtrate (100–200 ml) was further filtered through a Nuclepore filter, of which pore size was  $0.2\ \mu\text{m}$  ( $< 100\ \text{mmHg}$ ) (pico fraction). These filters were kept in glass vials, which contained 6 ml of N,N-dimethylformamide, for extraction of chlorophyll *a* (CHL) (SUZUKI and ISHIMARU, 1990). These vials were stored in the dark at  $-20^\circ\text{C}$  for 24 hours. The CHL was determined by the fluorometric method (PARSONS *et al.*, 1984). Calibration of the Turner Design Fluorometer Model 10R was conducted with pure chlorophyll *a* (Sigma Chemical Co.).

The rest of the filtrate from the Nuclepore filter of  $2.0\ \mu\text{m}$  pore size (50–100 ml) was filtered through a Nuclepore filter of  $0.2\ \mu\text{m}$  pore size. Picophytoplankton retained on this filter were immediately enumerated on board using an epifluorescence microscope (Nikon EDF). Under blue excitation (excitor 420–490 nm, dichroic mirror 510 nm, barrier 520 nm), yellow and red fluorescing cells are commonly observed (MURPHY and HAUGEN, 1985). The former is represented by

cyanobacteria (CY) while the latter contains small eukaryotes and prokaryotes (e.g., CAMPBELL and VAULOT, 1993). In the present study, picoeukaryotes could not be distinguished from picoprokaryotes. Red fluorescing cells are referred as “other picophytoplankton” (OP).

### 3. Results

#### 3.1. Zonation of sea area surveyed

Three major oceanographic fronts (APF, SAF, and STC) were recognized based on the degree of latitudinal gradients of surface water temperature and nutrient concentrations (Fig. 2a and b, respectively). The surface water temperature increased from 4.5 to 6.5°C, and the concentration of silicate decreased from 20  $\mu\text{M}$  to several  $\mu\text{M}$ , although the decrease of nitrate plus nitrite was not prominent around 55°30'S. Around 48°00'S, the surface water temperature jumped from 11 to 13.5°C, the concentration of nitrate plus nitrite decreased from 13  $\mu\text{M}$  to 5  $\mu\text{M}$ , and silicate became less than the detectable limit. The surface water temperature rapidly increased from 15.5 to 18°C, and the concentration of nitrate plus nitrite became less than the detectable limit around 42°15'S. These meridional gradients of the surface water temperature and the nutrient concentrations seem to correspond

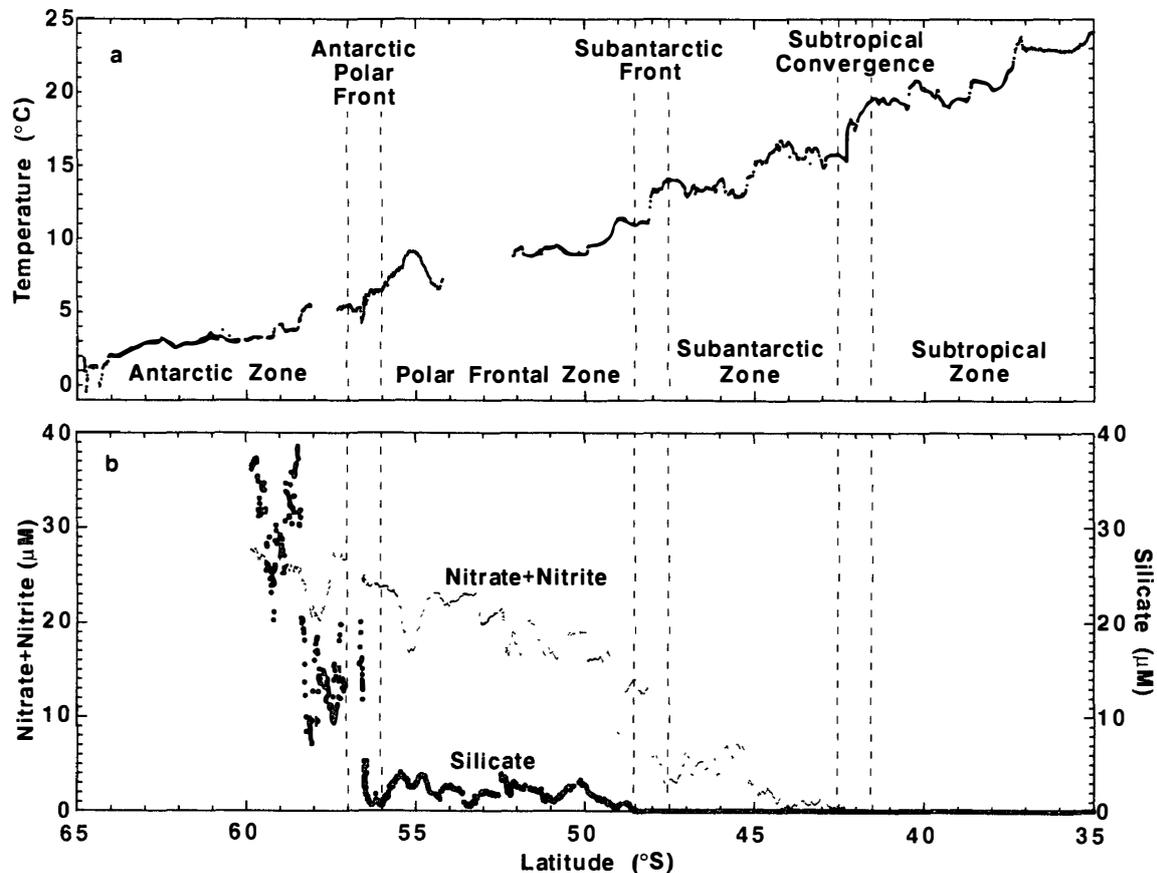


Fig. 2. Surface distribution of water temperature (a) and nutrient concentrations (b) along the northward cruise of JARE-33.

