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SIZE STRUCTURE OF PHYTOPLANKTON CARBON AND PRIMARY PRODUCTION IN THE SOUTHERN OCEAN SOUTH OF AUSTRALIA DURING THE SUMMER OF 1983–84

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Abstract: The size structure of phytoplankton carbon content and primary production were examined in the upper 125-m water column in the Southern Ocean south of Australia during the summer of 1983–84. At the surface, total phytoplankton carbon was $13.8 \pm 1.6\ \mu g/l$ in the Subantarctic Ocean and $45.6 \pm 27.4\ \mu g/l$ in the Antarctic Ocean. Phytoplankton in the 8 to 16-μm size class accounted for a large portion of phytoplankton carbon in the Subantarctic Ocean, whereas >64-μm forms were dominant in the Antarctic Ocean. The mean primary production was 0.952 mgC/m^3/h in the Subantarctic Ocean and 0.400 in the Antarctic Ocean; the >20-μm fraction accounted for a major part of the total production in both areas. Geographically, both phytoplankton carbon and primary production in the small cell size classes (<16 μm for phytoplankton carbon and <5 μm for primary production) were relatively constant, though those of netplankton (>16 and >5 μm, respectively) which were composed mainly of diatoms varied largely, determining the magnitude of the total values. Such large variation of biomass in netplankton as found in the surface water was also found down to the 125-m depth at all stations investigated. The importance of netplankton as primary producers in the Southern Ocean was discussed.

1. Introduction

The area south of Australia is divided into several well-defined circumpolar zones by two convergence zones; the Subtropical Convergence and the Antarctic Convergence. Since the 1960's, measurements of phytoplankton standing stocks in terms of chlorophyll *a* and estimates of primary production have been extensively done in the Southern Ocean. On the basis of the accumulated data, general distribution patterns of phytoplankton standing stocks and primary production were obtained (FUKUCHI, 1980 for chlorophyll *a*; EL-SAYED and TURNER, 1977 for primary production). However, most of the investigations dealt with phytoplankton communities as a whole, and little attention has been paid to the study of their size structure, whose ecological importance is well recognized (MALONE, 1980; SOURNIA, 1982).

Recently, it was revealed that the so-called netplankton are important components as primary producers in the Southern Ocean (*e.g.* YAMAGUCHI and SHIBATA, 1982). Since these studies were based on limited numbers of size-fractionations with one or two mesh sizes, more detailed information about size structure of phytoplankton is still poorly understood.

In this paper, we describe size structure of phytoplankton biomass in detailed forms and compare primary production in the Antarctic and Subantarctic Oceans south of Australia as a function of phytoplankton cell sizes. Phytoplankton biomass is given in terms of organic carbon content (PC) which is a desirable and useful measure for biomass (*e.g.* SMAYDA, 1978).

2. Materials and Methods

Samples were collected during the BIOMASS SIBEX cruise of R.V. HAKUHO MARU of Ocean Research Institute, University of Tokyo, along Section I from 13 December 1983 to 13 January 1984, at Stn. PI-2 on 16 January and along Section II from 19 to 28 January (Fig. 1). The Antarctic Convergence was located at 56.5°S along Section I and 55°S along Section II (NAKAI *et al.*, 1985). Therefore, Stns. 1–1, 2, 6–2 and 6–3 were located in the Subantarctic Ocean, Stns. 2–2, 3B, 5, PI-2, 6 and 6–1 were in the Antarctic Ocean. Water samples were collected from the surface to a 200-m depth with Niskin bottles mounted on a rosette with a CTDO (Niel Brown MK-IIIB). The oceanographic conditions during the cruise are described in NAKAI *et al.* (1985).

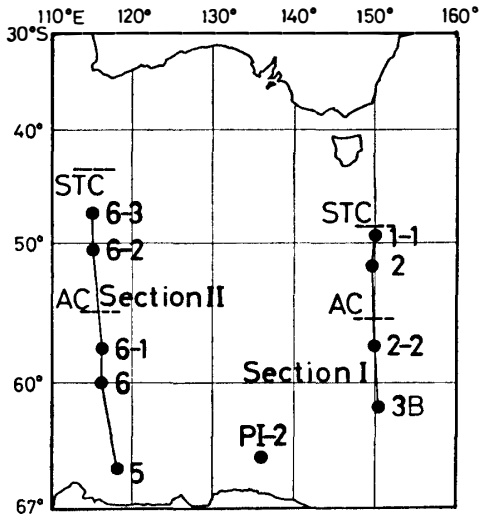

Fig. 1. Station locations (closed circles) during the KH-83-4 cruise, 13 December 1983 – 28 January 1984. STC and AC indicate the Subtropical Convergence and the Antarctic Convergence, respectively.

