J. Plant Biol. 41 (2) : 125~134 (1998)

Variation of the Phytoplankton Community Across the Subtropical Convergence Zone in the West Pacific Sector of the Southern Ocean During Early Austral Summer 1995/6

Lee, Hak Young* **and Richard M. Greene**[1]
Department of Biology, Pusan National University, Pusan 609-735, Korea
[1]*Department of Oceanography, Texas A&M University, College Station, TX77843*

Phytoplankton of the Southern Ocean, 140-148°E and 40-53°S, was sampled from early austral summer Nov. 1995 to Dec. 1995 to examine cell abundance, cell volume and biomass (cell carbon) distribution across the fronts. A total of 90 phytoplankton taxa were identified. They were 50 diatoms, 37 dinoflagellates, 2 silicoflagellates, and 1 prymnesiophyte. 73 species were observed from north of the subtropical convergence zone and 71 species from south of the subtropical convergence zone. *Pseudonitzschia* spp. was the most widely distributed species. Nanoplankton predominated cell number of phytoplankton throughout the stations. The abundance of diatoms was higher than that of dinoflagellates. Total biomass profiles were dependent to microphytoplankton biomass. Maximum cell number and biomass were observed from subsurface layer. Phytoplankton community changed across the subtropical convergence zone and 50-53°S (antarctic convergence zone), and physicochemical factors seem to controll the distribution.

Keywords: southern ocean, phytoplankton, biomass, subtropical convergence zone

The Southern Ocean which is known to be important global sinks of atmospheric CO_2, has unique physical and chemical characteristics: 1) the circumpolarity, 2) variability of light regime, 3) high concentrations of inorganic nutrients, etc. (El-Sayed, 1988a; El-Sayed and Fryxell, 1993). The circumpolar zonation with different physical characters divide the Southern Ocean with several different physicochemical environments (Deacon, 1982, 1984; Nowlin, 1985; Knox, 1994), and this circumpolarity of the Southern Ocean influences the distribution, abundance, productivity and behavior in the Southern Ocean marine organisms (Heywood and Priddle, 1987; Atkinson and Ward, 1988; Knox, 1994; Stein and Heywood, 1994). The phytoplankton species composition, abundance, biomass, and productivity also change across these circumpolar fronts (El-Sayed, 1988a; El-Sayed and Weber, 1982; Yamamoto, 1986; Froneman *et al.*, 1995; Fryxell and Hasle, 1979; Hart, 1934, 1942).

Though the study of Antarctic marine phytoplankton has more than 100 years history, the distribution, productivity and ecology of the phytoplankton of the Southern Ocean have been studied extensively since the establishment of Scientific Committee on Antarctic Research (SCAR) in 1957 (El-Sayed, 1968a, b, 1970a, b, 1978, 1985, 1987, 1988a, b, 1990; El-Sayed and Mandelli, 1965; El-Sayed and Turner, 1977; El-Sayed and Weber, 1982, 1986; El-Sayed *et al.*, 1979; Knox, 1970, 1994; Heywood and Whitaker, 1984; Hasle, 1969; Hosaka and Nemoto, 1986; Jacques and Fukuchi, 1994; Sakshaug and Holm-Hansen, 1984). Technological achievements of the 1980s and 1990s enhanced our knowledge of the Southern Ocean phytoplankton greatly. Moreover, through the several cruises of Antarctic research programs, a large body of valuable data was obtained on the geographic and temporal distributions of phytoplankton population (El-Sayed and Fryxell, 1993). Eltanin Cruise 36 (El-Sayed, 1970b) made great progress on the phytoplankton ecosystem of the west Pacific Sector of the Southern Ocean (El-Sayed and Fryxell, 1993). However,

---

*Corresponding author: Fax +82-51-581-2962 many ecological questions remain unknown, and the data of the phytoplankkton distribution pattern across the subtropical convergence zone (STCZ) are rare.

This research was performed as a part of the International Global Atmospheric Chemistry (IGAC) Project, Southern Hemisphere Aerosol Characterization Experiment (ACE-1) to compare species composition, cell numbers and biomass (cell carbon) of phytoplankton in the west Pacific Sector of the Southern Ocean across the STCZ.

MATERIALS AND METHODS

Sampling for this study was carried out from Nov. 16 1995 to Dec. 8 1995, early austral summer, on board *Southern Surveyor*. The location of stations are shown in Table 1. STCZ is supposed to run between 46°S and 48°S of this region (Nowlin and Klinck, 1986).

Water samples were collected at discrete depths within the upper 100 m of water column (Table 1). Subsamples of 1 liter were fixed with 1% glutaldehyde and a glass coverslip was added to each subsample to avoid silica dissolution. Each 1 liter water sample was settled for at least 2 days and approximately 900 mL of upper layer were carefully removed with a small tube. The remnant was settled in 50 mL settling chamber for 24 h and examined under an inverted microscope (Zeiss ICM 405) under ×400 magnification with phase contrast illumination. All phytoplankton larger than 2 μm (i. e., nanoplankton; 2-20 μm, and microphytoplankton; >20 μm) were counted and sized, and species identification were made for microphytoplankton. A minimum of 500 cells were counted for each sample to obtain more that 95% probability of encountings a taxon present at an 1% level (Shaw, 1964). Finally, the entire bottom of settling chamber was scanned at low magnifications (×100 and ×200) to enumerate the larger and less frequent phytoplankton. We found many empty diatoms from lower layers of water column and excluded from countings for accurate biomass calculation.

Table 1. The collection data of samples used in this

Station	Date (GMT)	Time (GMT)	Latitude	Longitude
TT1	21 Nov. 1995	05:56	-43 00.03	+140 53.82
TT2	21 Nov. 1995	15:44	-43 59.54	+141 49.66
TP4	30 Nov. 1995	16:39	-49 57.88	+145 45.88
TT5	27 Nov. 1995	10:15	-53 12.96	+145 28.53

+: East, -: South.

Cell volumes were calculated from the mean cell dimensions of the nearest geometric shapes, and biomass (cell carbon) were calculated using formula of Smayda (1978) for diatoms and Verity *et al.* (1992) for non-diatom phytoplankton.