to the APF, the SAF, and the STC, respectively, which are commonly observed in the Southern Ocean (LUTJEHARMS *et al.*, 1985; ISHINO, 1989; TOMCZAK and GODFREY, 1994). Consequently, the sea area was divided into four distinct zones, the ANZ (Stations 1–8 and I–II), the PFZ (Stations 10–16 and III–IV), the SAZ (Stations 18–22 and V), and the STZ (Stations 24–28). The data of Stations 9, 17, and 23 located in the frontal area were eliminated from the following calculation of

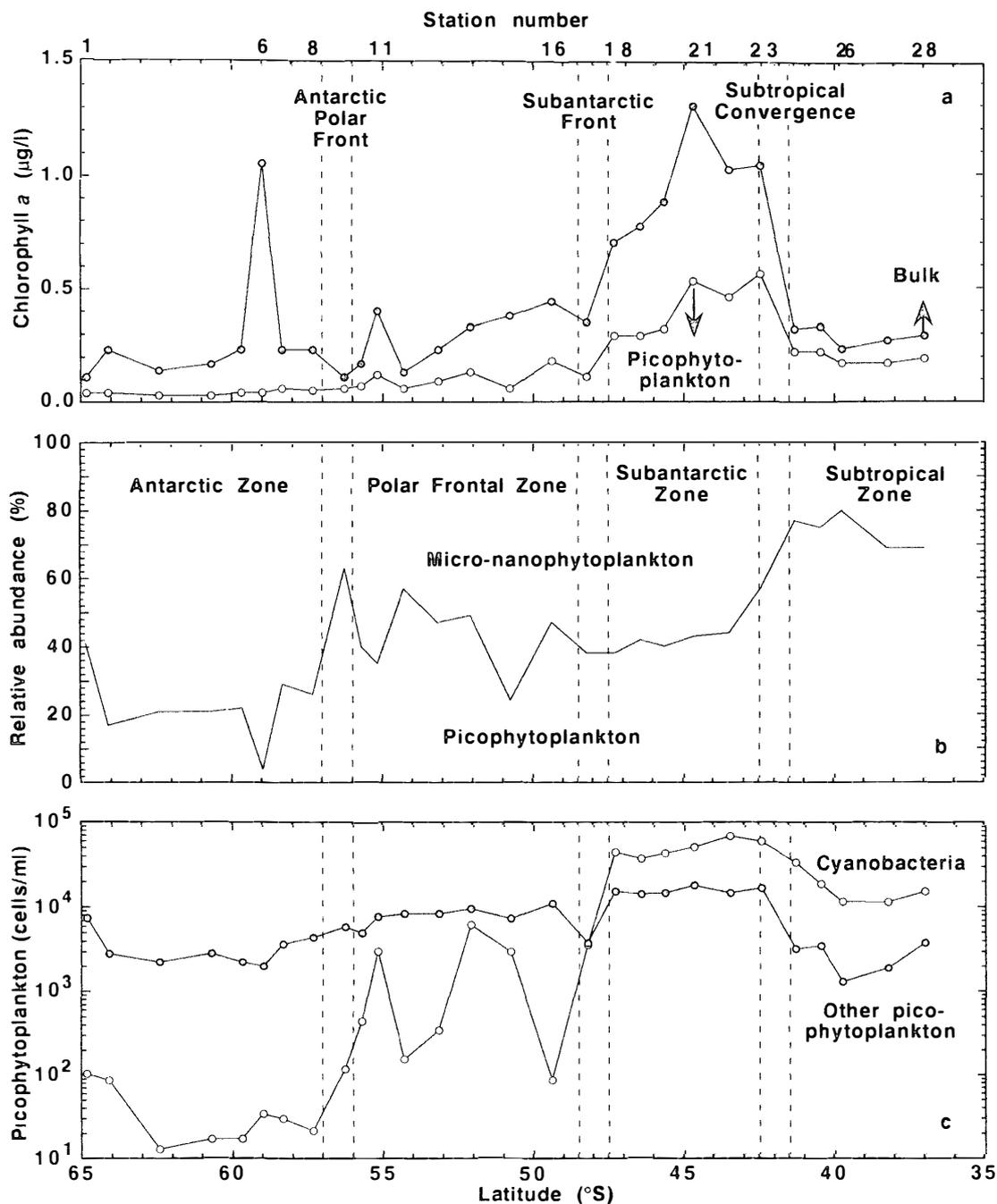


Fig. 3. Surface distributions of chlorophyll a concentration in the bulk (closed circles) and the pico (open circles) fractions (a). Percent contribution of the pico fraction (b). Cell densities of cyanobacteria (open circles) and other picophytoplankton (closed circles) (c).

Table 1. Summary of phytoplankton abundance in the surface water along the northward cruise of JARE-33. Mean values (1 SD) are shown.

Zone	Chlorophyll <i>a</i>			Contribution of pico-plankton (%)	Picophytoplankton cell density	
	Bulk ( $\mu\text{g/l}$ )	Micro-nanoplankton ( $\mu\text{g/l}$ )	Pico-plankton ( $\mu\text{g/l}$ )		Cyanobacteria ( $\times 10^3$ cells/l)	Other picophytoplankton ( $\times 10^3$ cells/l)
Subtropical Zone (n=5)	0.29 (0.04)	0.07 (0.02)	0.19 (0.03)	74 (5)	18 (9.1)	2.7 (1.1)
Subantarctic Zone (n=5)	0.93 (0.24)	0.53 (0.12)	0.38 (0.11)	41 (2)	49 (12)	15 (1.6)
Polar Frontal Zone (n=7)	0.30 (0.12)	0.14 (0.06)	0.10 (0.04)	43 (11)	1.9 (2.3)	8.2 (1.9)
Antarctic Zone (n=8)	0.30 (0.31)	0.24 (0.29)	0.04 (0.01)	23 (11)	0.041 (0.035)	3.5 (1.8)

the mean values representing water masses mentioned above.

