

Carbon and Nitrogen Primary Productivities in the Weddell Sea and the Bransfield Strait, Antarctica

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ABSTRACT. Carbon and nitrogen primary productivities using ¹⁴C-bicarbonate and ¹⁵N nitrate and ammonia were measured during the 7th KARP (Korea Antarctic Research Programme) cruise in the Weddell Sea and the Bransfield Strait, Antarctica. Carbon primary productivity ranged between 55.11 and 155.78 mg C m⁻² h⁻¹. The nitrogenous new productivity was between 1.105 and 4.464 μmoles N m⁻² h⁻¹, and regenerated productivity between 0.721 and 4.310 μmoles N m⁻² h⁻¹. The f-ratio, the fraction of new production from primary production, was approximately 0.65, which is the characteristics of eutrophic areas. The C:N productivity ratio ranged between 0.76 and 5.83 (mean = 2.61), significantly lower than the traditional Redfield ratio of 6.7. The low values were observed in the ice margin area. This indicates the unbalanced growth of phytoplankton between carbon and nitrogen metabolism. This imbalance could have a significant implication in the vertical flux of carbon dioxide. Other factors (e.g., the stability of water column, light condition) are plausible candidates for this unusual phenomenon of low C:N productivity ratio.

Key Words: carbon flux, C:N productivity ratio, new production

Introduction

The Antarctic Ocean is one of the HNLP (high nutrient low production) area characterized by the presence of excess nutrients (especially nitrate) in the surface water (Cullen 1991). Several factors were proposed as candidates for limiting the primary production in this area; low solar irradiance, low temperature, deep vertical mixing (Nelson and Smith 1991), and low trace metal concentration (eg., Fe; Martin *et al.* 1990a, 1990b, 1990c), and grazing by zooplankton (Frost 1991).

The Antarctic open waters are well mixed; the pycnocline and the 1% LPD (light penetration depth) are located at 80-100 m depth. Accordingly, productivity in this region is low due to low average light intensity experienced by phytoplankton popu-

lation, even though the ambient nutrient concentration in the surface mixed layer is high. In contrast, there are strong seasonal variations in productivity along the sea ice margin. In spring, this marginal ice zones (MIZ) in polar regions are places of high phytoplankton accumulation and high productivity due to the increase in vertical stability generated by the melting of ice (Figueiras *et al.* 1994 and references therein). Chlorophyll concentrations higher than 3 μg l⁻¹ were reported in MIZ during the spring bloom (Nelson and Smith 1986). There are also indications that a major fraction of primary production is passed up the food chain to large carnivores (Nelson and Smith 1986). However, there is a missing flux between the high productivity and downward vertical flux measured by sediment traps (Honjo 1990).

Objectives of this study are to investigate the mechanism of spring bloom in the Southern Ocean and to estimate primary productivity, new and

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regenerated productivities in this area. New production, which was introduced by Dugdale & Goering (1967), is equivalent to the export production (Eppley and Peterson 1979), and can sequester CO₂ from the system by converting it into organic carbon which is called the biological pump (Longhurst and Harrison 1989). Martin *et al.* (1990c) proposed a large scale iron enrichment experiment to scavenge the increasing atmospheric CO₂ by the burning of fossil fuel. However, the consequence of the large scale enrichment plan is uncertain and even controversial, and some models show results contrary to the anticipation (Banse 1990; Martin *et al.* 1990a; Joos *et al.* 1991; Peng and Broecker 1991).

Materials and Methods

The study area is located in the Weddell Sea and the Bransfield Strait near Antarctic Peninsula (Fig. 1). Samplings were conducted along 4 transects aboard the P/V Erebus January 1-12, 1994 as a part of the 7th KARP. The depth profiles of temperature, salinity, fluorescence, beam attenuation coefficient (wavelength = 665 nm, $r = 0.25$ m), and PAR (Photosynthetically Available Radiation; 400-700 nm) were collected using a Sea Bird Electronics CTD (Model #SBE 25-03) mounted with a Sea-Tech fluorometer, a transmissometer, and a scalar irradiance meter. Water samples were collected at 100, 49, 30, 15, 3.5, and 1% LPD (Light penetration depth) with 5 liter Niskin bottles attached to a Rosette sampler. Niskin bottles were modified by replacing the black rubber with silicone tubing to reduce the heavy metal toxicity. Polycarbonate bottles (250 ml or 2 liter) wrapped with perforated nickel screens (Stork Veco, Bedford, MA, USA) were used for on-deck incubation to simulate the *in situ* light intensity.