The water samples were fixed with 1% glutaraldehyde for one to ten hours, and then, 30 to 50 m*l* of the fixed samples were filtered through Gelman GA6 filters (4 mm in diameter) by gentle suction. The filters were mounted on cover slips with glycerin-jelly (TSUJI and YANAGITA, 1981), then stored in a desiccator at −80°C until microscopic inspections could be carried out. Dimensions of phytoplankton cells in the filtered samples were determined automatically using the Image Analyzer System fitted to an epifluorescence microscope (FURUYA, 1982), which can detect and measure only the organisms which contained chlorophyll *a*. For each sample, 600–1000 phytoplankton cells were measured. In order to facilitate the efficiency of the measurement, cell volume was estimated using the following equation under an assumption that every phytoplankton cell is an ellipsoid;

$$V = 1/6k\pi LW^2,$$

where L and W are maximum cell length (μm) and width (μm) measured, respectively, and k is a correcting coefficient. The k was determined from the mean ratio of total cell volume (V, μm^3) to that calculated from the formula of KOVALA and LARRANCE (1966) determined from five Antarctic and Subantarctic samples (0 m samples at Stns. 2, 3B, 5, 6, 7): the k was 0.677 (range; 0.231–1.200) for the $>$20-μm phytoplankton, 0.886 (range; 0.450–1.528) for the 5 to 20-μm, and 0.987 (range; 0.724–1.130) for the $<$5-μm phytoplankton. Cell volume was converted to PC using the size-dependent function by EPPLEY (in ANONYMOUS, 1974) for the $>$5-μm size class, and by MULLIN *et al.* (1966) for the $<$5-μm size class. The reason why we used these two functions in calculating PC is; (1) 78% of phytoplankton in the $>$5-μm size class in terms of cell volume were diatoms. The formula by EPPLEY (in ANONYMOUS, 1974) was based on the greatest number of data among the published formulas for diatoms; (2) the $<$5-μm size class was composed of flagellates and monads. The function of MULLIN *et al.* (1966) is based on data covering the smallest cell size (10 μm^3 in cell volume) among the formulas. Algal size was classified into five or six fractions according to a cell diameter of a sphere equivalent to the original cell volume.

Size fractionation of the sea water samples was carried out on the deck in the dark immediately after the sampling. The fractionations with Nitar screens (mesh sizes; 5 and 20 μm) were done by a reverse filtration. At Stn. 2, 1-μm Nuclepore filter was also used for size fractionations. The fractionated and non-fractionated samples were filtered through 0.3-μm glass fiber filters (Reeve Angel, 984H) for chlorophyll *a* and phaeopigment determinations with a Turner 111 fluorometer (STRICKLAND and PARSONS, 1972).

The ^{14}C uptake rate was determined for the surface population taken from Stns. 1–1, 3B, PI-2, 5, 6, 6–3 by the ^{14}C uptake method (STEEMANN NIELSEN, 1952). The water samples were filtered with 100-μm Nitar screen before incubations to remove larger zooplankton. 200-m*l* water samples in two light and two dark polycarbonate bottles were inoculated with 20 μCi $NaH^{14}CO_3$, and then incubated on the deck at the ambient temperature of the running surface seawater and under the natural light condition for about 5 hours. After the incubation, phytoplankton were collected on GS Millipore filters (0.22-μm pore size), and radioactivity on the filters was assayed using a liquid-scintillation counter (LKB Wallack, Rackbeta 1215).