### 3.2. Antarctic Zone

The CHL in the bulk fraction (bulk CHL) was less than  $0.30 \mu\text{g/l}$  in the surface water of the ANZ, excepting one high value at Station 6 ( $1.05 \mu\text{g/l}$ ) (Fig. 3a). The mean bulk CHL in the surface water was  $0.30 \pm 0.31 \mu\text{g/l}$  (Table 1). The relatively large standard deviation results from an uneven distribution. The vertical profile of the bulk CHL showed a prominent subsurface chlorophyll maximum (SCM) (Fig.

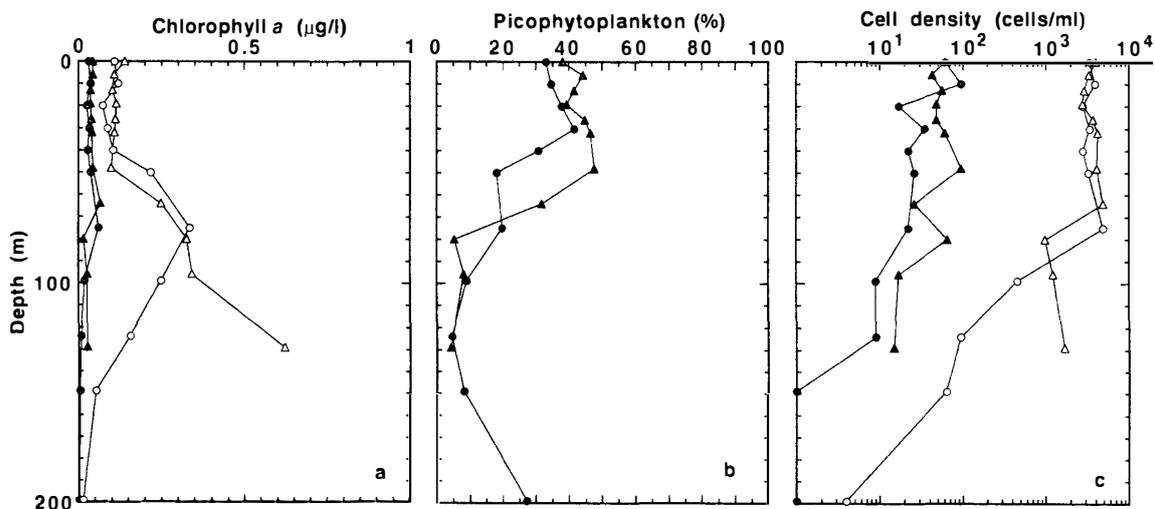


Fig. 4. Vertical distributions of chlorophyll *a* concentration in the bulk (open symbols) and the pico (closed symbols) fractions (a). Percent contribution of the pico fraction (b). Cell densities of cyanobacteria (closed symbols) and other picophytoplankton (open symbols) (c). Results were obtained at Stations I (circles) and II (triangles) in the Antarctic Zone.

4a). The SCM occurred at depths 75–124 m in Station I ( $0.16\text{--}0.33\ \mu\text{g/l}$ ) and 80–129 m in Station II ( $0.33\text{--}0.66\ \mu\text{g/l}$ ).

The CHL in the pico fraction (pico CHL) was less than  $0.06\ \mu\text{g/l}$  and the contribution of the fraction was less than 41% in the ANZ surface water (Fig. 3a and b, respectively). The pico CHL was not high at Station 6, where the lowest contribution of the pico fraction was obtained (4%). In the surface water the mean pico CHL was  $0.04 \pm 0.01\ \mu\text{g/l}$ , while the mean percent contribution was  $23 \pm 11\%$  (Table 1). The pico CHL was less than  $0.07\ \mu\text{g/l}$  throughout the water columns of Stations I and II (Fig. 4a). The percent contribution of the pico fraction was 31–42% in the upper 40 m of Station I and 32–48% in the upper 64 m of Station II (Fig. 4b).

The cell density of CY was less than  $0.1 \times 10^3$  cells/ml in the surface water of the ANZ (Fig. 3c) with the mean value of  $0.041 \pm 0.035 \times 10^3$  cells/ml (Table 1). The low CY density was observed through the water columns at Stations I and II (less than  $0.1 \times 10^3$  cells/ml) (Fig. 4c). OP numerically dominated in the picophytoplankton community (Fig. 3c). The mean value of cell density of OP was  $3.5 \pm 1.8 \times 10^3$  cells/ml in the surface water (Table 1). The OP density varied between  $2.8 \times 10^3$  and  $4.9 \times 10^3$  cells/ml in the upper 75 m of Station I and in the upper 64 m of Station II, and was not high in the SCM as observed for the pico CHL (Fig. 4c).

### 3.3. Antarctic Polar Front

A slight decrease of the bulk CHL occurred, while a small increase was noted in the pico CHL around the APF from south to north (Fig. 3a). The percent contribution of the pico fraction increased from south to north (Fig. 3b). The CY density increased from  $0.022 \times 10^3$  cells/ml at Station 8 to  $0.44 \times 10^3$  cells/ml at Station 10, while no marked change of the OP density was observed (Fig. 3c).

### 3.4. Polar Frontal Zone

The bulk CHL varied between 0.11 and  $0.44\ \mu\text{g/l}$  in the surface water of the PFZ, with an increasing trend from south to north (Fig. 3a). The mean bulk CHL was  $0.30 \pm 0.12\ \mu\text{g/l}$  (Table 1). There was no significant difference between the mean values of the bulk CHL in the PFZ and the ANZ ( $p > 0.05$ ). The bulk CHL was in the range of 0.10 and  $0.24\ \mu\text{g/l}$  in the upper 53 m at Station III and the range of 0.21 and  $0.37\ \mu\text{g/l}$  in the upper 100 m at Station IV (Fig. 5a). In this water mass the highest bulk CHL occurred at the surface water, being different from the profile in the ANZ.