Before the start of incubation, aliquots of 10 μ Ci of ¹⁴C-NaHCO₃ were added to 250 ml polycarbonate bottles for carbon primary production measurements. To measure new and regenerated production, ¹⁵N-KNO₃ (99%) and ¹⁵N-NH₄Cl (99%; Cambridge Isotope Laboratory, Woburn, MA, USA) were inoculated to make the final concentration of 1 μ M and

0.2 μ M for nitrate and ammonia, respectively. The incubation period was 3-6 hours around the local noon. For some experiments, 24 hour incubations were also conducted to investigate the effect of long term incubations. Light intensity (in quantum irradiance) was measured and integrated using the Li-Cor S902A Quantum sensor and Li-100 Data Logger.

After the incubation, ¹⁴C primary productivity samples were filtered onto 25 mm GF/F filters and acid fumed before measuring the radioactivity (dpm) with a liquid scintillation counter (Packard Tri-Carb, Model #2550). ¹⁵N New and regenerated samples were filtered onto pre-combusted (4 hours at 450°C) 25 mm GF/F filters and stored dry at 60°C. The analysis of ¹⁵N/¹⁴N ratio and PON contents were measured with a mass spectrometer (Europa Scientific Roboprep Tracermass GC-MS) in R.C. Dugdale lab of the University of Southern California according to Owens (1988). Calculations of new and regenerated production were done according to Wilkerson & Dugdale (1987). Because nitrate is supplied mainly via vertical mixing and turbulence, this portion of nitrogen production can be classified as new production. In contrast, ammonia is mostly recycled within the upper water column and can be classified as regenerated production. Additional sources of regenerated nitrogen, e.g., urea, dissolved free amino acid, may contribute to the regenerated production. However, this portion is not included in this study.

The "f-ratio", which is the portion of new production from primary production (Eppley and Peterson 1979), was calculated using the equation,

$$f\text{-ratio} = \text{Rho}_{\text{NO}_3} / (\text{Rho}_{\text{NO}_3} + \text{Rho}_{\text{NH}_4})$$

The vertically integrated water column production was calculated down to 1% LPD. Daily rates were converted from hourly rates by multiplying (total daily radiance)/(mean hourly irradiance for the incubation period).