3. Results

Size structure of PC at the surface was different between the Antarctic and Subantarctic Oceans (Fig. 2). The mean total PC was 45.6 ± 27.4 μgC/*l* in the Antarctic Ocean and 13.8 ± 1.6 μgC/*l* in the Subantarctic Ocean. In the Antarctic Ocean, PC was composed largely of cells larger than 16 μm. In these size classes, diatoms accounted for 74.2% on the average, and a peak abundance of 11.8 μgC/*l* (25.9% of the total) occurred at the $>$64-μm size class. PC in this size class varied largely as shown by the largest standard deviation (SD, 12.4 μgC/*l*) of PC among the size classes. In the Subantarctic Ocean, the averaged spectrum of PC showed a peak (3.6 μgC/*l*) at 8–16 μm. Compared with the Antarctic Ocean, PC was small in the $>$16-μm size classes where diatoms were also dominant (97.5% in terms of PC). SD of PC in each size class

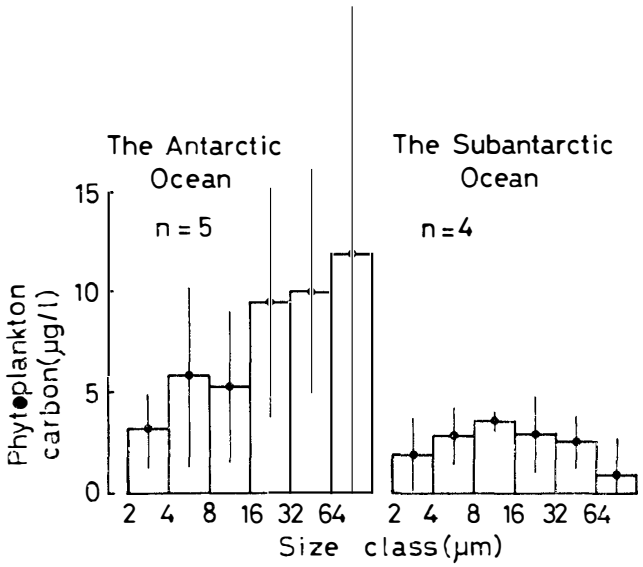

Fig. 2. Mean size frequency distributions of phytoplankton carbon at the surface with standard deviation in the Antarctic and the Subantarctic Oceans. The bars in the figure denote standard deviation. n: number of samples.

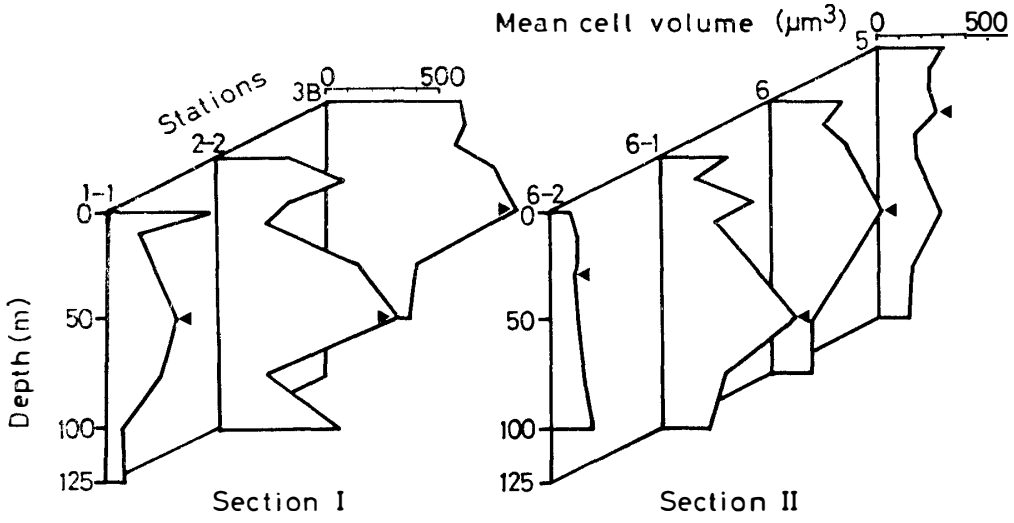

Fig. 3. Vertical profiles of mean cell volume in the upper 100- or 125-m depth along Sections I and II; solid triangles indicate phytoplankton carbon maximum layers.

was smaller in the Subantarctic Ocean than in the Antarctic Ocean. The difference of total PC between the two areas greatly depended upon that in the size classes larger than 16 μm (7.4 μgC/*l*). On the other hand, PC of the small size classes ($<16\,\mu$m) in both the Antarctic and Subantarctic Oceans showed small variations, indicating that PC of these size classes was relatively constant geographically.