The pico CHL varied between 0.06 and  $0.19\ \mu\text{g/l}$ , and the percent contribution of the pico fraction was 24–57% in the surface water of the PFZ (Fig. 3a and b, respectively). The mean pico CHL was two times higher in the PFZ ( $0.10 \pm 0.04\ \mu\text{g/l}$ ) than in the ANZ ( $0.04 \pm 0.01\ \mu\text{g/l}$ ) while the mean percent contribution of the pico fraction was also two times larger in the PFZ ( $43 \pm 11\%$ ) than in the ANZ ( $23 \pm 11\%$ ) (Table 1). The pico CHL was in the range of 0.03 and  $0.05\ \mu\text{g/l}$  in the upper 53 m at Station III and in the range of 0.06 and  $0.11\ \mu\text{g/l}$  in the upper 100 m

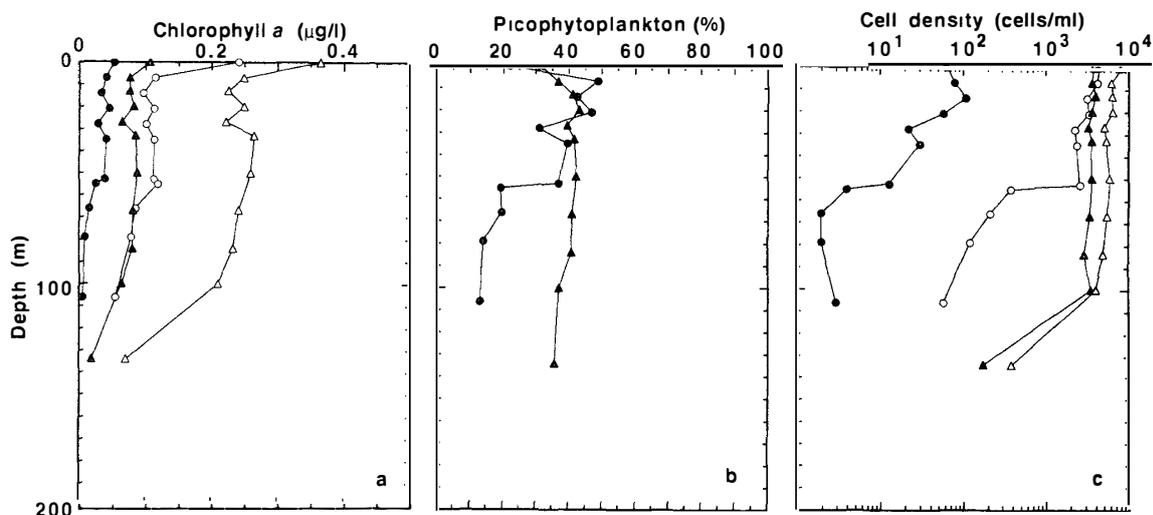


Fig. 5. Vertical distributions of chlorophyll a concentrations in the bulk (open symbols) and the pico (closed symbols) fractions (a). Percent contribution of the pico fraction (b). Cell densities of cyanobacteria (closed symbols) and other picophytoplankton (open symbols) (c). Results were obtained at Stations III (circles) and IV (triangles) in the Polar Frontal Zone.

at Station IV (Fig. 5a). The percent contribution of the pico fraction was 22–49% and 32–43% in the respective water columns (Fig. 5b).

The OP prevailed the CY in the PFZ (Fig. 3c). The mean cell densities of CY and OP were  $1.9 \pm 2.3 \times 10^3$  cells/ml and  $8.2 \pm 1.9 \times 10^3$  cells/ml, respectively (Table 1). Cell densities varied between  $0.013 \times 10^3$  and  $0.11 \times 10^3$  cells/ml and between  $2.2 \times 10^3$  and  $4.5 \times 10^3$  cells/ml in the upper 53 m of Station III, respectively (Fig. 5c). These cell densities were almost the same as those in the ANZ. On the other hand they ranged between  $3.0 \times 10^3$  and  $4.0 \times 10^3$  cells/ml and between  $4.1 \times 10^3$  and  $8.3 \times 10^3$  cells/ml in the upper 100 m of Station IV, respectively. No marked vertical change in the mean cell density in the upper 100 m water column was observed.

### 3.5. Subantarctic Front

A marked change in the bulk CHL occurred in the surface water around the SAF (Fig. 3a). The concentration increased from  $0.44 \mu\text{g/l}$  at Station 16 (PFZ) to  $0.70 \mu\text{g/l}$  at Station 18 (SAZ). The increase coincided with that of the water temperature (Fig. 2a). The pico CHL also changed there, increasing from  $0.18 \mu\text{g/l}$  at Station 16 to  $0.29 \mu\text{g/l}$  at Station 18 (Fig. 3a). No marked change in percent contribution of the pico fraction was observed between the PFZ and the SAZ (Fig. 3b). A drastic change in community structure of picophytoplankton was found around the SAF. The CY density at Station 18 in the SAZ was two orders of magnitude higher than that at Station 16 in the PFZ, although no marked increase of the OP density was found between these stations (Fig. 3c).

### 3.6. Subantarctic Zone

The bulk CHL was higher than  $0.5 \mu\text{g/l}$  in the surface water of the SAZ (Fig. 3a). The mean bulk CHL in the surface water of the SAZ was most abundant

