

SMALL-SCALE VARIATIONS IN PHYTOPLANKTON STANDING STOCK AND PRODUCTIVITY ACROSS THE OCEANIC FRONTS IN THE SOUTHERN OCEAN

Tamiji YAMAMOTO*

Faculty of Agriculture, Tohoku University,
1-1, Tsutsumidōri-Amamiyamachi, Sendai 980

Abstract: Observations on phytoplankton standing stock and productivity were carried out across the Antarctic Polar Front (PF) and the Subtropical Convergence (STC) employing a small-scale sampling scheme (1 sample per 1 or 2 miles) through 20 or 40 miles transects. Maximum of chlorophyll standing stock ($0.185 \mu\text{g chl. } a \cdot l^{-1}$) was found at the midst of physical and chemical changes in the PF transect, which was 2-fold higher than those in the Antarctic side and 3-fold higher than those in the Subantarctic side. Community forming the maximum standing stock consisted of a large number of the Antarctic species, *Nitzschia* spp. (72% of them was *Flagilariopsis* spp. in old nomenclature). On the other hand, the maximum standing stock ($0.309 \mu\text{g chl. } a \cdot l^{-1}$) in the STC transect was found at just north of the physical gradients at the front, and was associated with a warm saline water mass carrying nutrients of relatively low concentrations. Although the productivity also was maximum at the maximum standing stock, there was no indication of increase in the photosynthetic rates. Species appeared in the community of maximum standing stock in the STC transect included warm water forms such as *Ceratium arietinum* var. *glacilentum*, *C. massiliense*, *Oxytoxum scolopax*, *Podolampas spinifera* and *Prorocentrum rostratum* and a neritic form, *Protoperdinium pallidum*. Discussions were made for the formation of the maximum phytoplankton standing stock at the PF and the STC.

1. Introduction

Useful information on phytoplankton standing stock and primary production of the Southern Ocean has been gained during the past two decades, as exemplified by the works of EL-SAYED (1970), HOLM-HANSEN *et al.* (1977) and FUKUCHI (1980, 1982). It is well known that there exist two major oceanic fronts, *i.e.*, the Polar Front (PF) and the Subtropical Convergence (STC). These oceanic fronts are important not only as the hydrographic demarcations but also as the biogeographical boundaries. Based on the data of nine cruises of the icebreaker FUJI, FUKUCHI (1980) found that the maximum chlorophyll stock with considerable deviation occurs in the PF zone. EL-SAYED and WEBER (1982) encountered a higher-than-expected phytoplankton standing stock ($12.97 \mu\text{g} \cdot l^{-1}$ at 50 m, 0.1% of surface irradiance) and the productivity ($284.38 \mu\text{gC} \cdot l^{-1} \cdot d^{-1}$ at 10 m, 50% of surface irradiance) at the station located in the PF zone of the

* Present address: Aichi Prefectural Fisheries Experimental Station, Owari Branch, 3-36, Toyohama Toyoura, Minami-Chita, Chita-gun, Aichi 470-34.

Scotia Sea. PLANCKE (1977) showed that phytoplankton chlorophyll *a* and primary production were high at the northern edge of the STC employing a subsurface pumping method. FUKUCHI and TAMURA (1982) reported that the surface chlorophyll concentration increased rapidly just north of the PF during the southward leg along *ca.* 105°E and north of the STC during the northward leg along *ca.* 45°E.

The phenomenon that the maxima of chlorophyll standing stock and primary production are found in and around the PF and the STC is probably a fact. Nevertheless, the sampling intervals of 1 sample per hour (4.5–16 miles) conducted by PLANCKE (1977) and those (*ca.* 30–170 miles) by FUKUCHI (1980) and FUKUCHI and TAMURA (1982) seem to be too coarse to detect the precise location of the maxima of standing stock and productivity in and around the fronts. Since the physical changes in the surface layer across these oceanic fronts are expected to occur within one or half degree of latitudinal scale, sampling intervals are needed to be “fine” or finer “coarse” scales of 1–5 km according to HAURY *et al.* (1978).

During the BIOMASS SIBEX cruise of R. V. HAKUHO MARU, a small-scale sampling scheme of 1 sample per 1 or 2 miles was employed for the observations of phytoplankton standing stock and productivity across the PF and the STC. In the present paper, (1) the locations of the maxima of standing stock and productivity, north, middle or south of the fronts, (2) the kinds of species that constitute the communities are described and (3) the discussion of possible mechanisms for the formation of the maximum standing stock at the fronts is made.

2. Materials and Methods

Observations of the PF and the STC of the Southern Ocean were carried out during the BIOMASS SIBEX cruise (KH-83-4) of R.V. HAKUHO MARU, from November 22, 1983 to February 24, 1984 (Fig. 1). During the southbound trip along the 150°E meridian, the positions of the STC and the PF were confirmed by continuous records of surface temperature and salinity (HASUMOTO and NAKAI, 1985) and 26 XBT and 4 CTDO casts (NAKAI *et al.*, 1985).

Water samples were taken across the PF (56°30.1'S, 150°10.4'E–56°08.7'S, 149°59.3'E) on December 29, 1983 and the STC (STC-I; 46°59.6'S, 150°00.4'E–46°20.0'S, 149°48.2'E) on January 1, 1984. Seawater samplings were also made across the STC along 115°E (43°24.0'S, 114°54.1'E–43°01.7'S, 114°52.1'E) on January 27, 1984 (STC-II in Fig. 1). Observation of the PF along 115°E was not performed because of the indistinctness of physical structures.

Seawater was pumped up from *ca.* 4-m depth and pooled in 20 5-l polyethylene tanks successively for each observation. Sampling intervals were 1 mile for the PF and STC-II, and 2 miles for the STC-I. Concentrations of nitrate-N, nitrite-N and phosphate-P were determined using an auto analyzer AA-II (Technicon, USA), and manually for silicate-Si after STRICKLAND and PARSONS (1972). Chlorophyll *a* was measured fluorometrically with a Turner 111 model fluorometer (STRICKLAND and PARSONS, 1972). A 500 ml of each sample was fixed with 1% formaline, and identification and cell counting of diatoms, dinoflagellates and silicoflagellates were made on 25–250 ml aliquot as required. For each transect, the microscopic works were made