RESULTS

During the early austral summer of 1995/6, a total of 90 phytoplankton species and groups were identified. They were 50 diatoms, 37 dinoflagellates, 2 silicoflagellates, and 1 prymnesiophyte. In this number we included species groups which were unable to distinguish between taxa of a given genus (e.g., *Chaetoceros* spp.) and therefore we may have underestimated the actual number of species present. Only 25 species (17 diatoms, 7 dinoflagellates, and 1 silicoflagellate) were observed from all stations. *Pseudonitzschia* spp. which occurred at all the sampled depths of all stations was the most widely distributed species in this area. Diatoms such as *Chaetoceros peruvianus*, *C.* spp., *Corethron criophilum*, *Fragilariopsis kergulensis*, *Navicula* spp., *Nitzschia closterium*, *N.* spp., *Rhizosolenia* spp., *Thalassiothrix mediterrianea* var. *pacifica*, *Thalassiosira gravida*, and dinoflagellates such as *Exuviaella* spp., *Gymnodinium* spp., *Oxytoxum variable*, and *Protoperidinium antarcticum* also occurred from all the stations but missed from several sampled depths. The predominance of these species appears to be typical in many regions of the Southern Ocean (Heywood and Whitacker, 1984; El-Sayed and Fryxell, 1993) although other species may dominate under different conditions (Knox, 1994). As rare microphytoplankton species, 7 species of diatoms (*Chaetoceros pelagicus*, *Dactyliosolen antarcticus*, *Nitzschia bicapitata*, *Planktoniella sol*, *Pseudoeunotia doliolus*, *Rhizosolenia stolterfothii*, *Tropidoneis antarctica*) and 2 species of dinoflagellates (*Ceratium pentagonum*, *Dinophysis antarcticum*) were found only from 1 to 3 sampled depths. The most diverse phytoplankton flora was observed at station TT2 with 57 species (42 diatoms, 13 dinoflagellates, 1 silicoflagellate, and 1 prymnesiophyte), and the least at station TP5 with 51 species (34 diatoms, 15 dinoflagellates, 2 silicoflagellates). Total species numbers between south and north of the STCZ were nearly same. Only the species number of diatoms decreased slightly from south of the STCZ while dinoflagellates decreased slightly from north of the STCZ. At the north of the STCZ, 46 diatoms, 24 dinoflagellates, 2 silicoflagellates and 1 prymnesiophyte were observed, and 42 diatoms, 26 dinoflagellates, 2 silicoflagellates and 1 prymnesiophyte from south of the STCZ. Species composition changed across the STCZ. Phytoplankton species such as *Azpeitia africanus*, *Chaetoceros convolutus*, *Nitzschia bicapitata* and *Planktoniella sol* were only found from north of the STCZ and *Chaetoceros bulbosus*, *C. pelagicus*, *Eucampia antarctica*, *Rhizosolenia stolterfothii*, *Tropidoneis antarctica*, *Ceratium pentagonum*, *Dinophysis antarcticum*, and *Oxytoxum caudatum* from south of the STCZ.

In vertical distribution, the most diverse phytoplankton flora were observed at 40 m depth with 70 species from north of the STCZ and at 80 m depth with 64 species from south of the STCZ.

The highest cell numbers of phytoplankton were observed at 40 m depth of TT1 (4×10^5 cells/L), and followed by 20 m depth of TT1 (2.5×10^5 cells/L), and the lowest from 80 m depth of TT2 (1.7×10^4 cells/L) (Fig. 1). Station TT1 which is adjacent to Australia and Tasmania Island showed high cell numbers both nanophytoplankton and microphytoplankton. At all stations, nanophytoplankton was the major contributer to the total cell number and the distribution pattern of total phytoplankton was dependent to nanophytoplankton. In TT1, nanophytoplankton accounted more than 75% of total cell numbers of phytoplankton. However, cell numbers of microphytoplankton from depths of 20, 40, and 80 m in station TP5 were as high as nanophytoplankton.

Diatoms were the most important component of the microphytoplankton and they accounted 44.2-93.5% of microphytoplankton and 15.8-51.8% of total phytoplankton cell number. Five species or species groups of diatoms (*Chaetoceros* spp., *Nitzschia closterium*, *N.* spp., *Fragilariopsis kergulensis*, *Pseudonitzschia* spp.) accounted for more than 50% of total cell number of diatoms (Fig. 2). However, dominant diatom differed across the STCZ. From north of the STCZ, *Pseudonitzschia* spp. predominated other diatoms and *Nitzschia closterium* from TP4, and the subantaritic species *Fragilariopsis kergulensis* from TP5.

Dinoflagellates occurred less frequently than diatoms. They never exceeded 20% of total cell numbers of phytoplankton (Fig. 1). However, dinoflagellates accounted around 50% of microphytoplankton at station TT1. *Exuviaella* spp., *Gymnodinium* spp.,