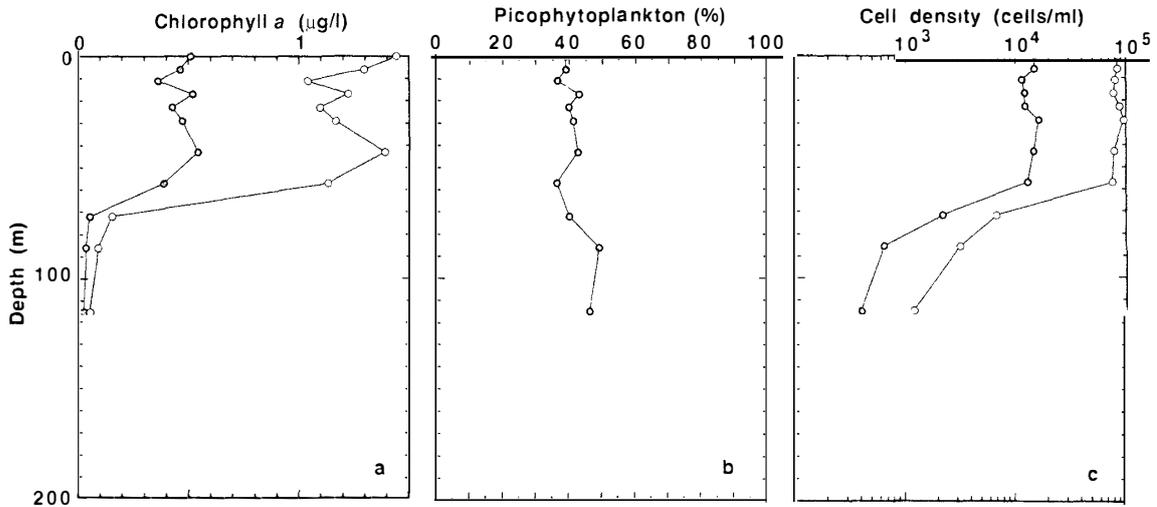


Fig. 6. Vertical distributions of chlorophyll a concentrations in the bulk (open symbols) and the pico (closed symbols) fractions (a). Percent contribution of the pico fraction (b). Cell densities of cyanobacteria (closed symbols) and other picophytoplankton (open symbols) (c). Results were obtained at Station V in the Subantarctic Zone.

among water masses ( $0.93 \pm 0.24 \mu\text{g/l}$ ) (Table 1). The mean value was significantly larger in the SAZ than in the ANZ ( $p < 0.01$ ), the PFZ ( $p < 0.001$ ), and the STZ ( $p < 0.01$ ). In particular, bulk CHL higher than  $1 \mu\text{g/l}$  was observed in the northern part of the SAZ ( $42^\circ\text{S}$ – $45^\circ\text{S}$ ). Bulk CHL higher than  $1.0 \mu\text{g/l}$  ( $1.10$ – $1.44 \mu\text{g/l}$ ) was also noted in the upper 57 m at the northern end of the SAZ (Station V) with the highest concentration at the surface (Fig. 6a).

The pico CHL was abundant in the SAZ (Fig. 3a) with a mean concentration of  $0.38 \pm 0.11 \mu\text{g/l}$  (Table 1). The same pico CHL was observed in the upper 57 m at Station V (Fig. 6a). The mean percent contribution of the pico fraction was  $41 \pm 2\%$  in the SAZ. The difference between the mean percentage in the PFZ and the SAZ was not significant ( $p > 0.05$ ). A similar percent contribution of picophytoplankton was obtained in the upper 57 m at Station V (Fig. 6b).

Cell densities of CY and OP were abundant in the surface water of the SAZ (Fig. 3c). Their mean cell densities were  $49 \pm 12 \times 10^3$  cells/ml and  $15 \pm 1.6 \times 10^3$  cells/ml, respectively (Table 1). The cell densities of the two groups occurred evenly in the upper 57 m of Station V (Fig. 6c).

### 3.7. Subtropical Convergence

The most remarkable change in the bulk CHL occurred in the surface water around the STC in the study area (Fig. 3a). The concentration decreased from  $1.02 \mu\text{g/l}$  at Station 22 (SAZ) to  $0.32 \mu\text{g/l}$  at Station 24 (STZ). The pico CHL apparently changed around the STC, decreasing from  $0.46 \mu\text{g/l}$  at Station 22 to  $0.22 \mu\text{g/l}$  at Station 24 (Fig. 3a). The percent contribution of the pico fraction increased around the STC, from 44% at Station 22 to 77% at Station 24 (Fig. 3b). The CY density decreased from  $68 \times 10^3$  cells/ml at Station 22 to  $34 \times 10^3$  cells/ml at Station 24 (Fig. 3c). On the other hand, OP density decreased from  $15 \times 10^3$  cells/ml at Station 22

to  $3.3 \times 10^3$  cells/ml at Station 24 (Fig. 3c). High densities of CY and OP were observed in the low temperature water around the STC.

### 3.8. Subtropical Zone

The bulk CHL was low in the surface water of the STZ (Fig. 3a) with a mean concentration of  $0.29 \pm 0.04 \mu\text{g/l}$  (Table 1). No significant difference of the mean bulk CHL was obtained between the STZ and the PFZ ( $p > 0.05$ ) and between the STZ and the ANZ ( $p > 0.05$ ). The pico CHL in the STZ was, however, higher than those in the PFZ and the ANZ. The mean percent contribution of the pico fraction in the surface water was significantly higher in the STZ ( $74\% \pm 5\%$ ) than in the ANZ ( $p < 0.001$ ), the PFZ (0.001), and the SAZ ( $p < 0.001$ ) (Table 1).

In the surface water of the STZ, CY numerically prevailed over OP (Fig. 3c). The mean CY density was  $18 \pm 9.1 \times 10^3$  cells/ml (Table 1). On the other hand, the mean OP density was  $2.7 \pm 1.1 \times 10^3$  cells/ml in this water mass.

## 4. Discussion

### 4.1. Total phytoplankton

The bulk CHL varied remarkably with change of water temperature around the STC and the SAF, as observed by FUKUCHI *et al.* (1986). The mean bulk CHL in the SAZ was most abundant among four water masses. The high CHL concentrations in the northern part of the SAZ may be attributed to active growth of phytoplankton (PLANCKE, 1977; FURUYA *et al.*, 1986). FURUYA *et al.* (1986) demonstrated that warm and saline water mass of the STZ intruded southward into the subsurface layer, producing a temperature inversion and an associated shallower pycnocline in the northern part of the SAZ along  $150^\circ\text{E}$ . The temperature inversion confines the subantarctic phytoplankton population in the shallower mixed layer, resulting in elevated chlorophyll *a* and primary production (FURUYA *et al.*, 1986). However, the elevated abundance of the bulk CHL was not recorded in the SAZ in the eastern Atlantic and the Western Indian sectors during the same season (FUKUCHI, 1980) but was noted in the SAZ south of Australia during early austral summer (FUKUCHI *et al.*, 1986). The high bulk CHL seems to be unique for the SAZ south of Australia and New Zealand.