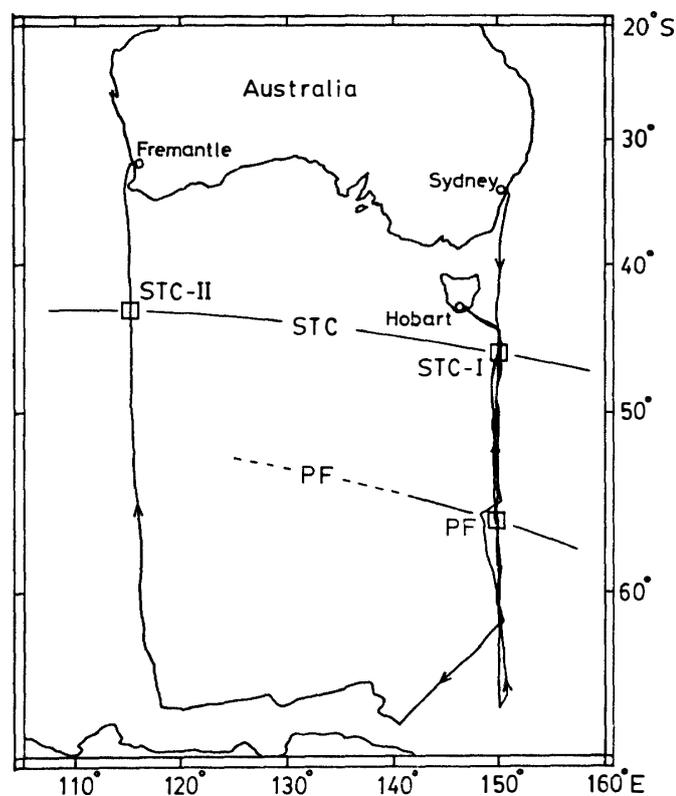


Fig. 1. Cruise track of R. V. HAKUHO MARU from December 11, 1983 to January 31, 1984 and the sampling locations.

for selected 6 samples, *i.e.*, each 2 samples in the chlorophyll maximum and each 2 at both terminals of the transect, which are indicated by arrows in Figs. 2, 3 and 4. Continuous record of salinity at 4-m depth was obtained on board using a salinograph (Union Electronics, ST-MK-15). The salinity records were calibrated for 5 seawater samples on each transect with a salinometer (Guildline, Autosal 8400). Temperature at the same depth was also monitored continuously.

Photosynthetic activity was measured for arbitrarily selected 9 samples taken from two STC transects. In the PF transect, the radioisotope experiments were not done owing to the stormy weather. Sampled water of 200 ml was dispensed into three transparent glass bottles and inoculated with $5 \mu\text{Ci}$ of $\text{NaH}^{14}\text{CO}_3$. Although the method was basically according to STEEMANN NIELSEN (1952), $10^{-5} \text{mol} \cdot \text{l}^{-1}$ DCMU (dissolved in water) was added to one of them before the addition of ^{14}C solution. This bottle was used as a control instead of treating it in dark (LEGENDRE *et al.*, 1983). The incubations were conducted for 4 to 5 h under a condition of *ca.* 9800 lx. During the incubations, bottles were shaken every 1 h. Temperature of the incubation in the STC-I transect was set at $12.0 \pm 0.2^\circ\text{C}$, and was $11.8 \pm 1^\circ\text{C}$, $12.7 \pm 1^\circ\text{C}$ and $13.9 \pm 1^\circ\text{C}$ for the samples taken from the cold, middle and warm sides of the STC-II transect, respectively. After the filtration of incubated water through Millipore HA filter, 0.5N HCl was pipetted on the filter according to LEAN and BURNISON (1979). Radioactivity of ^{14}C taken up by phytoplankton was counted on board with LKB 1215 Rackbeta II.

3. Results

3.1. The Antarctic Polar Front

Temperature and salinity changed from *ca.* 3.8°C and 33.75‰ in the Antarctic side to *ca.* 7.4°C and 34.10‰ in the Subantarctic side (Fig. 2). Nutrient salts were higher in the Antarctic side than in the Subantarctic side. The ranges were 20.8–29.1 $\mu\text{g-at}\cdot\text{l}^{-1}$ in nitrate-N, 0.21–0.31 $\mu\text{g-at}\cdot\text{l}^{-1}$ in nitrite-N, 1.40–1.70 $\mu\text{g-at}\cdot\text{l}^{-1}$ in phosphate-P and 7.0–17.6 $\mu\text{g-at}\cdot\text{l}^{-1}$ in silicate-Si. In these nutrient forms, the change in silicate-Si was more than 2-fold between both terminal samples of the transect. Chlorophyll *a* showed a maximum concentration of 0.185 $\mu\text{g}\cdot\text{l}^{-1}$ at the middle of the transect, and it was *ca.* 2-fold higher than those in the Antarctic side and *ca.* 3-fold higher than those in the Subantarctic side. The width of the dense community is considered to be 5 miles between the sample Nos. 7 and 12.

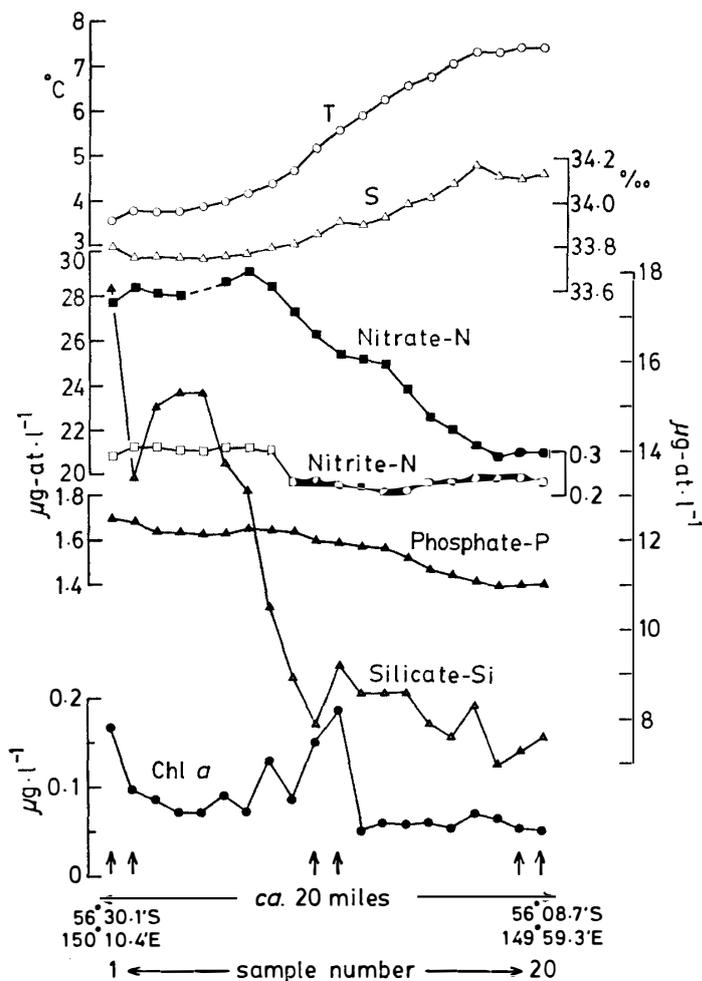


Fig. 2. Horizontal variations in phytoplankton standing stock, photosynthetic activity and environmental factors in the surface layer (*ca.* 4-m depth) across the PF on December 29, 1983. Six arrows at the bottom of the figure indicate the samples used for the microscopic works.