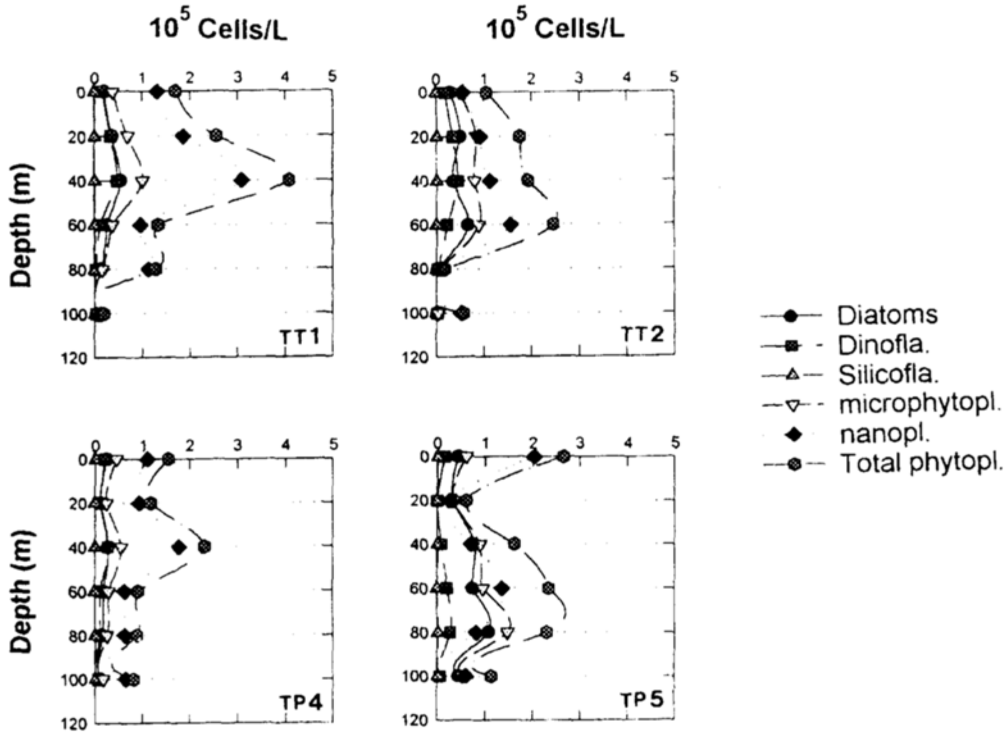

Fig. 1. Vertical distribution of the phytoplankton cell numbers from each station.

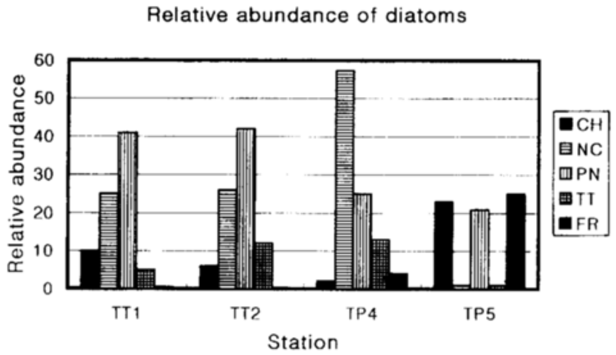

Fig. 2. Relative abundance (%) of major diatoms from each station. CH=*Chaetoceros* spp.; NC=*Nitzschia closterium*; PN=*Pseudonitzschia* spp.; TT=*Thalassiothrix mediterrianea* var. *pacifica*; FR=*Fragilariopsis kergulensis*.

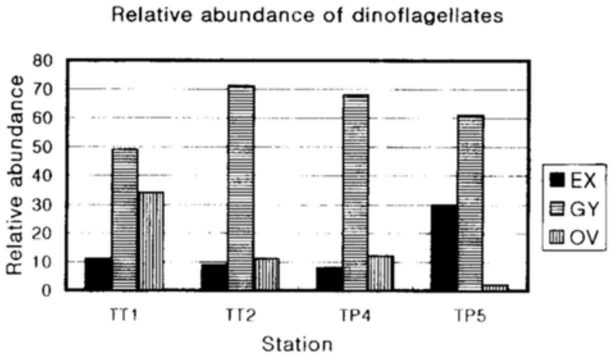

Fig. 3. Relative abundance (%) of major dinoflagellates from each station. EX=*Exuviaella* spp.; GY=*Gymnodinium* spp.; OV=*Oxytoxum variable*.

and *Oxytoxum variable* were major dinoflagellates. They accounted more than 90% of total dinoflagellates (Fig. 3). *Gymnodinium* spp. predominated both north and south of the STCZ and *Oxytoxum variable* from north of the STCZ and *Exuviaella* spp. from south of the STCZ were second dominant species.

Other phytoplanktons such as silicoflagellates, prymnesiophytes, and coccolithophorids were observed less than 0.5% of total phytoplankton cell numbers throughout the stations (Fig. 1). However, many coccolithophorids were found from samples collected during this cruise for cell cycle analysis. Therefore, coccolithophorids are considered as one of the common phytoplankton group in this area.

The vertical distribution of the phytoplankton cell number showed a moderately strong sub-surface maximum. The maximum cell numbers of phytoplankton were observed in the upper 60 m layer. The vertical profiles of diatoms and nanoplankton showed similar pattern of total phytoplankton and they composed major portion of total cell numbers. Dinoflagellates, silicoflagellates and prymnesiophytes, however, showed no clear difference in vertical distribution. They occurred fairly constant numbers from all depths of all stations. From the south of the STCZ, vertical profile of cell numbers showed 2 peaks by abrupt decrease at 20 m depth. The cell number decreased below 80 m depth except TP5 where cell numbers of 80 m depth exceeded upper layer.

Cell numbers of each species also changed across the STCZ. *Pseudonitzschia* spp. showed high abundance at TP5 station and *Nitzschia closterium* occurred highly at TT2. From station TP5, *Fragilariopsis kergulensis* occurred highly. *Gymnodinium* spp. and *Oxytoxum variable* showed high abundance from all stations, but less than the cell numbers of dominant diatoms. Other dinoflagellates, such as *Exuviaella* spp. and *Protoperidinium antarcticum* occurred moderately from several stations.

Vertical profiles of biomass of phytoplankton showed similar pattern with cell number profiles (Fig. 4). However, the biomass profiles of total phytoplankton followed those of microphytoplankton. Maximum biomass was observed at 40 m depth of TT1 with 22 μg C/L. Nanophytoplankton which dominated diatoms and dinoflagellates in cell numbers showed less biomass except 60 m depth of TT1 where nanophytoplankton occupied more than 50% of total biomass. The biomass of nanophytoplankton never exceeded 20% of total phytoplankton biomass from south of the STCZ. Biomass distribution of each taxonomic group also changed across the STCZ and between TP4 and TP5. From north of the STCZ, diatoms and dinoflagellates increased from surface to 40 m depth and decreased from 40 m to 100 m depth. From south of the STCZ, diatoms and dinoflagellates decreased at 20 m depth and constant level below 60 m depth. At TP5, biomass of dinoflagellates dominated other groups. Biomass of each species also changed across the STCZ. From north of the STCZ, *Thalassiosira gravida* and *Protoperidinium* spp. were dominant groups, and *Thalassiosira gravida* and *Protoperidinium* spp. at TP4, and *Tropidoneis antarcticum* and *Gymnodinium* spp. at TP5.