Results

Hydrographic features

CTD results and nutrient distributions were

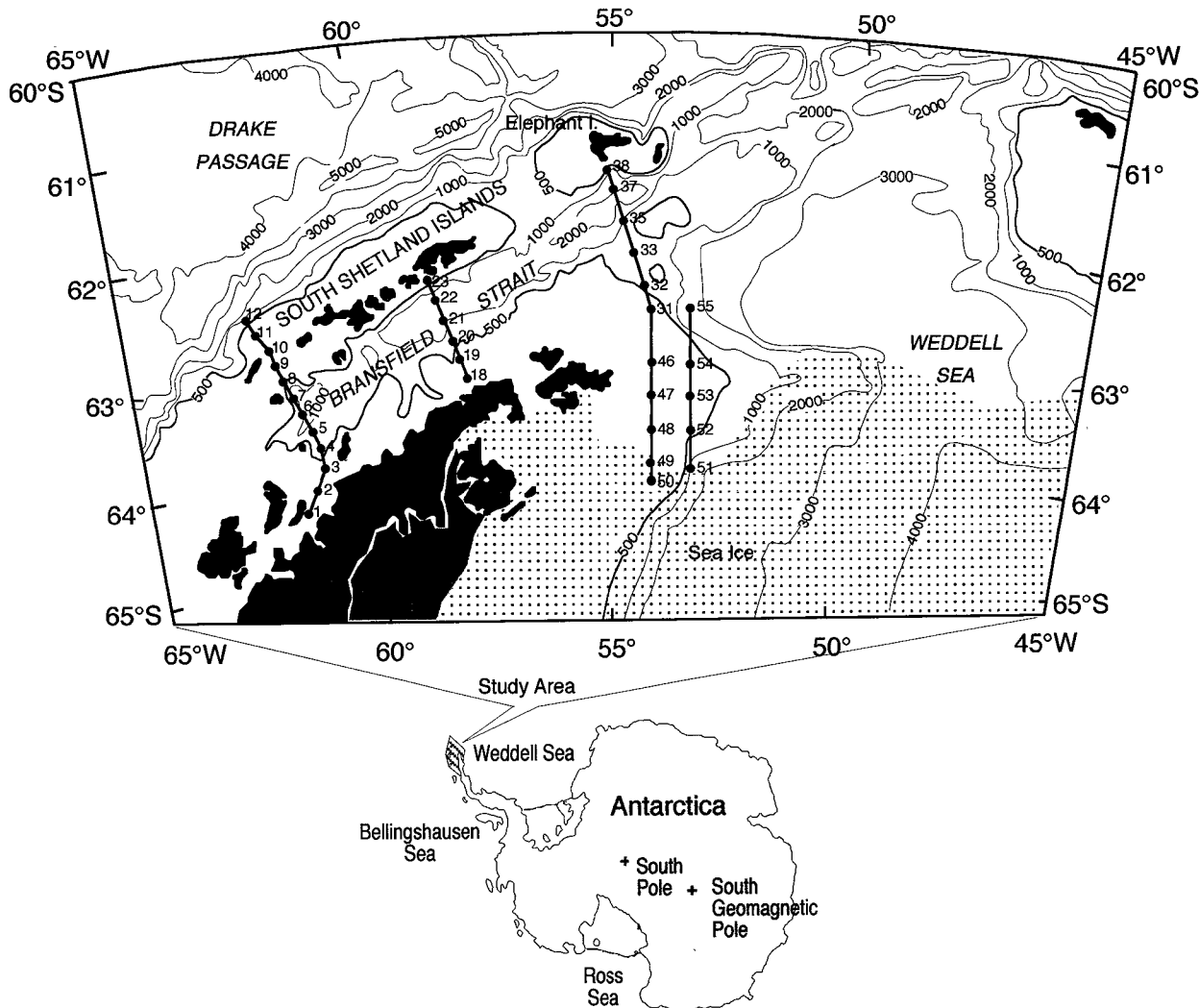


Fig. 1. Map showing the study area and sampling stations during the 7th KARP cruise in January 1994.

described elsewhere (Kang *et al.* 1995; Park and Chung 1995). The study area can be divided into two regions according to the general hydrographic features: the well mixed open ocean area and the stratified MIZ (Smith *et al.* 1988). There was a considerable difference between the two regions in phytoplankton biomass (represented as chlorophyll fluorescence) as well as the vertical structures of temperature and salinity (Kang *et al.* 1995). The MIZ showed high phytoplankton biomass and stratified (low temperature and salinity due to the meltwater) and the offshore region showed low biomass and vertically homogeneous profile of T, S.

Quantum irradiance

The hourly averaged quantum irradiance during the

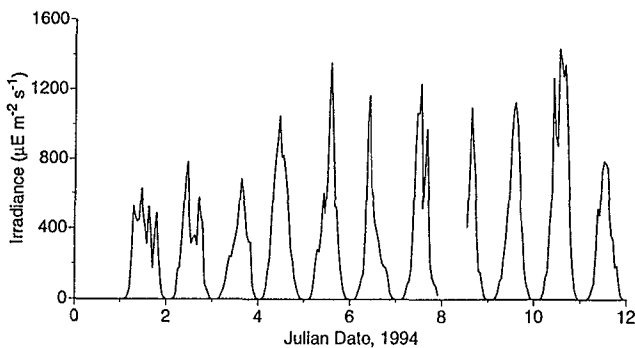
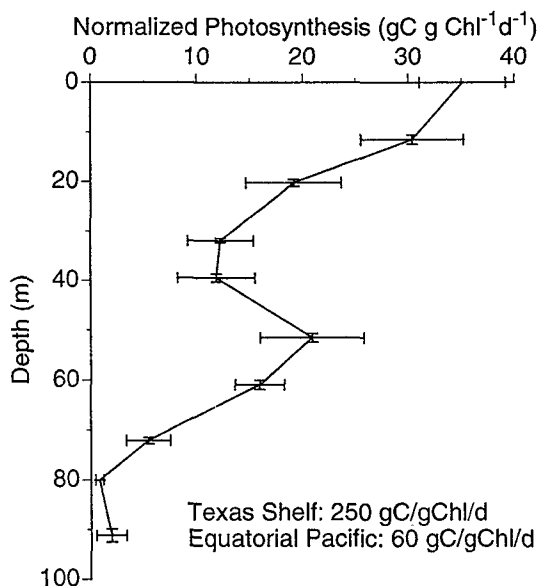
sampling period is shown in Fig. 2. The maximum irradiance during the mid-day was approximately $1400 \mu\text{moles quanta m}^{-2} \text{s}^{-1}$. The light period was longer than 18 hours. During this time of the year, light may have been sufficient to support the maximum growth of phytoplankton provided that other factors are favorable.