The mean cell volume of phytoplankton in the upper 100 or 125-m water columns tended to be larger in the Antarctic Ocean than in the Subantarctic Ocean (Fig. 3); the mean cell volume varied from 130 to 870 μm^3 in the Antarctic Ocean, and from 60 to

490 μm^3 in the Subantarctic Ocean. Below the surface, the largest mean cell volume was found in the PC-maximum layers at all stations except Stns. 5 and 6–2, that is, relatively large phytoplankton predominated in the PC-maximum layers. At Stns. 5 and 6–2 where PC-maximum layers were located shallower (30 m) than those at the other stations (50–75 m), the largest mean cell volume was found 45–70 m below the PC-maximum layers and the mean cell volume was relatively constant among layers.

Relative abundance of PC in the upper 100- or 125-m water column from Stn. 5 to Stn. 6–2 along Section II is shown in Fig. 4. In the Antarctic Ocean, the size structure of PC at Stn. 5 was different from those at Stns. 6 and 6–1; two size classes between 8 and 32 μm constantly accounted for large portions (55.3–79.1%) of the total at Stn. 5, while PC in these classes changed from 20.8 to 67.5% at Stns. 6 and 6–1. In particular, above 30 m where the maximum value of total PC was detected at Stn. 5, PC in the 16 to 32-μm size class was estimated at 20.9–38.5 $\mu g/l$ and it constituted the major portion (35.3–36.6%) of the totals. On the other hand, below that layer, the 8 to 16-μm size class occupied a larger portion (32.7–49.9%) of the total than the 16 to 32-μm size class (21.5–29.1%). The major fraction of total PC at Stns. 6 and 6–1 occurred in the two

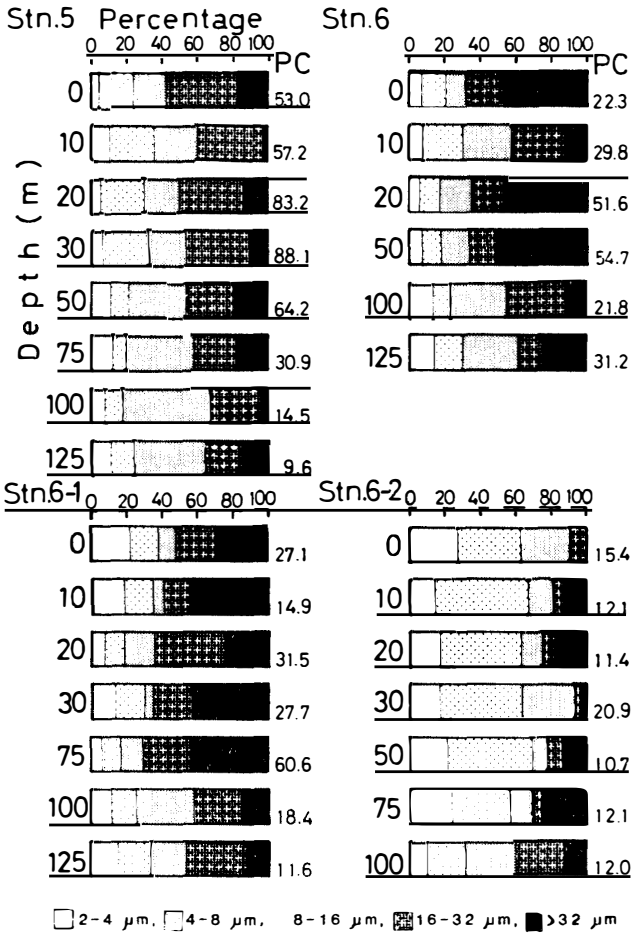

Fig. 4. Percentages of size fractionated phytoplankton carbon to the total (PC, $\mu g/l$) in each layer above the 100- or 125-m depth from Stn. 5 to Stn. 6–2 along Section II.