However, the profiles of each taxonomic group showed different pattern from cell number profiles, because some species, such as *Tropidoneis antarcticum*, *Protoperidinium antarcticum*, and several *Rhizosolenia species*, though occurred not high abundance, showed high biomass owing to their

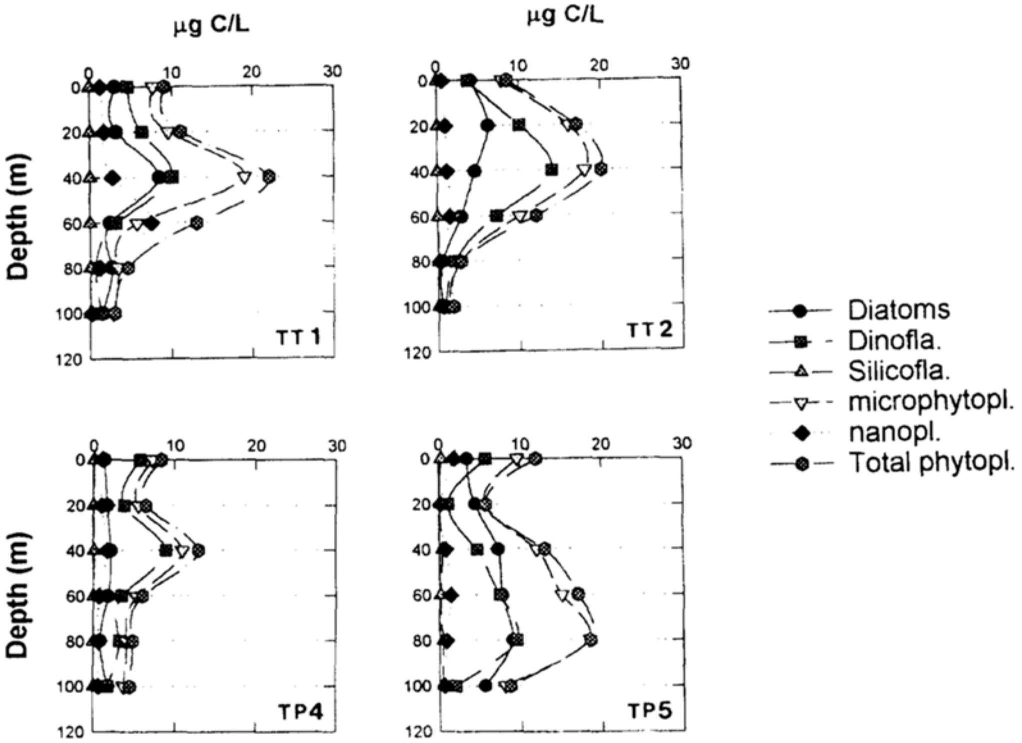

Fig. 4. Vertical distribution of the phytoplankton biomass from each station.

high unit carbon contents (Smayda, 1978). At TP4, all phytoplankton groups showed low biomass and total biomass showed lowest level among the stations. The vertical distribution of phytoplankton biomass showed similar pattern with that of cell numbers. However, the proportion of each taxonomic group differed from cell number profiles. The vertical distribution of biomass showed moderately strong subsurface maximum. Like cell number profiles, maximum biomass observed from upper 60 m depth except TP5 where maximum biomass were observed from 60 and 80 m depths.

Five groups of diatoms, *Chaetoceros* spp., *Pseudonitzschia* spp., *Rhizosolenia* spp., *Thalassiosira gravida*, and *Tropidoneis antarctica* occupied more than 50% of total diatom biomass (Fig. 5). *Thalassiosira gravida* showed large relative biomass from north of the STCZ and *Chaetoceros* spp. at TP4 and *Tropidoneis* from TP5. *Chaetoceros* spp. showed high relative biomass from south of the STCZ.

The biomass of dinoflagellates was determined by *Exuviaella* spp., *Gymnodinium* spp., and *Protoperidinium* spp. These three species occupied more than 80% of total biomass of dinoflagellates (Fig. 6). Their dominance varied from station to station. *Exuviaella* spp. showed maximum relative biomass from TT1, *Protoperidinium* spp. from TT2 and TP4, and *Gymnodinium* spp. from TP5.

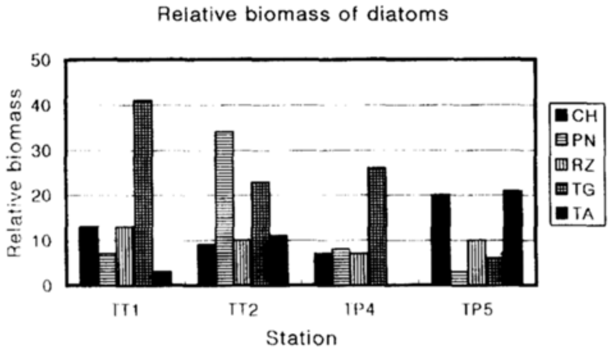

Fig. 5. Relative biomass (%) of major diatoms from each station. CH=*Chaetoceros* spp.; PN=*Pseudonitzschia* spp.; RZ=*Rhizosolenia* spp.; TG=*Thalassiosira gravida*; TA=*Tropidoneis antarctica*.