3.2. The Subtropical Convergence-I

Variations in all items measured across the STC-I are illustrated in Fig. 3. Temperature changed from *ca.* 11.0°C to *ca.* 12.5°C. Although salinity was stable in the Subantarctic side (34.40‰), it varied in the middle to the Subtropical side in the range of 34.40–34.80‰. It is noted that temperature and salinity attained their maxima of 12.7°C and 34.80‰ at the site of sample No. 14, and decreased again to 11.9°C and 34.56‰ at sample No. 18. The variations of nutrients coincided with each other, especially in nitrate, nitrite and phosphate, and revealed a mirror image to those of temperature and salinity. Concentration of each nutrient form varied within the ranges of 2.6–9.8 $\mu\text{g-at}\cdot\text{l}^{-1}$ in nitrate-N, 0.17–0.23 $\mu\text{g-at}\cdot\text{l}^{-1}$ in nitrite-N, 0.51–0.86 $\mu\text{g-at}\cdot\text{l}^{-1}$ in phosphate-P and 0.5–2.3 $\mu\text{g-at}\cdot\text{l}^{-1}$ in silicate-Si. These values were 2/3–1/10 lower than those in the PF transect.

Chlorophyll *a* showed a similar pattern of variation to those in temperature and

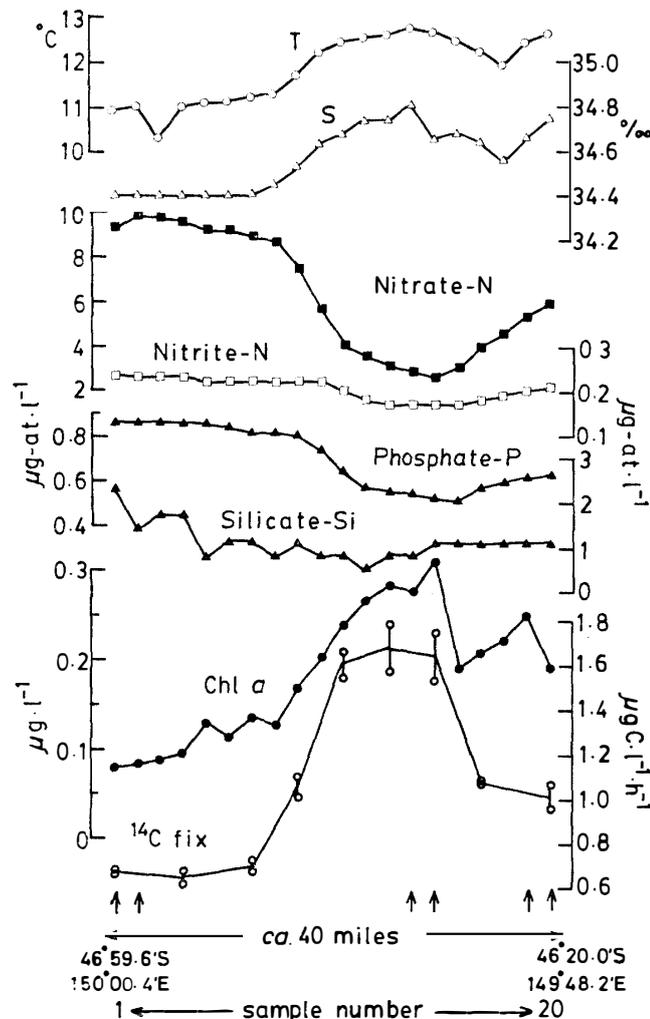


Fig. 3. Horizontal variations in phytoplankton standing stock, photosynthetic activity and environmental factors in the surface layer (*ca.* 4-m depth) across the STC-I on January 1, 1984. See Fig. 2 for six arrows at the bottom.

salinity, attaining the maximum of $0.309 \mu\text{g}\cdot\text{l}^{-1}$ in sample No. 15 from the lowest of $0.078 \mu\text{g}\cdot\text{l}^{-1}$ in sample No. 1. Phytoplankton productivity was high as much as $1.664 \mu\text{gC}\cdot\text{l}^{-1}\cdot\text{h}^{-1}$ on the average near the chlorophyll maximum (sample No. 13), and was the minimum of $0.638 \mu\text{gC}\cdot\text{l}^{-1}\cdot\text{h}^{-1}$ in sample No. 4. However, the photosynthetic rates ($\mu\text{gC}\cdot\mu\text{g chl. a}^{-1}\cdot\text{h}^{-1}$) did not show significant differences among three regions; 6.83 on the average for three samples in the Subantarctic side, 5.94 for three samples in the middle region and 5.29 for two samples in the Subtropical side, statistically non-significant (t -test, $p=0.10$). Distance of 16 miles between sample Nos. 8 and 16 can be regarded as the width of the dense community accompanied with higher productivity than those in the surrounding waters.

3.3. The Subtropical Convergence-II

Salinity showed smooth change (34.61–34.71‰) across the STC-II in contrast to that in the STC-I, although the temperature change was sharper (ca. 12.2–14.4°C) than

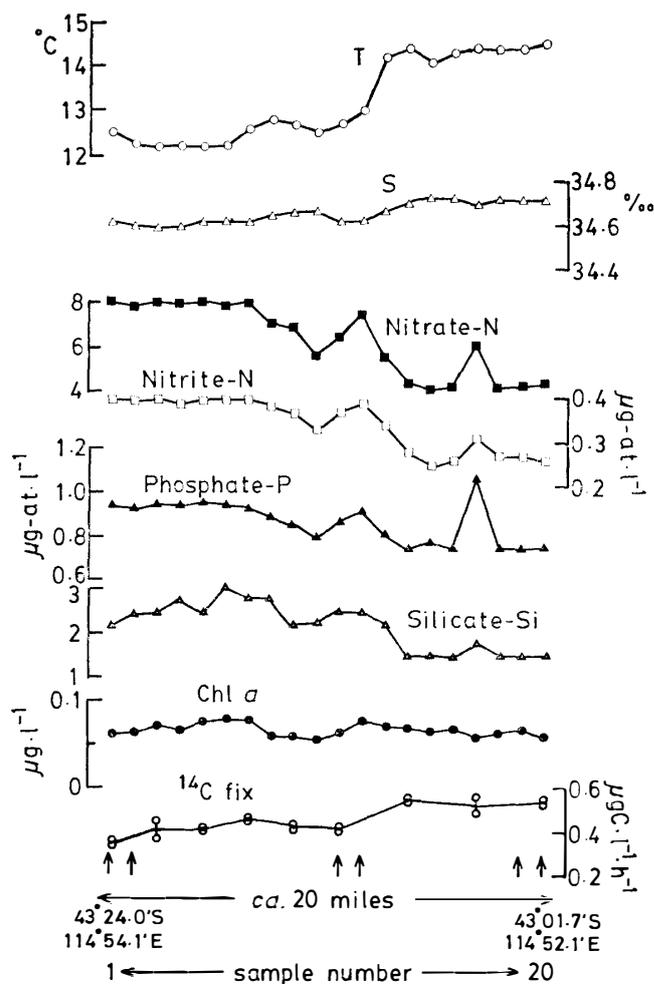


Fig. 4. Horizontal variations in phytoplankton standing stock, photosynthetic activity and environmental factors in the surface layer (ca. 4-m depth) across the STC-II on January 27, 1984. See Fig. 2 for six arrows at the bottom.