Although the bulk CHL in the surface waters of the PFZ was almost the same as that of the ANZ, the vertical profiles were different from each other. In the former the maximum concentration occurred at the surface water, while in the latter an SCM was formed as noted by KURODA and FUKUCHI (1982) and FUKUI *et al.* (1986). The SCM, commonly observed in a stratified water column, in particular, of the subtropical open waters (CULLEN, 1982), is usually associated with a density discontinuity, and extinction of the surface light intensity (0.1 and 10%), and formation of a nutricline (CULLEN, 1982). In the ANZ surface water, nutrients (nitrate plus nitrite and silicate) were abundant. KURODA and FUKUCHI (1982) found that the SCM occurred at a depth deeper than the euphotic zone in the well-mixed water column. Moreover, they documented that the occurrence of the

SCM in the ANZ coincided with a remarkable minimum layer of water temperature, which was usually observed at depths between 80 and 150 m. Physical mechanisms forming the SCM in the ANZ seem to be different from those in the STZ. The occurrence of an SCM is one of the typical features in vertical distribution of phytoplankton in the ANZ.

No significant difference of the bulk CHLs was obtained among in the STZ, the PFZ, or the ANZ. The low abundance in the STZ seems to result from the depletion of nutrients. While the low abundances in the PFZ and the ANZ cannot be explained by the depletion of nutrients since we detected high concentrations of nutrients in these waters. FUKUCHI (1980) pointed out that the surface chlorophyll stock in the Antarctic Ocean water was not high, since about 80% of chlorophyll *a* data were less than 0.5  $\mu\text{g/l}$ . The present mean value in the ANZ is slightly less than the mean value in the ANZ of the eastern Atlantic and the western Indian sectors (FUKUCHI, 1980) and of the Pacific sector (EL-SAYED, 1970). The low abundance of phytoplankton with high macronutrient concentration is considered to be due to the presence of the deep mixed layer (SMITH and NELSON, 1985), to a lack of micronutrient such as iron (MARTIN and FITZWATER, 1988), and to heavy zooplankton grazing (HEWES *et al.*, 1985).

#### 4.2. Picophytoplankton

The phytoplankton community in the STZ was dominated by the pico fraction while those in the ANZ, the PFZ, and the SAZ were dominated by the micro-nano fraction. The dominance of the pico fraction has been revealed in other subtropical surface waters, where nutrients are usually depleted (CHISHOLM, 1992). From the south to the north along the line, the percent contribution of the pico fraction rapidly increased and the bulk CHL largely decreased around the STC. The low bulk CHL in the STZ resulted from decrease of the micro-nano fraction. In general, a phytoplankton community with low CHL is dominated by small phytoplankton (*e.g.*, picophytoplankton) and that with high CHL is dominated by large ones (*e.g.*, microphytoplankton) (ODATE and MAITA, 1988/1989; CHISHOLM, 1992). We revealed, however, low phytoplankton abundance with low picophytoplankton and high micro-nanophytoplankton in the ANZ and PFZ. The low contribution of the pico fraction in the ANZ was noted (KOSAKI *et al.*, 1985). Although no separation in the micro-nanophytoplankton fraction was conducted during the present study, nanophytoplankton seem to largely contribute to the bulk CHL of the ANZ and the PFZ as shown in the earlier studies (KOSAKI *et al.*, 1985; WEBER and EL-SAYED, 1987; SULLIVAN *et al.*, 1990). The low abundance of phytoplankton predominated by micro-nanophytoplankton in nutrient-rich water is one of the features of the polar marine ecosystems.

Moreover, the picophytoplankton community was mainly composed of OP and the extremely low CY density was revealed in the ANZ. The low CY density is a typical feature of phytoplankton community in the polar seas (WATERBURY *et al.*, 1986; MARCHANT *et al.*, 1987). The CY density increased around the APF from the south to the north. WATERBURY *et al.* (1986) showed that CY density

increased from a few cells/ml ( $3.5^{\circ}\text{C}$ ) to  $6.5 \times 10^3$  cells/ml ( $5^{\circ}\text{C}$ ). Their observations are consistent with our results showing that the CY density increased in accordance with a temperature change from  $4.5$  to  $6.5^{\circ}\text{C}$  around the APF.

A drastic change in the picophytoplankton community occurred around the SAF, where the surface water temperature jumped from  $11^{\circ}\text{C}$  (south) to  $13.5^{\circ}\text{C}$  (north). The CY density reached a value of more than two orders of magnitude, although a marked increase of OP was not found. CY was more abundant than OP north of the SAF, while OP was more abundant than CY south of the SAF. The picophytoplankton community is dominated by CY in waters warmer than *ca.*  $10^{\circ}\text{C}$  and by OP in waters colder than *ca.*  $10^{\circ}\text{C}$  (ODATE, 1989; ODATE *et al.*, 1990). The change in the composition of the picophytoplankton community is likely to be related to water temperature or chemical variables of the surrounding water optimizing CY (MURPHY and HAUGEN, 1985; ODATE, 1989; ODATE *et al.*, 1990). Then, the SAF is important for the geographical distribution of the picophytoplankton community.

The CY density decreased around the STC with the increase of water temperature. This pattern is different from former findings in waters of the Northern Hemisphere (MURPHY and HAUGEN, 1985; ODATE, 1989; ODATE *et al.*, 1990) but is consistent with observations in the Southern Ocean (WATERBURY *et al.*, 1986). The difference between them may result from the occurrence of suitable conditions for CY growth around the STC in the Southern Ocean (FURUYA *et al.*, 1986). On the other hand, high OP density occurred in the low water temperature around the STC. A similar trend has been noted around the subarctic boundary in the North Pacific (ODATE *et al.*, 1990) and the North Atlantic (MURPHY and HAUGEN, 1985).