DISCUSSION

The horizontal and vertical distribution of species number, cell number, and biomass of phytoplankton from our stations showed the transitional pattern across the STCZ and 50-53°S (supposed antarctic convergence zone) where physicochemical charact-

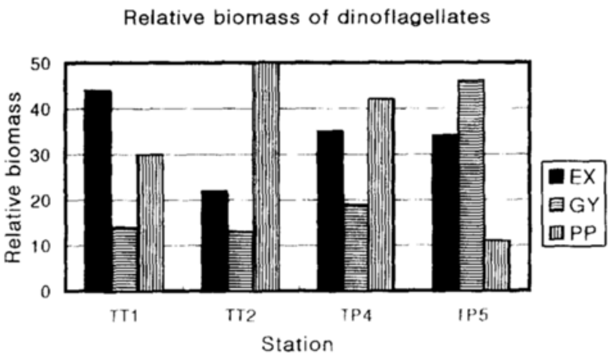

Fig. 6. Relative biomass (%) of major dinoflagellates from each station. EX=*Exuviaella* spp.; GY=*Gymnodinium* spp.; PP=*Protoperidinium* spp.

ers of water mass changed (Nowlin and Klinck, 1987; El-Sayed and Fryxell, 1993). The distribution of phytoplankton in the Southern Ocean is known to be implicated with the availability of micronutrients (Martin *et al.*, 1990), elemental ratios (Sommer and Stabel, 1986), light (Jacque, 1983; El-Sayed, 1988a), temperature (Saijo and Kawashima, 1964; Neori and Holm-Hansen, 1982), water column stability (Sverdrup, 1953; El-Sayed and Fryxell, 1993), and biological factors (Uribe, 1982; Weber and El-Sayed, 1985; El-Sayed and Fryxell, 1993). The different phytoplankton communities of this study area also seems to be implicated with above factors, which change across the fronts of this area (El-Sayed and Fryxell, 1993).

The maximum cell number and biomass from TT1 seems to be resulted from the influence of adjacent continent, Australia. The localized high productivity and biomass are common in the vicinity of oceanic islands (Grindley and David, 1985; Le Jehan and Trequer, 1985; Perissinotto *et al.*, 1992) by the presence of dissolved iron (Martin, 1990; Martin *et al.*, 1990), input of nutrients from depth as a result of turbulence around the island (Simpson *et al.*, 1982), and turbulence-induced variations of light regime (El-Sayed and Fryxell, 1993). Though the continent seemed to influence the cell numbers of phytoplankton from this study area, no continent originated phytoplankton was observed from our samples.

The species richness of the phytoplankton in this area was low compared to over 100 species of diatoms, some 60 species of dinoflagellates, and a few species of other algal classes for microphytoplankton flora of Antarctic waters (Heywood and Whitaker, 1984; Knox, 1994). Species composition of each station varied both diatoms and dinoflagellates. Especially, the dinoflagellate flora showed drastic differences between stations. Only 7 species out of 36 total dinoflagellates were commonly observed from all the stations. However, 32 diatoms and 11 dinoflagellates were commonly observed from north of the STCZ and 28 diatoms and 10 dinoflagellates from south of the STCZ. Therefore, we can conclude that the similarity of species composition of intra-frontal station is higher than inter-frontal station.

The dominance of diatoms over dinoflagellates from our stations also seems to be due to the lack of krill grazing (Kopczynska, 1990). Major grazers from this study area were tintinnids and aloricate cilliates which appeared around 3.0×10^2-2.5×10^3 cells/L (unpublished data). The grazers also changed in species and number across the fronts.

Phaeocystis sp. is generally considered an important summer bloom species in the Southern Ocean (Kang and Fryxell, 1993). However, this was not the case in this investigation, during which diatoms were far more important numerically. Knox (1990) and Andreoli (1995) also found the diatom dominance in the early summer from the Southern Ocean.

Nanophytoplankton which often dominate the Antarctic phytoplankton (Bröckel, 1981; Hosaka and Nemoto, 1986; Weber and El-Sayed, 1987; Hewes *et al.*, 1990; Knox, 1994) was not so high in this study (Figs. 1 and 4). Low proportions of cell numbers and biomass of the nanophytoplankton from this research were uncertain, because the percentage of nanophytoplankton was too low compared to other data from the southern ocean: 69-85% (Fay, 1973), 52-72% (Weber and El-Sayed, 1985), and 66% as the average of several studies for widely distributed localities (Knox, 1994). The nanophytoplankton was hitherto mainly considered to be small diatoms (5 to 10 μm), prymnesiophytes, cryptomonads and other green flagellates (Smetacek *et al.*, 1990; Buma *et al.*, 1992; El-Sayed and Fryxell, 1993; Knox, 1994) and it was true from our samples. As the nanophytoplankton of this study area, small diatoms, chlorophytes, chrysophytes and dinoflagellates were commonly observed. Though nanophytoplankton was the most important group in cell number, the less abundant medium-sized, and occasionally the large species can be dominated from Pacific region of the Southern Ocean (Hasle, 1969) and we found the same results in this study area (Fig. 4).

This research confirmed the predominance of colonial and chainforming phytoplankton species which commonly observed from many regions of the Southern Ocean (Heywood and Priddle, 1987; Priddle, 1990; Knox, 1994). However, the species composition differed from each studied region (Heywood and Priddle, 1987; Priddle, 1990; Knox, 1994; Andreoli *et al.*, 1995). The chainforming diatoms seem to have benefits of the protection against small grazers and minimizing sinking (El-Sayed and Fryxell, 1993). Gelatinous colonies of the small *Thalassiosira gravida* was commonly found as more than 40 celled-chain form from station TP5, and with that form they dominated other diatoms at upper 40 m depth.

Nitzschia bicapitata, known as a cosmopolitan species (Hasle, 1976), which predominated both the Pacific (Lee and Fryxell, 1996) and Indian (Range *et al.*, 1994) equatorial Oceans, was found with low cell numbers in TT1 and TT2, and *Pseudoeunotia doliolus*, warm water species (Hasle, 1976), commonly observed from those oceans, encountered only in TT1 (i.e., north of the STCZ). Other warm water species were absent from our sampled staitons. This result means that there is a water mass barrier between the equatorial and the Southern Pacific Ocean and this barrier could be a barrier to phytoplankton distribution.

Phytoplankton cell numbers and biomass can be changed according to the sampling time of a day (Priddle, 1990). However, we could not find any difference in the horizontal and vertical distribution of phytoplankton depending on sampling time of a day.