that in the STC-I transect (Fig. 4). Concentrations of nutrients (nitrate-N, 4.1–8.2 $\mu\text{g-at}\cdot\text{l}^{-1}$; nitrite-N, 0.25–0.40 $\mu\text{g-at}\cdot\text{l}^{-1}$; Phosphate-P, 0.73–1.05 $\mu\text{g-at}\cdot\text{l}^{-1}$; Silicate-Si, 1.5–3.1 $\mu\text{g-at}\cdot\text{l}^{-1}$) were at the same levels in the STC-I transect. And the increase and decrease in all nutrient forms concurred with each other throughout the transect. No marked variation or peak formation was found in chlorophyll *a* distribution. ^{14}C fixations of phytoplankton were significantly different between 6 samples in the Subantarctic side (0.417 $\mu\text{gC}\cdot\text{l}^{-1}\cdot\text{h}^{-1}$ on average) and 3 samples in the Subtropical side (0.529 $\mu\text{gC}\cdot\text{l}^{-1}\cdot\text{h}^{-1}$ on average) (*t*-test, $p=0.01$). The average photosynthetic rates were 6.16 for the former and 8.83 for the latter, and these were also significantly different (*t*-test, $p=0.01$).

3.4. Structures of phytoplankton communities

Phytoplankton numerical abundance and compositions are shown in Fig. 5. Microscopic works were done for six samples taken at three different sites of each transect. Data are averaged between each two neighboring samples. Species identified were listed in Tables 1, 2 and 3. While diatoms were a dominant group in the PF transect (Fig. 5 and Table 1), dinoflagellates were abundant in the two STC transects (Fig. 5 and Tables 2 and 3).

In the PF transect, diatoms occupied more than 99% in both the chlorophyll maximum and the Antarctic side, and 84% in the Subantarctic side (Fig. 5). The cell number of diatoms reached $1.2\times 10^5\text{l}^{-1}$ at the site of chlorophyll maximum, and most of them (1.0×10^5) were *Nitzschia* spp. Species that occurred more in the chlorophyll

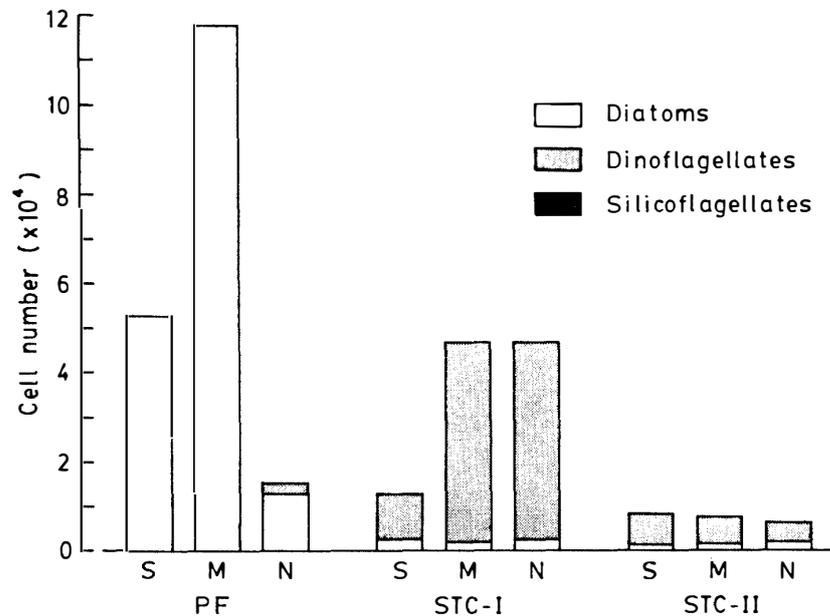


Fig. 5. Numerical abundance of diatoms, dinoflagellates and silicoflagellates at the south (S), middle (M) and north (N) of the Polar Front (PF), the Subtropical Convergence (STC)-I and II. Numerical contribution of silicoflagellates was very small compared to the total in each sample so that it could not be pictured in.

maximum than those in both terminal samples of the transect were *Actinocyclus* sp., *Chaetoceros decipiens*, *C. peruvianum*, *Coscinodiscus furcatus*, *C. gyratus*, *Dactyliosolen antarcticus*, *Nitzschia* spp., *Rhizosolenia alata*, *Thalassionema elegans*, *Tropidoneis belgicae* of diatoms, and *Ceratium pentagonum* of dinoflagellate (Table 1).

In the transect of STC-I, dinoflagellates predominated over diatoms throughout the entire line (83–96%), being contrary to the results on the PF (Fig. 5). While dinoflagellates were abundant in both the chlorophyll maximum and the Subtropical side (ca. 4.4×10^4 cells l^{-1}), diatoms showed relatively constant distribution throughout the

Table 1. Phytoplankton species and their abundances (cells l^{-1}) at the middle and both ends of the PF transect on December 29, 1983.

Species	Antarctic side	Middle	Subantarctic side
Diatoms			
<i>Actinocyclus</i> sp. 1	—	10	—
<i>Asteromphalus hookerii</i>	30	65	4
<i>A. pervulus</i>	190	40	8
<i>Chaetoceros atlanticum</i>	20	90	8
<i>C. boreale</i>	15	20	—
<i>C. bulbosus</i>	15	—	—
<i>C. concavicornis</i>	40	70	4
<i>C. decipiens</i>	—	10	—
<i>C. peruvianum</i>	—	20	8
<i>Chaetoceros</i> spp.	—	35	4
<i>Corethron criophilum</i>	335	300	8
<i>Coscinodiscus bullatus</i>	—	—	2
<i>C. furcatus</i>	—	10	2
<i>C. gyratus</i>	55	160	56
<i>C. inflatus</i>	10	30	—
<i>C. lentiginosus</i>	115	50	16
<i>C. oculoides</i>	40	—	2
<i>C. ritscherii</i>	200	205	16
<i>C. tumidus</i>	10	70	2
<i>C. variolatus?</i>	—	—	2
<i>Dactyliosolen antarcticus</i>	75	100	—
<i>Eucampia balaustium</i>	15	20	10
<i>Navicula</i> spp.	720	600	145
<i>Nitzschia</i> spp.	42410	101580	11293
<i>Rhizosolenia alata</i>	90	120	25
<i>R. fragilissima</i>	30	20	10
<i>R. hebetata</i> f. <i>semispina</i>	105	340	43
<i>R. styliformis</i>	10	—	—
<i>Thalassionema elegans</i>	275	5520	262
<i>Thalassiosira</i> spp.	4345	2840	423
<i>Thalassiothrix antarctica</i>	2845	4440	138
<i>Tropidoneis antarctica</i>	200	170	12
<i>T. belgicae</i>	70	225	38
Unidentified diatoms	25	40	10
Total (%)	52290 (99.4)	117200 (99.5)	12551 (83.7)

Table 1. Continued.