size classes larger than 16 μm: 38.9–69.6% at Stn. 6 and 42.2–70.4% at Stn. 6–1. Especially, in the layers where maximum phytoplankton carbon occurred (50 m at Stn. 6 and 75 m at Stn. 6–1), PC of netplankton (>16 μm) was large (35.8 μg/*l* and 42.6 μg/*l*, respectively) and constituted major portions of the total PC (65.5% and 70.4%). The percentage of PC in the two size classes below 8 μm was clearly higher (30.9–69.8%) in the Subantarctic Ocean (Stn. 6–2) than those at the other stations (17.1–39.2%). However, PC in the two large size classes (>16 μm) was obviously small (1.4–4.8 μgC/*l*) and occupied small portions (6.9–40.2%) of the totals. PC in both the 16 to 32-μm and >32-μm size classes was also variable (SD: 6.18 μgC/*l* for 16–32 μm and 7.64 for >32 μm) in the upper 100- or 125-m water column at all the stations investigated as well as PC in those size classes at the surface (Fig. 2). Such variation of PC of the netplankton mainly determined the magnitude of total PC throughout the water column.

Relative abundances of PC in the >20-, 20 to 5- and <5-μm size classes to the total were compared with those of chlorophyll *a* (Table 1). In the Antarctic Ocean (Stns. 3B, PI-2, 5, 6, 6–1), 56.4% of total PC was occupied by the >20-μm size class, 32.9% by 20–5 μm, 10.7% by the <5-μm class, whereas in terms of chlorophyll *a*, the >20-μm fraction accounted for 40.8% of the total, 20–5 μm for 35.6% and <5 μm for 23.6% on the average. In the Subantarctic Ocean (Stns. 1–1, 2, 6–2, 6–3), percentage of >20-μm phytoplankton to the total biomass was 46.2% by PC and 23.5% by chlorophyll *a*. In both areas, the relative abundance of PC in the >20-μm size class was larger than that of chlorophyll *a*.

The ratio of phytoplankton carbon to chlorophyll *a* at the surface increased southward (Fig. 5). The ratios ranged from 129.8 (Stn. 1–1) to 509.0 (Stn. 5). The mean ratio was 159.9±39.5 in the Subantarctic Ocean and 331.9±101.5 in the Antarctic Ocean.

The mean value (9.52×10^{-1}mgC/m^3/h) of primary production of the total phytoplankton population in the Subantarctic Ocean (Stns. 1–1 and 6–3) was 2.4 times as much as that (4.00×10^{-1}) in the Antarctic Ocean (Stns. 3B, PI-2, 5, and 6). The mean photosynthetic index of total phytoplankton population was also higher in the Sub-

*Table 1. Mean and standard deviation of size fractionated phytoplankton carbon (PC, μg/*l*) and chlorophyll (Chl. a, $\times10^{-2}$$\mu$g/*l*) at the surface in the Antarctic and the Subantarctic Oceans. Percentages to the totals are shown in parentheses.*

Areas	Size class	PC	(%)	Chl. *a*	(%)
Antarctic Ocean (*n*=5)	>20 μm	25.7±16.7	(56.4)	5.6±3.4	(40.8)
	20–5 μm	15.0± 7.5	(32.9)	4.9±5.2	(35.6)
	<5 μm	4.9± 1.9	(10.7)	3.2±3.0	(23.6)
	Total	45.6±27.4		13.7±6.9	
Subantarctic Ocean (*n*=4)	>20 μm	6.4± 2.4	(46.2)	2.1±3.0	(23.5)
	20–5 μm	5.3± 1.8	(38.1)	3.4±4.1	(39.1)
	<5 μm	2.2± 1.9	(15.7)	3.3±1.0	(37.4)
	Total	13.8± 1.6		8.8±3.5	

n: number of samples.

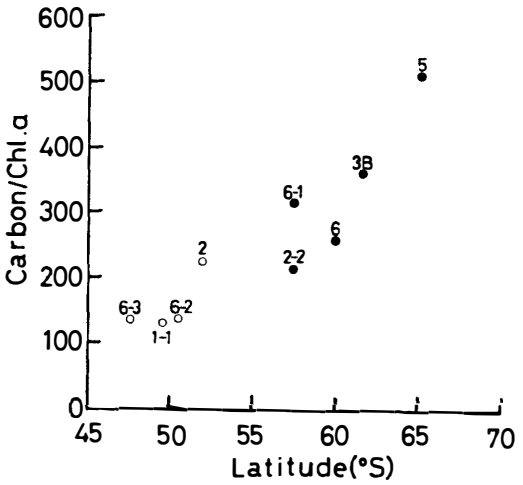

Fig. 5. Variation of the ratio of phytoplankton carbon to chlorophyll a along latitude; ● Antarctic stations, ○ Subantarctic stations. The number near each circle indicates station number.