The Southern Ocean is known to have higher (80-85%) endemism of the phytoplankton than any other oceanic region (Knox, 1994) and we found several endemic species of Antarctic water (Heywood and Whitaker, 1984). However, the genus *Ceratium* which is known to be absent from south of the Antarctic convergence (Kopczynska *et al.*, 1986; Knox, 1994) was observed from all stations (*Ceratium lineatum*) including TP5 which is supposed to lie south of the Antarctic convergence.

In general, the vertical distribution of phytoplakton biomass of the Southern Ocean also exhibits subsurface (50-70 m depths) maxima (El-Sayed and Fryxell, 1993) and our samples also showed moderately strong subsurface maxima at 20 to 60 m depths (Figs. 1 and 4).

Pakhomov and McQuaid (1996) found the importance of the STCZ as a strong biogeographical border to the distribution of warmer water zooplankton species, and clear species shifting of phytoplankton community was also observed from this study (Figs. 2 and 3).

The results obtained from this study are suggestive that the frontal systems of the Southern Ocean can act as the circumpolar biological borders to the distribution of phytoplankton community. Temperature and salinity are the principle factors controlling distribution of marine phytoplakton (Burckle, 1978) and the fronts are the transitional zone of temperature and salinity. Thefore, the phytoplankton community transition across the STCZ of this area also seems to be resulted from the difference of these factors. However, more frequent and sufficient sampling can reveal the biological importance of the STCZ and factors controlling the phytoplankton distribution.

LITERATURE CITED

Allanson, B.R., R.C. Hart and J.R.E. Lutjeharms. 1981. Obeservations of the nutrients, chlorophyll and primary production of the Southern Ocean south of Africa. *S. Afr. J. Antarct. Res.* **10**: 3-14.

Andreoli, C., C. Tolomio, I. Moro, M. Radice, E. Moschin and S. Bellato. 1995. Diatoms and dinoflagellates in Terra Nova Bay (Ross Sea-Antarctica) during austral summer 1990. *Polar Biol.* **15**: 465-475.

Andrews, K.J.H. 1966. The distribution and life-history of Calanoides acutus (Giesbrecht). *Discovery Reports* **34**: 117-162.

Atkinson, A. and P. Ward. 1988. Summer-winter differences in copepod distribution around South Georgia. *Hydrobiologia*, **167/168**: 325-334.

Baker, A.C. 1959. The distribution and life history of Euphausia tricantha Holt and Tattersall. *Discovery Reports* **29**: 309-340.

Bröckel, K. 1981. The importance of nanoplankton within the pelagic Antarctic ecosystem. *Kiel Meeresforsch [special issue]* **5**: 61-67.

Burckle, L.H. 1978. Marine diatoms. *In* Introduction to Marine Micropaleontology B.V. Haq and A. Boersma (eds.). Elsevier, New York, pp. 245-266.

Buma, A.G.J., W.W.C. Gieskes and H.A. Thomsen. 1992. Abundance of Cryptophyceae and chlorophyll b containing organisms in the Weddell Sea Scotia Confluence area in the spring of 1988. *Polar Biol.* **12**: 45-52.

Deacon, G.E.R. 1982. Physical and biological zonation in the Southern Ocean. *Deep-Sea Res.* **29**: 1-15.

Deacon, G.E.R. 1984. The Antarctic Circumpolar Ocean. Cambridge University Press, Cambridge, pp. 259.

El-Sayed, S.Z. 1968a. On the productivity of the southwest Atlantic Ocean and the waters west of the Antarctic Peninsula. *In* Biology of the Antarctic Seas III. Antarctic Research Series 11. W. Schmitt and G. Llano (eds.). American Geophysical Union, Washington, D.C. pp. 15-47.

El-Sayed, S.Z. 1968b. Primary productivity of the Antarctic and sub-Antarctic. *In* Primary Productivity and Benthic Marine Algae of the Antarctic and sub-Antarctic. Antarctic Map Folio Series, folio 10. V.C. Bushnell (ed.). American Geographical Society. New York. pp. 1-6.

El-Sayed, S.Z. 1970a. On the productivity of the Southern Ocean. *In* Antarctic Ecology, Vol. 1. M.W. Holdgate (ed.). Academy Press, London, pp. 119-135.

El-Sayed, S.Z. 1970b. Phytoplankton production in the South Pacific sector of Antarctica. *In* Scientific Exploration of the South Pacific., W.S. Worster (ed.). National Academy of Science. Washington, DC, pp. 193-210.

El-Sayed, S.Z. 1978. Primary productivity and estimates of potential yields on the Southern Ocean. *In* Polar Research. To the Present and the Future. M.A. Mcwhinnie (ed.). AAAS Selected Symposia 7, pp. 141-160.

El-Sayed, S.Z. 1985. Plankton of the Antarctic seas. *In* Key Environments Antarctica. W.N. Bonner and D.W. H. Walton (eds.). Pergamon Press, Oxford, pp. 135-153.

El-Sayed, S.Z. 1987. Biological productivity of the Antarctic waters: present paradoxes and emerging paradigms. *In* Antarctic Aquatic Biology. S.Z. El-Sayed and A.P. Toma (eds.). BIOASS Scientific Series, 7. SCAR, Cambridge, pp. 1-22.

El-Sayed, S.Z. 1988a. Seasonal and interannual variabilities in Antarctic phytoplankton with reference to krill distribution. *In* Antarctic Ocean and Resources Variability. D. Sahrhage (ed.). Springer-Verlag, Berlin & Heidelberg, pp. 101-119.

El-Sayed, S.Z. 1988b. Productivity of the Southern Ocean: a closer look. *Comparative Biochemistry & Physiology* **90**: 489-498.

El-Sayed, S.Z. and G.A. Fryxell. 1993. Phytoplankton. *In* Antarctic Microbiology. E.I. Friedmann (ed.). Wiley-Liss, Inc., New York, pp. 65-122.

El-Sayed, S.Z. and H.R. Jitts. 1973. Phytoplankton production in the Southeastern Indian Ocean. *In* The Biology of the Indian Ocean, Vol. 3. B. Zeitshel, (ed.). Springer-Verlag, New York, pp. 131-142.