Species	Antarctic side	Middle	Subantarctic side
Dinoflagellates			
<i>Amphidinium turbo?</i>	—	—	4
<i>Amphidinium</i> sp. 1	—	—	36
<i>Ceratium fusus</i>	—	—	28
<i>C. lineatum</i>	5	20	36
<i>C. pentagonum</i>	—	35	—
<i>Cochlodinium</i> sp. 1	—	—	4
<i>Dinophysis parvula?</i>	10	—	—
<i>D. punctata?</i>	—	—	4
<i>Gonyaulax minuta?</i>	—	—	6
<i>Gymnodinium</i> spp.	—	70	446
<i>Gyrodinium glaciale?</i>	—	—	154
<i>Oxytoxum curvatum?</i>	—	—	10
<i>O. laticeps</i>	—	—	20
<i>O. nanum</i>	—	135	1468
<i>O. variable</i>	—	—	48
<i>Pronoctiluca pelagica</i>	—	10	14
<i>Prorocentrum micans?</i>	—	—	2
<i>P. triestinum?</i>	—	—	36
<i>Protoperidinium elegantissimum?</i>	—	10	—
<i>P. pallidum</i>	—	20	10
<i>Protoperidinium</i> spp.	—	—	20
<i>Scrippsiella</i> spp.	—	30	16
Unidentified dinoflagellates	10	60	44
Total (%)	25 (0.0)	390 (0.3)	2406 (16.0)
Silicoflagellates			
<i>Distephanus speculus</i>	310 (0.6)	220 (0.2)	48 (0.3)
Grand total	52625	117810	15005

transect ($ca. 2.0 \times 10^3$ cells $\cdot l^{-1}$). Total cell number of these organisms ($ca. 1.3-4.7 \times 10^4 l^{-1}$) was about 1/2 of those in the PF transect. *Gymnodinium* and *Oxytoxum* were leading genera in the dinoflagellate group throughout the entire transect (Table 2). And the following species characteristically appeared in the samples of chlorophyll maximum; *Ceratium arietinum* var. *glacilentum*, *C. massiliense*, *Dissodinium bicornis*, *Oxytoxum scolopax*, *Podolampas spinifera*, *Prorocentrum rostratum*, and *Protoperidinium pallidum* (Table 2).

Although the situation in the STC-II transect in which the dominance of dinoflagellates was similar to that in the STC-I, the total cell number was about 1/5 compared to those in the STC-I (Fig. 5). In the STC-II transect (Table 3), dinoflagellates slightly decreased from the Subantarctic side towards the Subtropical side, while diatoms showed a reverse pattern.

On these three transects observed in the present study, the following diatoms sharply decreased from the Antarctic side to the Subantarctic side; *Asteromphalus hookerii*, *A.*

Table 2. Phytoplankton species and their abundances (cells l⁻¹) at the middle and both ends of the STC-I transect on January 1, 1984.

Species	Subantarctic side	Middle	Subtropical side
Diatoms			
<i>Asteromphalus pervulus</i>	4	—	—
<i>Chaetoceros concavicornis</i>	8	—	—
<i>C. peruvianum</i>	20	60	60
<i>C. schimperianum</i>	84	20	190
<i>Chaetoceros</i> spp.	52	40	180
<i>Corethron criophilum</i>	30	35	35
<i>Coscinodiscus gyrratus</i>	24	—	—
<i>C. ritscherii</i>	8	—	—
<i>C. subtilis?</i>	4	—	—
<i>Coscinodiscus</i> spp.	—	—	80
<i>Eucampia balaustium</i>	3	—	—
<i>Navicula</i> spp.	83	27	80
<i>Nitzschia</i> spp.	1441	1189	1345
<i>Planktoniella sol</i>	—	5	10
<i>Rhizosolenia alata</i>	3	—	5
<i>R. hebetata</i> f. <i>semispina</i>	10	5	—
<i>Thalassionema elegans</i>	180	280	260
<i>Thalassiosira</i> spp.	213	140	85
<i>Tropidoneis antarctica</i>	3	—	—
<i>T. belgicae</i>	32	5	—
Unidentified diatoms	—	60	20
Total (%)	2202 (17.5)	1866 (4.0)	2350 (5.0)
Dinoflagellates			
<i>Amphidinium hadai?</i>	228	160	40
<i>Amphidinium</i> sp. 1	124	480	460
<i>Amphidinium</i> sp. 2	4	20	—
<i>Amphidoma</i> sp. 1	24	1660	260
<i>Ceratium arietinum</i> v. <i>glacilentum</i>	—	5	—
<i>C. furca</i>	—	—	5
<i>C. fusus</i>	5	64	30
<i>C. lineatum</i>	193	720	560
<i>C. massiliense</i>	—	10	—
<i>Dinophysis hastata</i>	—	—	5
<i>D. meteori?</i>	5	—	—
<i>D. ovum</i>	—	—	20
<i>D. ruudii?</i>	—	20	—
<i>D. schroederi</i>	—	—	10
<i>Dinophysis</i> sp. 1	—	60	—
<i>Dissodinium bicornis</i>	—	14	5
<i>Gonyaulax minuta</i>	4	—	50
<i>G. polygramma</i>	8	—	—
<i>Gymnodinium guttula?</i>	8	—	—
<i>G. minor?</i>	3140	2960	1100
<i>G. soyai?</i>	48	420	210
<i>Gymnodinium</i> spp.	2472	6520	8200

Table 2. Continued.