Primary Production

The primary productivity measured by $^{14}\text{C-NaHCO}_3$ uptake method, was as high as $8 \text{ mg C m}^{-3} \text{ h}^{-1}$. The mean values for each station were $2.5\text{--}3.3 \text{ mg C m}^{-3} \text{ h}^{-1}$ (Table 1). The depth integrated values were $55.11\text{--}155.78 \text{ mg C m}^{-2} \text{ h}^{-1}$. It was high at the stations in the MIZ of the Weddell Sea and low at offshore stations. The highest daily productivity value (3738.7 mg C

Table 1. Primary production, new and regenerated production, and C:N productivity ratio during the 7th KARP cruise

ST #	1% LPD	Hourly prod. (mg C m ⁻² h ⁻¹)	Daily prod. (mg C m ⁻² d ⁻¹)	New prod. (μmoles N m ⁻² h ⁻¹)	Reg. prod (μmoles N m ⁻² h ⁻¹)	f-ratio	C:N ratio
2	32 m	64.01	1152.2	1.171	1.118	0.51	2.33
6	75 m	56.99	648.9	3.901	2.369	0.62	0.75
10	90 m	152.73	1667.7	1.602	0.988	0.61	4.91
11	86 m	97.61	1414.8	2.470	0.850	0.74	2.44
46	20 m	110.82	1058.9	3.859	1.153	0.76	1.84
47	36 m	55.11	799.9	3.840	1.300	0.74	0.89
51	38 m	100.48	1078.1	4.464	4.310	0.50	0.95
52	38 m	76.60	2161.4	3.418	3.127	0.52	0.97
19R	80 m	113.73	1519.4	1.105	0.721	0.60	5.19
23R	60 m	155.78	3738.7	1.192	1.036	0.53	5.82

**Fig. 2.** Hourly averaged plot of solar irradiance during the 7th KARP cruise in January 1994.**Fig. 3.** Vertical profile of the average chlorophyll normalized photosynthesis (P^b) during the 7th KARP cruise in January 1994 with data from Cullen (1990) for comparison.

the north of the MIZ. However, the station of the maximum production per unit area does not coincide with the maximum production per unit volume, due to the differences in the euphotic depth.

The vertical distribution of chlorophyll normalized photosynthesis (P^b) averaged up to 35 g C g Chl⁻¹ d⁻¹ (Fig. 3). This value is significantly lower than those of other areas, such as the Texas shelf (250 g C g Chl⁻¹ d⁻¹) and the equatorial Pacific (60 g C g Chl⁻¹ d⁻¹; Cullen 1990). The reasons could be due to high chlorophyll concentration in this area (higher than 3 mg m⁻³; Fig. 4) and partly due to low average light intensity experienced by phytoplankton resulting from deep vertical mixing (Kang *et al.* 1995). The maximum P^b was observed at the surface and peaked again at around 50 m depth. The surface maximum appears to have resulted from high irradiance and relatively low chlorophyll concentration compared to 10 or 20 m (Fig. 4). The increase in P^b at 50 m depth seems to be due to low chlorophyll concentration and due to the increased nutrient concentration at that depth. However, this is the composite of different hydrographic regimes and there could be some artifacts.