El-Sayed, S.Z. and E.F. Mandelli. 1965. Primary production and standing crop of phytoplankton in the Weddell Sea and Drake Passage. *In* Biology of the Antarctic Seas II. G. Llano (ed.). American Geophysical Society, Washington, DC, pp. 87-106.

El-Sayed, S.Z., D.A. Stockwell, H.R. Reheim, S. Taguchi and M.A. Meyer. 1979. On the productivity of the southwestern Indian Ocean. *In* CNFRA, Campagne Oceanographique MD 08/Benthos aux iles Crozet, Marion et Prince Edward: premiers resultats scientifiques. Extrait de la Publication 44 du C.N.F.R.A.P. M. Arnaud and J.C. Hureau (eds.). pp. 83-110.

El-Sayed, S.Z. and J.T. Turner. 1977. Productivity of the Antarctic and tropical-subtropical regions: a comparative study. *In* Polar oceans. M.J. Dunbar (ed.). Arctic Institute of North America, Calgary, pp. 463-504.

El-Sayed, S.Z. and L.H. Weber. 1982. Spatial and temporal variations in phytoplankton biomass and primary productivity in the Southwest Atlantic and Soctia Sea. *Polar Biol.* **1**: 83-90.

El-Sayed, S.Z. and L.H. Weber. 1986. Size fractionation of Atlantic phytoplankton. *Antarctic Journal of the United States* **19**: 141-143.

Fay, R.R. 1973. Significance of nanoplankton in primary production of the Ross Sea, Antarctica, during the 1972 austral summer. PhD thesis, Texas A&M University, College Station, Texas. 184 pp.

Froneman, P.W., C.D. McQuaid and R. Perissinotto. 1995. Biogeographic structure of the microphytoplankton assemblages of the south Atlantic and Southern Ocean during austral summer. *J. Plankton Res.* **17**: 1791-1802.

Froneman, P.W., R. Perissinotto, C.D. McQuaid and R. K. Laubscher. 1995. Summer distribution of netphytoplankton in the Atlantic sector of the Southern Ocean. *Polar Biol.* **15**: 77-84.

Fryxell, G.A. and G.R. Hasle. 1979. The genus *Thalassiosira*: *T. trifulta* sp. nov. and other species with tricolumnar support on strutted processes. *Beihefte zur Nova Hedwigia* **64**: 13-32.

Fryxell, G.A. and C.A. Kendrick. 1988. Austral spring microalgae across the Weddell Sea ice edge: spatial relationships found along northward transect during AMERIEZ 83. *Deep-Sea Res.* **35**: 1-20.

Grindley, J.R. and P. David. 1985. Nutrient upwellings and its effects in the lee of Marion Island. *In* Antarctic nutrient cycles and food webs. W.R. Siegfried, P.R. Condy and R.M. Laws (eds.). Springer-Verlag, Berlin, Heidelberg and New York. pp. 42-60.

Hart, T.J. 1934. On the phytoplankton of the southwest Atlantic and the Bellingshausen Sea. *Discovery Reports* **16**: 413-446.

Hart, T.J. 1942. Phytoplankton periodicity in Antarctic surface waters. *Discovery Reports* **21**: 261-356.

Hasle, G.R. 1969. Phytoplankton and hydrography of the Pacific part of the Antarctic Ocean. *Nature* (London) **177**: 616-617.

Hasle, G.R. 1976. The biogeography of marine planktonic diatoms. *Deep-Sea Res.* **23**: 319-338.

Hempel, G. 1985. On the biology of polar seas, particularly the Southern Ocean. *In* Marine biology of polar regions and effects of stress on marine organisms. J.S. Gray and M.E. Christiansen (eds.). Wiley, Chichester, pp. 3-33.

Hews C.D., E. Sakshaug, F.M.H. Reid and O. Holm-Hansen. 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.

Heywood, R.B. and J. Priddle. 1987. Retention of phytoplankton by an eddy. *Continental Shelf Research* **7**: 937-955.

Heywood, R.B. and T.M. Whitaker. 1984. The Antarctic marine flora. *In* Antarctic Ecology, Vol. 2, R.M. Laws (ed.). Academic Press, London, pp. 373-419.

Hosaka, N. and T. Nemoto. 1986. Size structure of phytoplankton carbon and primary production in the Southern Ocean south of Australia during the summer of 1983-1984. *Memoirs National Institute of Polar Research, Special Issue* **40**: 15-24.

Jaques, G. 1983. Some ecophysiological aspects of the Antarctic phytoplankton. *Polar Biol.* **11**: 315-328.

Jaques G. and M. Fukuchi. 1994. Phytoplankton of the Indian Antarctic Ocean. *In* Southern Ocean Ecology: the Biomass Perspective. S.E. El-Sayed (ed.). Cambridge University Press, London, pp. 63-78.

Kang, S.H. and G.A. Fryxell. 1993. Phytoplankton in the Weddell Sea, Antarctica: composition, abundance and distribution in water-column assemblages of the marginal ice-edge zone during austral autumn. *Mar. Biol.* **116**: 335-348.

Knox, G.A. 1970. Antarctic marine ecosystems. *In* Antarctic Ecology, Vol. 1. M.W. Holdgate (ed.). Academic Press, London, pp. 69-96.

Knox, G.A. 1990. Primary production and comsumption in McMurdo Sound, Antarctica. *In* Antarctic ecosystems. Ecological change and conservation. K.R. Kerry and G. Hempel (eds.). Springer, Berlin, Heidelberg, New York, pp. 115-128.

Knox, G.A. 1994. The Biology of the Southern Ocean. Cambridge University Press, London, 444 pp.

Kopczynska, E.E. 1990. Dominance of microflagellates over diatoms in the Antarctic areas of deep vertical mixing and krill concentrations. *J. Plankton Res.* **14**: 1031-1054.

Kopczynska, E.E., L.H. Weber and S.Z. El-Sayed. 1986. Phytoplankton species composition and abundance in the Indian Sector of the Antarctic Ocean. *Polar Biol.* **6**: 161-169.

Lange, C.B., U.F. Treppke and G. Fischer. 1994. Seasonal diatom fluxes in the Guinea basin and their relationships to trade winds, hydrography and upwelling events. *Deep-Sea Res.* **41**: 1843-1868.