Species	Subantarctic side	Middle	Subtropical side
<i>Gyrodinium glaciale?</i>	816	3500	4950
<i>Oxytoxum curvatum?</i>	—	—	20
<i>O. gracile</i>	—	920	410
<i>O. laticeps</i>	296	3980	5680
<i>O. longiceps</i>	4	—	—
<i>O. nanum</i>	2280	12660	11230
<i>O. parvum</i>	—	60	50
<i>O. scolopax</i>	—	20	—
<i>O. sublatum</i>	4	—	—
<i>O. turbo</i>	—	—	20
<i>O. variabile</i>	70	2300	5460
<i>O. viide</i>	4	—	—
<i>Oxytoxum</i> sp. 1	—	1780	1210
<i>Podolampas spinifera</i>	—	5	—
<i>Pronoctiluca pelagica</i>	4	5	—
<i>Prorocentrum obtusidens</i>	285	3210	2140
<i>P. rostratum</i>	—	60	—
<i>P. triestinum?</i>	132	1060	550
<i>Protoperidinium conicum</i>	—	20	20
<i>P. minusculum</i>	—	20	10
<i>P. orientale</i>	16	20	20
<i>P. pallidum</i>	—	9	—
<i>P. pellucidum</i>	—	32	85
<i>P. sourniai</i>	16	40	40
<i>P. tenuissimum</i>	8	5	25
<i>P. tristylum?</i>	4	—	—
<i>P. trochoideum</i>	—	470	260
<i>Protoperidinium</i> spp.	24	260	80
<i>Scrippsiella</i> spp.	38	460	1020
Unidentified dinoflagellates	116	440	90
Total (%)	10380 (82.5)	44449 (96.0)	44325 (95.0)
Silicoflagellates			
<i>Dictyocha fibula</i>	— (0.0)	5 (0.0)	10 (0.0)
Grand total	12582	46320	46685

pervulus, *Chaetoceros atlanticum*, *C. boreale*, *C. bulbosus*, *C. concavicornis*, *Corethron criophilum*, *Coscinodiscus inflatus*, *C. ritscherii*, *C. tumidus*, *Dactyliosolen antarcticus*, *Rhizosolenia hebetata* form *semispina*, *R. styliformis*, *Thalassiosira* spp., *Thalassiothrix antarctica* and *Tropidoneis antarctica*. On the other hand, the following species increased from the middle of the STC-I and -II to the Subtropical side; *Planktoniella sol*, *Oxytoxum parvum*, *Prorocentrum obtusidens*. And while *Pronoctiluca pelagica* was found both at the north of the PF and at the south of the STC, *A. hookerii*, *C. criophilum*, *R. alata*, *R. hebetata* form *semispina*, *T. belgicae* and *C. lineatum* were found both at the south of the PF and at the north of the STC.

Table 3. Phytoplankton species and their abundances (cells l^{-1}) at the middle and both ends of the STC-II transect on January 27, 1984.

Species	Subantarctic side	Middle	Subtropical side
Diatoms			
<i>Asteromphalus hookerii</i>	3	10	15
<i>Chaetoceros atlanticum</i> v. <i>audax</i>	3	—	—
<i>C. atlanticum</i> v. <i>neapolitanum</i>	—	—	43
<i>C. compressum</i>	—	—	28
<i>C. glaciles?</i>	—	—	3
<i>C. lacinosum</i>	—	5	28
<i>C. pendulum</i>	—	8	40
<i>C. peruvianum</i>	80	103	43
<i>C. schimperianum</i>	24	8	—
<i>Chaetoceros</i> spp.	4	8	48
<i>Corethron criophilum</i>	208	143	120
<i>Coscinodiscus</i> sp. 1	11	—	—
<i>Navicula</i> spp.	85	65	145
<i>Nitzschia</i> spp.	423	733	776
<i>Planktoniella sol</i>	3	30	290
<i>Rhizosolenia alata</i>	15	13	3
<i>R. hebetata</i> f. <i>semispina</i>	3	3	5
<i>Thalassiosira</i> spp.	10	55	250
<i>Thalassiothrix delicatula</i>	180	24	8
<i>T. mediterranea</i>	4	8	—
<i>Tropidoneis belgicae</i>	104	48	48
<i>T. fusiformis</i>	—	—	64
Unidentified diatoms	20	—	6
Total (%)	1180 (14.3)	1264 (17.0)	1963 (31.9)
Dinoflagellates			
<i>Amphidinium</i> sp. 1	188	72	88
<i>Amphidinium</i> sp. 3	4	8	—
<i>Amphidoma</i> sp. 1	56	16	8
<i>Ceratium fusus</i>	3	3	—
<i>C. lineatum</i>	25	25	60
<i>Cladopyxis brachiolata</i>	—	—	3
<i>Gymnodinium minor?</i>	152	152	192
<i>G. soyai?</i>	52	—	—
<i>Gymnodinium</i> spp.	2044	1632	1560
<i>Gyrodinium</i> spp.	604	552	642
<i>Oxytoxum coronatum?</i>	—	8	16
<i>O. glacile</i>	208	160	120
<i>O. laticeps</i>	182	112	64
<i>O. nanum</i>	2060	2464	608
<i>O. parvum</i>	—	8	16
<i>O. variabile</i>	352	280	480
<i>Oxytoxum</i> sp. 1	216	184	64
<i>Pronoctiluca pelagica</i>	—	8	—
<i>Prorocentrum obtusidens</i>	8	10	18
<i>P. rostratum</i>	8	—	8

Table 3. Continued.

Species	Subantarctic side	Middle	Subtropical side
<i>P. triestinum?</i>	56	80	88
<i>Protoperdinium minusculum</i>	—	8	—
<i>P. sourniai</i>	20	24	8
<i>P. trochoideum</i>	268	152	56
<i>Protoperdinium</i> spp.	12	8	16
<i>Scripsiella</i> spp.	516	176	56
Unidentified dinoflagellates	24	48	30
Total (%)	7060 (85.7)	6190 (83.0)	4183 (68.1)
Grand total	8240	7454	6146

4. Discussion

Dense phytoplankton standing stocks of 5-mile width and of 16-mile width were observed respectively in the PF and the STC-I transects during this cruise (Figs. 2 and 3). FUKUCHI (1980) summarized the phytoplankton chlorophyll stock in the Southern Ocean, and showed that those in the Antarctic region are lower than those in the Bering Sea which is located at the equivalent latitude in the northern hemisphere. EL-SAYED and MANDELLI (1965) discussed the limiting factors of phytoplankton production in the Antarctic region, and suggested that light and temperature are the two most important factors. In the summer season, however, as they also mentioned and the other reports (FRANCESCHINI, 1978; HOLM-HANSEN *et al.*, 1977) said, the amount of solar radiation is sufficient for the photosynthesis of phytoplankton in the surface layer. Furthermore, the Antarctic water is sufficiently high in nutrients as shown in Fig. 2 in this study and in the other reports (*e.g.*, FUKASE, 1962; HOLM-HANSEN *et al.*, 1977; EL-SAYED and TAGUCHI, 1981; JACQUES, 1983), although there are some indications that silicate may limit the growth of diatoms in the region (HOLM-HANSEN *et al.*, 1977; JACQUES, 1983).

NEORI and HOLM-HANSEN (1982) have found that photosynthetic rates of the Antarctic phytoplankton increased with increasing temperature up to 7°C from ambient sub-zero temperatures. The increase in photosynthetic rates was also found at *ca.* 12°C by JACQUES (1983) for the Antarctic natural assemblages. Therefore, temperature can necessarily be presumed to be a most important factor limiting the growth of the Antarctic phytoplankton community.