Table 2. Primary production (P, mgC/m³/h) and photosynthetic index (PI, mgC/mgChl. a/h) in each size class and total of phytoplankton with the ambient temperature (temp., °C) and mean light intensity (light, $\times 10^{20}$ quanta/m²/s) during incubations at the surface.

Stations	20 μm		20–5 μm		5 μm		Total		Temp.	Light
	P	(PI)	P	(PI)	P	(PI)	P	(PI)		
Antarctic Ocean										
3B	2.69×10^{-1}	(3.0)	0.93×10^{-2}	(0.2)	6.72×10^{-2}	(7.5)	3.45×10^{-1}	(2.5)	0.2	1.76
PI-2	1.38×10^{-2}	(2.8)	6.53×10^{-2}	(4.7)	5.99×10^{-2}	(1.7)	1.39×10^{-1}	(2.6)	−1.6	1.57
5	1.00×10^{-1}	(9.9)	5.97×10^{-1}	(4.1)	2.42×10^{-1}	(2.9)	9.39×10^{-1}	(3.9)	0.0	3.32
6	9.80×10^{-2}	(2.4)	4.55×10^{-2}	(1.5)	3.15×10^{-2}	(2.1)	1.75×10^{-1}	(2.0)	1.8	2.30
Subantarctic Ocean										
1-1	7.24×10^{-1}	(7.2)	3.95×10^{-1}	(3.1)	2.61×10^{-1}	(4.1)	1.38	(4.8)	7.8	4.00
6-3	1.72×10^{-1}	(4.2)	2.22×10^{-1}	(5.1)	1.29×10^{-1}	(2.9)	5.23×10^{-1}	(4.0)	11.1	2.20

antarctic Ocean (4.4 mgC/mgChl. *a*/h; range 4.0–4.8) than in the Antarctic Ocean (2.8; range 2.0–3.9). The highest value of primary production was found in the >20-μm fraction at Stns. 1–1, 3B and 6, and in the 5 to 20-μm fraction at Stns. PI-2, 5 and 6–3 (Table 2). The primary production was relatively constant in the <5-μm fraction among stations as shown by the smallest SD (8.97×10^{-2}mgC/m³/h) among the cell size classes. The geographic variations of primary production in the 5 to 20-μm and >20-μm fractions were large (SD: 2.13×10^{-1}mgC/m³/h for 5–20 μm and 2.35×10^{-1} for >20 μm) and they determined the magnitude of the total primary productions. Among the size classes, photosynthetic index was the highest in the >20-μm fraction at Stns. 1–1, 5 and 6, in the 5 to 20-μm fraction at Stns. PI-2 and 6–3, and in <5 μm at Stn. 3B. The mean value of photosynthetic indices in each size class was estimated to be the highest in the >20-μm fraction in both the Subantarctic (5.7 mgC/mgChl. *a*/h) and the Antarctic (4.3 mgC/mgChl. *a*/h) Oceans. Although the photosynthetic index of the total population was relatively constant among stations (SD: 1.0 mgC/mgChl. *a*/h), that in each size class was variable (SD: 2.7 mgC/mgChl. *a*/h for >20 μm, 1.8 for

20–5μm and 1.9 for $<5\,\mu$m). The geographic variation of photosynthetic indices in the major biomass fraction ($>20\,\mu$m) largely determined the magnitude of the totals as shown by the largest SD of photosynthetic indices in this fraction. In the Antarcic Ocean, size structures of primary production at the southern stations (Stns. PI-2 and 5) were different from those at the northern stations (Stns. 3B and 6); at the southern stations, the highest percentages of primary productions to the totals were found in the 5 to 20-μm fraction, whereas the >20-μm fractions contributed only 10.7–9.9% of the totals. On the contrary, at the northern stations, the highest contributions to the total primary productions occurred in the >20-μm size class (56.0–77.9%).

Picoplankton ($<1\,\mu$m) standing stock and primary production were examined at Stn. 2 in the Subantarctic Ocean: they occupied 18.2% ($4.72\times10^{-3}\,\mu$gChl. a/l) of the total chlorophyll a and 9.8% ($3.75\times10^{-2}\,\mu$gC/m^3/h) of the total primary production.