A latitudinal variation of the CY density was more than that of the OP density in the area surveyed, where surface water temperature and nutrient concentrations largely changed. South of the SAZ, the concentration of nitrate plus nitrite (more than several  $\mu\text{M}$ ) may be abundant enough for picophytoplankton growth. The fluctuation of the cell densities seems to be due to the change of water temperature (MURPHY and HAUGEN, 1985; EL HAG and FOGG, 1986; MARCHANT *et al.*, 1987; ODATE, 1989; ODATE *et al.*, 1990). The different variation patterns in cell densities of CY and OP may be due to the difference in their functional responses to the temperature, resulting in the apparent change in community structure of picophytoplankton around the fronts.

## 5. Concluding Remarks

Four different water masses (ANZ, PFZ, SAZ, and STZ) were separated by three oceanographic fronts (APF, SAF, and STC) south of Australia during late austral summer. The phytoplankton abundance and picophytoplankton community structure in each water mass are summarized as follows.

1) ANZ: The bulk CHL was low ( $0.30 \pm 0.31 \mu\text{g/l}$ ) although an uneven horizontal distribution occurred and the bulk CHL maximum was found below the

surface (75–129 m). Percent contribution of the pico CHL was low ( $23 \pm 11\%$ ). Cell density of CY was extremely low ( $0.041 \pm 0.035 \times 10^3$  cells/ml) and OP prevailed ( $3.5 \pm 1.8 \times 10^3$  cells/ml).

2) PFZ: The bulk CHL was  $0.30 \pm 0.12 \mu\text{g/l}$  and its maximum was at the surface. Contribution of the pico fraction was  $43 \pm 11\%$ . CY density ( $1.9 \pm 2.3 \times 10^3$  cells/ml) was less than OP ( $8.2 \pm 1.9 \times 10^3$  cells/ml).

3) SAZ: The bulk CHL was most abundant among four distinct zones ( $0.93 \pm 0.24 \mu\text{g/l}$ ) and contribution of the pico fraction was less than half ( $41 \pm 2\%$ ). CY density ( $49 \pm 12 \times 10^3$  cells/ml) was more than OP ( $15 \pm 1.6 \times 10^3$  cells/ml).

4) STZ: The bulk CHL was  $0.29 \pm 0.04 \mu\text{g/l}$  and phytoplankton community was dominated by the pico fraction ( $74 \pm 5\%$ ), in which CY was numerically more abundant ( $18 \pm 9.1 \times 10^3$  cells/ml) than OP ( $2.7 \pm 1.1 \times 10^3$  cells/ml).

Since these changes evidently occurred around the fronts, the fronts play an important role for geographical distribution of phytoplankton in the Southern Ocean as described before.

### Acknowledgments

The authors are indebted to Captain M. SAITOH of the icebreaker SHIRASE, Japan Maritime Self-Defense Force, and his officers and crew, and to the colleagues of the JARE-33 for their cooperation during the cruise. A part of the present study was supported by a Grant-in-Aid for Scientific Research on Priority Areas from the Ministry of Education, Science and Culture in 1991 and 1993 (Grant Nos. 03248208 and 05760151 to T.O.).

### References

- BRÖKEL, K. von (1981): The importance of nanoplankton within the pelagic Antarctic ecosystem. *Kiel Meeresforsch.*, **5**, 61–67.
- CAMPBELL, L. and VAULOT, D. (1993): Photosynthetic picoplankton community structure in the subtropical North Pacific Ocean near Hawaii (station ALOHA). *Deep-Sea Res.*, **40**, 2043–2060.
- CHISHOLM, S. W. (1992): Phytoplankton size. *Primary Productivity and Biochemical Cycles in the Sea*, ed. by P. G. FALKOWSKI and A. D. WOODHEAD. New York, Plenum Press, 213–237.
- CULLEN, J. J. (1982): The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. *Can. J. Fish. Aquat. Sci.*, **39**, 791–803.
- EL HAG, A. G. D. and FOGG, G. E. (1986): The distribution of coccoid blue-green algae (Cyanobacteria) in the Menai Straits and the Irish Sea. *Br. Phycol. J.*, **21**, 45–54.
- EL-SAYED, S. Z. (1970): On the productivity of the Southern Ocean. *Antarctic Ecology*, Vol. 1, ed. by M. W. HOLDGATE. London, Academic Press, 119–135.
- EL-SAYED, S. Z. and TAGUCHI, S. (1981): Primary production and standing crop of phytoplankton along the ice-edge in the Weddell Sea. *Deep-Sea Res.*, **28**, 1017–1032.
- FUKASE, S. (1962): Oceanographic condition of surface water between the south end of Africa and Antarctica. *Nankyoku Shiryo (Antarct. Rec.)*, **15**, 53–110.
- FUKUCHI, M. (1980): Phytoplankton chlorophyll stocks in the Antarctic Ocean. *Nippon Kaiyo Gakkaiishi (J. Oceanogr. Soc. Jpn.)*, **36**, 73–84.
- FUKUCHI, M. and HATTORI, H. (1987): Surface water monitoring system installed on board the