SVERDRUP *et al.* (1942) suggested that a wind stress would carry the surface water in the Antarctic region towards the PF, whereas a thermohaline circulation dominates in the Subantarctic region which carries the light surface waters towards the PF. Then, the cold low salinity water of the Antarctic region and the relatively warm saline water of the Subantarctic region are mixed at the PF. Therefore, it is plausible to consider that the growth activity of the Antarctic phytoplankton is accelerated at the PF as a result of the increase in temperature by the admixture with the warmer Subantarctic water. *Nitzschia* spp. which amounted to *ca.* 86% in the chlorophyll maximum of the PF transect included a large number of *Fragilariopsis* spp. (*ca.* 72%) in old nomenclature. Any species in the genera are reported as the Antarctic ones (HENDEY, 1937; KOZLOVA,

1964). It is assumed that their growth activities were enhanced by the temperature increase at the PF and resulted in the chlorophyll maximum at the midst of the front.

During this cruise, incubation experiments were done using ^{14}C radioisotope for the surface phytoplankton assemblages at 10 stations along the cruise track (YAMAMOTO, 1985). The temperatures of the incubations were usually set at the ambient and several degrees lower and higher than the ambient ones. Although the photosynthetic activities of the Antarctic phytoplankton increased with increasing temperature, those of both the Subantarctic and the Subtropical communities showed the maxima at the ambient temperatures, and were reduced at both the lower and higher temperatures than the ambient ones. These results imply that the increase in temperature by the admixture process at the fronts may be effective only for the situation at the PF.

The increase in ambient nutrient concentrations at the PF might provide more suitable condition to the Subantarctic species than in the original habitat. SAVIDGE (1976) observed a marked increase in phytoplankton photosynthesis resulting from admixture of the two water types on opposite sides of the front in the Irish Sea. Among some species which showed the increase in cell number at the PF, *C. peruvianum* seems to be the representative species whose origin is in the region north of the PF (Table 1). However, the increase in nutrient levels is assumed to give only a minor influence to the Subantarctic phytoplankton assemblages, because the nutrient levels in the Subantarctic water were not so low as preventing the growth from the viewpoint of half-saturation constants of nutrient uptake kinetics (THOMAS and DODSON, 1968; EPPLEY *et al.*, 1969).

Although available information on micronutrients is scarce in the studied area, CARLUCCI and CUHEL (1977) showed that several kinds of vitamins, particularly B_{12} , at the surface of the area south off Australia are nearly undetectable. Therefore, vitamins at least do not seem to become stimulants for the growth of phytoplankton by the admixture of two water masses at the PF.

Maxima of standing stock and productivity in the STC-I transect were found just north of the sharp gradients in surface temperature and salinity, and these were associated with a warm (12.7°C) and saline (34.80‰) water mass carrying nutrients of relatively low concentrations (Fig. 3). Since the water mass of such values of temperature and salinity is not found elsewhere within the 40-mile transect, the origin of the water must be sought in the north of the transect. As described by DEACON (1937), the Subantarctic surface water is driven towards the north by east by the prevailing westerly wind according to Ekman's theory, while the Subtropical current north of the STC has a southward component. In this region, south of Australia, the formation of a sharp convergence is less often than in the area of an extensive ocean lies to the north, because the north-south movement of surface water is supposed to be restricted by the Australian continent. He also mentioned that the easterly surface current south of Tasmania is deflected southwards and becomes involved in a large number of eddies which can almost certainly be attributed to the influence of the exceptionally rugged bottom topography. In the case of STC-I south of the Tasmanian Island, it can be concluded that a warm saline water parcel from the Subtropical region, probably near the Tasmanian Island, is entangled in an eddy during its formation process.

There is an indication that species appeared more in the chlorophyll maximum rather than in both sides, *i.e.*, *C. arietinum* var. *glacilentum*, *C. massiliense*, *O. scolopax*,

P. spinifera, *P. rostratum* are considered to be warm water forms, and *P. pallidum* is ubiquitous in neritic or estuarine environments according to WOOD (1954, 1968) and TAYLOR (1976). Furthermore, the appearance of *Chaetoceros schimperianum*, *Navicula* spp., *Nitzschia* spp., *Gonyaulax minuta* and *Proto-peridinium tenuissimum*, which were found in both terminal samples from the STC-I transect, would strengthen the rotating water movement by an eddy.

PLANCKE (1977) also found that the phytoplankton maxima exist just north of the STC, although she was not concerned with the formation mechanisms. FURUYA *et al.* (1985) observed that the less dense water mass south of the STC was overlying on the comparatively dense water mass of the opposite side of the STC, and these two water masses formed a shallow pycnocline at 27-m depth. And they examined that the phytoplankton community in the upper water was actively growing, consuming the available nutrients *in situ*. They have also described that diatom carbon occupied more than 90% of the total in the upper 20m layers of the central part of the STC. On the contrary, dinoflagellates revealed a predominancy of 96% of the maximum standing stock of the STC-I in the present study (Table 2). FURUYA and co-workers carried out observations for 20 to several hours prior to this observation on the same day of January 1, 1984. Whereas there is a fundamental difference in the expression of phytoplankton abundance between the present study (cell number) and theirs (cell carbon), it is difficult to explain this unexpected contradiction at this stage.

In the present paper, for the formation of the maxima of phytoplankton standing stock and productivity, the "admixture" and the "eddy" were adopted as most plausible assumptions for the PF and the STC, respectively. Phytoplankton community of the maximum standing stock in the STC-I transect did not show significantly higher photosynthetic rates than those in the two communities on both sides. However, if the eddy is anticyclonic (DEACON, 1937), and it was at the initial phase of the formation when the observations were done, the standing stock in the eddy center is expected to increase in the near future due to nutrient supply from the deeper layers. Photosynthetic rates of the maximum standing stock at the PF are supposed to be higher than those in the both sides because of the increase in temperature as a physiological enhancement on growth activity, although no measurements of productivities were made on the PF transect. Complicated physical and chemical conditions at the oceanic fronts would give rise to some different cases other than the two mechanisms discussed above. Further investigations should be done on the oceanic fronts in the Southern Ocean.

Acknowledgments

The author wishes to express his sincere thanks to Prof. T. NEMOTO, Ocean Research Institute, University of Tokyo, and to the captain and crew of R. V. HAKUHO MARU for making this research possible. The author is deeply indebted to Dr. K. FUKAMI for his aid in the field operations.