4. Discussion

The present study demonstrated that both PC and primary production in the small cell size classes ($<16\,\mu$m for PC and $<5\,\mu$m for primary production) were geographically constant at the surface, compared to those in the diatom-dominated large size classes ($>16\,\mu$m and $>5\,\mu$m, respectively). PC in the >16-μm size class was also variable vertically. Thus, phytoplankton in the large size classes were the major components determining the total biomass and primary production in the Southern Ocean, supporting the finding of FURUYA and MARUMO (1983) for the size distribution of PC in the western Pacific Ocean in summer. The constant biomass in the two size classes below 8μm found in the present study agrees with the report of FURUYA and MARUMO (1983). However, PC in the 8 to 16-μm size class was also constant in the present study though it varied largely in FURUYA and MARUMO (1983).

Relative abundance of netplankton was evaluated to be lower in terms of chlorophyll a than of PC (Table 1). As the result of the present study derived from chlorophyll a by filteration and PC by the image analysis, the definition of phytoplankton size differed between these two methods; the phytoplankton size obtained by filteration represents the colony size rather than the cell size, though the PC spectra were based on the cell size. If the difference of algal size definition between the two methods had influenced the difference of relative abundance in each size class between PC and chlorophyll a, the percentage of netplankton biomass would be estimated higher in terms of chlorophyll a than of PC. However, we got the opposite trend, therefore, the difference of the algal size definition has little effect on the relative abundance of PC and chlorophyll a in each size class. Probably, a large relative abundance of netplankton resulted partly from that phytoplankton cells even larger than mesh size passed through it, or that the ratio of PC to chlorophyll a might increase with phytoplankton cell size.

The ratio of PC to chlorophyll a increased southword at the surface in the Southern Ocean. SMITH and MORRIS (1980) demonstrated that the ratio of carbon to chlorophyll a increases with decrease in the temperature because changes in abundance of saturated lipids occur under such very low tempeeature and low light intensities as observed in the Antarctic Ocean. Accordingly, the ratio of the total phytoplankton standing stock in the Antarctic Ocean to that in the Subantarctic Ocean is estimated to be fairly large

(almost twice according to the result on the average) when they are estimated in terms of PC instead of chlorophyll *a*.

Chlorophyll *a* and primary production of the <1-μm phytoplankton at the Subantarctic station (Stn. 2) were very low, compared with the larger fractions. LI *et al.* (1983) showed that in the euphothic zone of the eastern tropical Pacific Ocean, particles which could pass through a 1-μm pore contributed 25–90% of the biomass (in terms of chlorophyll *a*) and 20–80% of primary production. Thus, the contributions of <1-μm fraction to the total phytoplankton biomass and production in the Subantarctic Ocean were obviously smaller than those in the tropical ocean. REID (1983) showed that proportions of PC in the picoplankton fraction ($<2\,\mu$m) to the total were only 0.1–0.3% in the Scotia Sea as determined by the Utermöhl settling technique. She also showed the picoplankton carbon contributed only a small portion of the total in the Antarctic Ocean in comparison with the tropical and subtropical oceans. Thus, it is considered that picoplankton in both the Antarctic and Subantarctic Oceans occupy only a small part of the total phytoplankton biomass in comparison with those in tropical and subtropical oceans.

The >20-μm phytoplankton accounted for a major portion of total primary production; the mean contribution of the phytoplankton in this fraction was estimated at about 48.0% in the Antarctic Ocean and 42.7% in the Subantarctic Ocean. The value of the Antarctic Ocean is almost the same as that for the Ross Sea (46%) obtained by FAY (1973) but clearly higher than that for the Weddell Sea (25.8%) reported by EL-SAYED and TAGUCHI (1981).

Geographically, the photosynthetic index in each size class of natural phytoplankton communities varied largely. Such large variation of the value in each size class resulted in the regional change in those of the total populations. Especially in the Subantarctic Ocean, a high photosynthetic index in the major biomass fraction ($>20\,\mu$m) brought about the high value of total population on the average.

In conclusoin, the variations of both phytoplankton biomass and primary production of the netplankton largely influenced the magnitude of the totals in the Southern Ocean.

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