Laubscher, R.K., R. Perssinotto and C.D. McQuaid. 1993. Phytoplankton production and biomass at frontal zones in the Atlantic sector of the Southern Ocean. *Polar Biol.* **13**: 471-481.

Lee, H.Y. and G.A. Fryxell. 1996. Bicapitate Nitzschia species: abundant nanoplankton in aggregates during November-December (1992) in the equatorial Pacific. *J. Plankton Res.* **18**: 1271-1294.

le Jehan, S. and P. Treguer. 1985. The distribution of inorganic nitrogen, phosphorus, silicon and dissolved organic matter in the surface and deep waters of the Southern Ocean. *In* Antarctic Nutrient Cycles and Food Webs. W.R. Siegfried, P.R. Condy and R.M. Laws (eds.). Springer-Verlag, Berlin, pp. 22-41.

Lutjeharms, J.R.E., N.M. Walters and B.R. Allanson. 1985. Oceanic frontal systems and biological enhancement. *In* Antarctic Nutrient Cycles and Food Webs. W.R. Siegfried, P.R. Condy and R.M. Laws (eds.). Springer-Verlag, Berlin, pp. 11-21.

Martin, J.H. 1990. Glacial-interglacial CO_2 change: the iron hypothesis. *Paleoceanography* **5**: 1-13.

Martin, J.H., R.M. Gordon, S.E. Fitzwater. 1990. Iron in Antarctic waters. *Nature* **345**: 156-158.

Neori, A. and O. Holm-Hansen. 1982. Effect of temperature on rate of photosynthesis in Antarctic phytoplankton. *Polar Biol.* **1**: 33-38.

Nowlin, W.D. 1985. General circulation of the Southern Ocean: status and recommendation for research. A report by SCOR Working Group, September 1985.

Nowlin, W.D. and J.M. Klinck. 1986. The physics of the Antarctic Circumpolar Current. *Revs. Geophys.* **24**: 469-491.

Pakhomov, E.A. and C.D. McQuaid. 1996. Distribution of surface zooplankton and seabirds across the Southern Ocean. *Polar Biol.* **16**: 271-286.

Perissinotto, R., R.K. Laubscher and C.D. McQuaid. 1992. Marine productivity (enhancement) around Bouvet and the South Sandwich Islands (Southern Ocean). *Mar. Ecol. Prog. Ser.* **88**: 41-53.

Priddle, J. 1990. Antarctic planktonic ecosystem. *In* Polar Marine Diatoms. B.W. Mullins and J. Priddle (eds.). British Antarctic Survey. Natural Environment Research Council, Cambridge, pp. 25-34.

Saijo, Y. and T. Kawashima. 1964. Primary production in the Antarctic Ocean. *Journal of the Oceanographic Society of Japan* **19**: 190-196.

Sakshaug, E. and O. Holm-Hansen. 1984. Factors governing pelagic production in polar oceans. 1-18. *In* Marine Phytoplankton and Productivity. O. Holm-Hansen, L. Bolis and R. Gilles (eds.). Springer-Verlag, Berlin, pp. 1-18.

Shaw, A.B. 1964. Time in Stratigraphy. McGraw-Hill, New York, pp. 109.

Simpson, J.H., P.B. Terr, M.L. Argote-Espinoza, A. Edwards, H.J. Jones and G. Savidge. 1982. Mixing and phytoplankton growth around an island in a Stratfield sea. *Continental Shelf Research* **1**: 15-31.

Smayda, T.J. 1978. From phytoplankters to biomass. *In* Phytoplankton Manual. A. Sournia (ed.). Unesco, New York, pp. 273-279.

Smetacek, V.S., R. Scharek and E.M. Nothing. 1990. Seasonal and regional variation in the pelagial and its relationship to the life history cycle of krill. *In* Antarctic Ecosystems. Ecological Change and Conservation. K.R. Kerry and G. Hempel (eds.). Springer-Verlag, Berlin and Heidelberg, pp. 103-114.

Sommer, U. and H.H. Stabel. 1986. Near surface nutrient and phytoplankton distribution in the Drake Passage during early December. *Polar Biol.* **6**: 107-110.

Stein, M. and R.B. Heywood. 1994. Antarctic environment-physical oceanography: the Antarctic Peninsula and Southwest Atlantic region of the Southern Ocean. *In* Southern Ocean Ecology: the Biomass Perspective. S.E. El-Sayed (ed.). Cambridge University Press, London. pp. 11-24.

Sverdrup, H.U. 1953. On conditions for the vernal blooming of phytoplankton. *Journal du Conseil International pour l'Exploration de la Mer.* **18**: 287-295.

Uribe, F. 1982. Influence of the phytoplankton and primary production of the Antarctic waters in relationship with the distribution and behavior of krill. *Instituto Antartico Chileno Scientific Series* **28**: 147-163.

Verity, P.G., C.Y. Robertson, C.R. Tronzo, M.G. Andews, J.R. Nelson and M.E. Sieracki. 1992. Relationships between cell volume and the carbon and nitrogen content of marine photosynthetic nanoplankton. *Limnol. Oceanogr.* **37**: 1434-1446.

Weber, L.H. and S.Z. El-Sayed. 1985. Spatial variability of phytoplankton and the distribution and abundance of krill in the Indian sector of the Southern Ocean. *In* Antarctic Nutrient Cycles and Food Webs. W.R. Siegfried, P.R. Condy and R.M. Laws (eds.). Springer-Verlag, Berlin, pp. 284-293.

Weber, L.H. and S.Z. El-Sayed. 1987. Contribution of net-, nano- and picoplankton to the phytoplankton standing crop and primary productivity of the Southern Ocean. *J. Plankton Res.* **9**: 973-994.

Yamamoto, T. 1986. Small-scale variations in phytoplankton standing stock and productivity across the oceanic fronts in the Southern Ocean. *Memoirs National Institute of Polar Research, Special Issue* **40**: 25-41.

Received March 26, 1998
Accepted April 20, 1998