References

- CARLUCCI, A. F. and CUHEL, R. L. (1977): Vitamins in the South Polar Seas: Distribution and significance of dissolved and particulate vitamin B₁₂, thiamine, and biotin in the southern Indian Ocean. Adaptations within Antarctic Ecosystems, ed. by G. A. LLANO. Washington, D. C., Smithsonian Inst., 115–128.
- DEACON, G. E. R. (1937): The hydrology of the Southern Ocean. *Discovery Rep.*, **15**, 1–124.
- EL-SAYED, S. Z. (1970): On the productivity of the Southern Ocean (Atlantic and Pacific sectors). *Antarctic Ecology*, Vol. 1, ed. by M. W. HOLDGATE. London, Academic Press, 119–135.
- EL-SAYED, S. Z. and MANDELLI, E. F. (1965): Primary production and standing crop of phytoplankton in the Weddell Sea and Drake Passage. *Biology of the Antarctic Seas, II*, ed. by G. A. LLANO. Washington, D. C., Am. Geophys. Union, 87–106 (*Antarct. Res. Ser.*, Vol. 5).
- 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.
- EL-SAYED, S. Z. and WEBER, L. H. (1982): Spatial and temporal variations in phytoplankton biomass and primary productivity in the southwest Atlantic and the Scotia Sea. *Polar Biol.*, **1**, 83–90.
- EPPLEY, R. W., ROGERS, J. N. and MCCARTHY, J. J. (1969): Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton. *Limnol. Oceanogr.*, **14**, 912–920.
- FRANCESCHINI, G. A. (1978): Solar radiation over the Weddell and Ross Seas. *Antarct. J. U. S.*, **13**, 172–173.
- FUKASE, S. (1962): Oceanographic condition of surface water between the south end of Africa and Antarctica. *Nankyoku Shiryo* (*Antarct. Rec.*), **15**, 53–111.
- FUKUCHI, M. (1980): Phytoplankton chlorophyll stocks in the Antarctic Ocean. *J. Oceanogr. Soc. Jpn.*, **36**, 73–84.
- FUKUCHI, M. (1982): Ichiji seisan (Primary production). *Nankyoku no Kagaku*, 7. *Seibutsu (Science of Antarctica, 7. Biology)*, ed. by Kokuritsu Kyokuchi Kenkyûjo. Tokyo, Kokon Shoin, 11–37.
- FUKUCHI, M. and TAMURA, S. (1982): Chlorophyll *a* distribution in the Indian sector of the Antarctic Ocean in 1978–1979. *Nankyoku Shiryo* (*Antarct. Rec.*), **74**, 143–162.
- FURUYA, K., HASUMOTO, H., NAKAI, T. and NEMOTO, T. (1985): Phytoplankton in the Subtropical Convergence during the austral summer; Community structure and growth activity. *Deep-Sea Res.* (in press).
- HASUMOTO, H. and NAKAI, T. (1985): Continuous measurements of sea surface temperature and salinity. *Prelim. Rep. Hakuho Maru Cruise, KH-83-4*, 8–16.
- HAURY, L. R., MCGOWAN, J. A. and WIEBE, P. H. (1978): Patterns and processes in the time-space scales of plankton distributions. *Special Pattern in Plankton Communities*, ed. by J. H. STEELE. New York, Plenum Press, 277–327.
- HENDEY, N. I. (1937): The plankton diatoms of the Southern Seas. *Discovery Rep.*, **14**, 151–364.
- HOLM-HANSEN, O., EL-SAYED, S. Z., FRANCESCHINI, G. A. and CUHEL, R. L. (1977): Primary production and the factors controlling phytoplankton growth in the Southern Ocean. Adaptations within Antarctic Ecosystems, ed. by G. A. LLANO. Washington, D. C., Smithsonian Inst., 11–50.
- JACQUES, G. (1983): Some ecophysiological aspects of the Antarctic phytoplankton. *Polar Biol.*, **2**, 27–33.
- KOZLOVA, O. G. (1964): Diatoms of the Indian and Pacific Sectors of the Antarctic, ed. by A. P. LISITSYN, tr. from Russian by S. HOFFMANN. Jerusalem, Israel Program for Scientific Translations, 191 p.
- LEAN, D. R. and BURNISON, B. K. (1979): An evaluation of errors in the ¹⁴C method of primary production measurement. *Limnol. Oceanogr.*, **24**, 917–928.
- LEGENDRE, L., DEMERS, S., YENTSCH, C. M. and YENTSCH, C. S. (1983): The ¹⁴C method; Patterns of dark CO₂ fixation and DCMU correction to replace the dark bottle. *Limnol. Oceanogr.*, **28**, 996–1003.
- NAKAI, T., HASUMOTO, H. and NEMOTO, T. (1985): Hydrographic characteristics. *Prelim. Rep. Hakuho Maru Cruise, KH-83-4*, 3–7.

- NEORI, A. and HOLM-HANSEN, O. (1982): Effect of temperature on rate of photosynthesis in Antarctic phytoplankton. *Polar Biol.*, **1**, 33–38.
- PLANCKE, J. (1977): Phytoplankton biomass and productivity in the Subtropical Convergence area and shelves of the western Indian Subantarctic islands. *Adaptations within Antarctic Ecosystems*, ed. by G. A. LLANO. Washington, D. C., Smithsonian Inst., 51–73.
- SAVIDGE, G. (1976): A preliminary study of the distribution of chlorophyll *a* in the vicinity of fronts in the Celtic and western Irish Seas. *Est. Coast. Mar. Sci.*, **4**, 617–625.
- STEEMANN NIELSEN, E. (1952): The use of radioactive carbon (^{14}C) for measuring organic production in the sea. *J. Cons. Int. Explor. Mer*, **18**, 117–140.
- STRICKLAND, J. D. H. and PARSONS, T. R. (1972): A practical handbook of seawater analysis. *Bull., Fish. Res. Board Can.*, **167**, 310 p.
- SVERDRUP, H. U., JOHNSON, M. W. and FLEMING, R. H. (1942): *The Oceans; Their Physics, Chemistry, and General Biology*. Englewood Cliffs, Prentice-Hall, 1060 p.
- TAYLOR, F. J. R. (1976): Dinoflagellates from the International Indian Ocean Expedition. *Bibl. Bot.*, **132**, 234 p.
- THOMAS, W. H. and DODSON, A. N. (1968): Effects of phosphates concentration on cell division rates and yield of a tropical oceanic diatom. *Biol. Bull.*, **134**, 199–208.
- WOOD, E. J. F. (1954): Dinoflagellates in the Australian region. *Aust. J. Mar. Freshwater Res.*, **5**, 171–351.
- WOOD, E. J. F. (1968): *Dinoflagellates of the Caribbean Sea and Adjacent Areas*. Miami, University of Miami Press, 143 p.
- YAMAMOTO, T. (1985): Effect of temperature on photosynthetic activity in Antarctic phytoplankton. *Prelim. Rep. Hakuho Maru Cruise*, **KH-83-4**, 30–32.

(Received April 1, 1985; Revised manuscript received October 24, 1985)