- icebreaker SHIRASE. Proc. NIPR Symp. Polar Biol., **1**, 47–55.
- FUKUCHI, M., FUKUDA, Y., OHNO, M. and HATTORI, H. (1986): Surface phytoplankton chlorophyll distribution continuously observed in the JARE-26 cruise (1984/85) to Syowa Station, Antarctica (SIBEX II). Mem. Natl Inst. Polar Res., Spec. Issue, **44**, 15–23.
- FUKUI, F., OTOMO, K. and OKABE, S. (1986): Nutrient depression in the blooming area of Prydz Bay, Antarctica. Mem. Natl Inst. Polar Res., Spec. Issue, **44**, 43–54.
- FURUYA, K., HASUMOTO, H., NAKAI, T. and NEMOTO, T. (1986): Phytoplankton in the Subtropical Convergence during the austral summer: community structure and growth activity. Deep-Sea Res., **33**, 621–630.
- HART, T. J. (1942): Phytoplankton periodicity in Antarctic surface waters. Discovery Rep., **21**, 261–356.
- HASLE, G. R. (1969): An analysis of the phytoplankton of the Pacific Southern Ocean: Abundance, composition and distribution during the Bratigg Expedition, 1947–1948. Hvalrådets Skr., **52**, 1–168.
- HEMPEL, I. (1985): Field observations on the developmental ascent of larval *Euphausia superba* (Crustacea). Polar Biol., **6**, 121–126.
- HEWES, C. D., HOLM-HANSEN, O. and SAKSHAUG, E. (1985): Alternative carbon pathways at lower trophic levels in the Antarctic food web. Antarctic Nutrient Cycles and Food Webs, ed. by W. R. SIEGFRIED *et al.* Berlin, Springer, 277–283.
- HEWES, C. D., SAKSHAUG, E., REID, F. M. H. and HOLM-HANSEN, O. (1990): Microbial autotrophic and heterotrophic eucaryotes in Antarctic waters: relationships between biomass and chlorophyll, adenosine triphosphate and particulate organic carbon. Mar. Ecol. Prog. Ser., **63**, 27–35.
- HOSHIAI, T. (1968): Chlorophyll-a contents in the surface water observed during the cruise of FUJI to the Antarctic in 1965–1966. Nankyoku Shiryo (Antarct. Rec.), **32**, 55–62.
- ISHINO, M. (1989): 2. Kaiyo butsuri (Kaikyô) (Physical oceanography (Hydrographic condition)). Nankyoku no Kagaku, 8. Kaiyô (Science in Antarctica, 8. Oceanography), ed. by Natl Inst. Polar Res. Tokyo, Kokon Shoin, 6–35.
- KURODA, K. and FUKUCHI, M. (1982): Vertical distribution of chlorophyll *a* in the Indian sector of the Antarctic Ocean in 1972–1973. Nankyoku Shiryo (Antarct. Rec.), **74**, 127–142.
- KOSAKI, S., TAKAHASHI, M., YAMAGUCHI, Y. and ARUGA, Y. (1985): Size characteristics of chlorophyll particles in the Southern Ocean. Trans. Tokyo Univ. Fish., **6**, 85–97.
- LUTJEHARMS, J. R. E., WALTERS, N. M. and ALLANSON, B. R. (1985): Oceanic frontal systems and biological enhancement. Antarctic Nutrient Cycles and Food Webs, ed. by W. R. SIEGFRIED *et al.* Berlin, Springer, 11–21.
- MARCHANT, H. J., DAVIDSON, A. T. and WRIGHT, S. W. (1987): The distribution and abundance of chroococcoid cyanobacteria in the Southern Ocean. Proc. NIPR Symp. Polar Biol., **1**, 1–9.
- MARTIN, J. H. and FITZWATER, S. E. (1988): Iron deficiency limits phytoplankton growth in the Northeast Pacific subarctic. Nature, **331**, 341–343.
- MURPHY, L. S. and HAUGEN, E. M. (1985): The distribution and abundance of phototrophic ultraplankton in the North Atlantic. Limnol. Oceanogr., **31**, 47–58.
- ODATE, T. (1989): Seasonal changes in cell density of cyanobacteria and other picophytoplankton populations in Funka Bay, Japan. Nippon Purankuton Gakkaiho (Bull. Plankton Soc. Jpn.), **36**, 53–61.
- ODATE, T. and MAITA, Y. (1988/1989): Regional variation in the size composition of phytoplankton communities in the western North Pacific Ocean, spring 1985. Biol. Oceanogr., **6**, 65–77.
- ODATE, T., YANADA, M., CASTILLO, L. V. and MAITA, Y. (1990): Distribution of cyanobacteria and other picophytoplankton in the western North Pacific Ocean, summer 1989. Nippon Kaiyô Gakkaiishi (J. Oceanogr. Soc. Jpn.), **46**, 184–189.
- PARSONS, T. R., MAITA, Y. and LALLI, C. M. (1984): A Manual of Chemical and Biological Methods for Seawater Analysis. Oxford, Pergamon, 173 p.
- PLANCKE, J. (1977): Phytoplankton biomass and productivity in the Subtropical Convergence area and

- shelves of the western Indian sub-Antarctic islands. Adaptations within Antarctic Ecosystems, ed. by G. A. LLANO. Houston, Gulf Publ., 51–73.
- SMITH, W. O. and NELSON, D. M. (1985): Phytoplankton bloom produced by a receding ice edge in the Ross Sea: spatial coherence with density field. *Science*, **227**, 163–166.
- SULLIVAN, C. W., COTA, G. F., KREMPIN, D. W. and SMITH, W. O. (1990): Distribution and activity of bacterioplankton in the marginal ice zone of the Weddell-Scotia Sea during austral spring. *Mar. Ecol. Prog. Ser.*, **63**, 239–252.
- SUZUKI, R. and ISHIMARU, T. (1990): An improved method for the determination of phytoplankton chlorophyll using N,N-dimethylformamide. *Nippon Kaiyô Gakkaishi (J. Oceanogr. Soc. Jpn.)*, **46**, 190–194.
- TOMCZAK, M. and GODFREY, J. S. (1994): *Regional Oceanography: An Introduction*. Oxford, Pergamon, 422 p.
- WATERBURY, J. B., WATSON, S. W., VALOIS, F. W. and FRANKS, D. G. (1986). Biological and ecological characterization of marine unicellular cyanobacterium *Synechococcus*. *Can. Bull. Fish. Aquat. Sci.* **214**, 71–120.
- WEBER, L. H. and EL-SAYED, S. Z. (1987): Contributions of the net, nano- and picoplankton to the phytoplankton standing crop and primary productivity in the Southern Ocean. *J. Plankton Res.*, **9**, 973–994.

*(Received May 11, 1994; Revised manuscript received September 19, 1994)*