Nitrogen Primary Production

Rho_{NO_3} (nitrate transport rate; $\mu\text{M h}^{-1}$) and Rho_{NH_4} (ammonia transport rate; $\mu\text{M h}^{-1}$) indicate nitrate and ammonia uptake rate per unit volume of seawater and are equivalent to new and regenerated production, respectively. V_{NO_3} (biomass specific nitrate

m⁻² d⁻¹) was observed at ST#23, which was located to

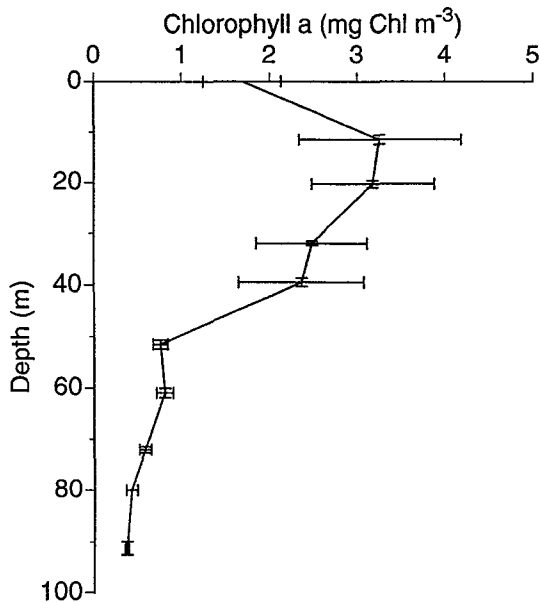


Fig. 4. Vertical profile of the average chlorophyll *a* concentration from productivity stations during the 7th KARP cruise in January 1994.

uptake rate; h^{-1}) and V_{NH_4} (biomass specific ammonia uptake rate; h^{-1}) are equivalent to the growth rate of phytoplankton based on nitrate and ammonia nutrition, respectively. Nitrogen production, measured by $^{15}N-KNO_3$ and $^{15}N-NH_4Cl$ uptake method, ranged from 1.105 to 4.464 $\mu moles N m^{-2} h^{-1}$ and from 0.721 to 4.310 $\mu moles N m^{-2} h^{-1}$ for new and regenerated production, respectively (Table 1). Nitrate and ammonia transport rate (Rho_{NO_3} and Rho_{NH_4}) versus irradiance show typical P-I curves with saturation around 50% of surface irradiance (Fig. 5). The maximum nitrate transport rate averaged from all productivity stations was 0.082 $\mu M N h^{-1}$ and was twice as high as the maximum ammonia transport rate.

f-ratio

The *f*-ratios from all of the incubations ranged between 0.51 and 0.76 (average 0.62), indicating high new production compared to regenerated production (Table 1). There was no significant difference in the *f*-ratio between the MIZ and offshore stations. The vertical distribution of *f*-ratio was very similar from surface down to 3.5% LPD (approximately 0.6; Fig. 6). It increased to 0.73 at 1% LPD, which was mostly due to the increased nitrate concentration below the thermocline. There was no sig-

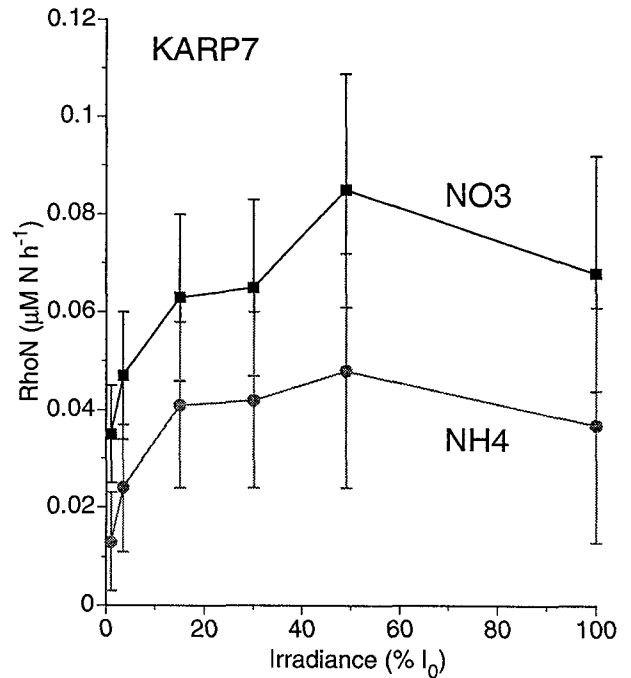


Fig. 5. Irradiance versus nitrate transport rate (Rho_{NO_3}) and ammonia transport rate (Rho_{NH_4}) during the 7th KARP cruise in January 1994.

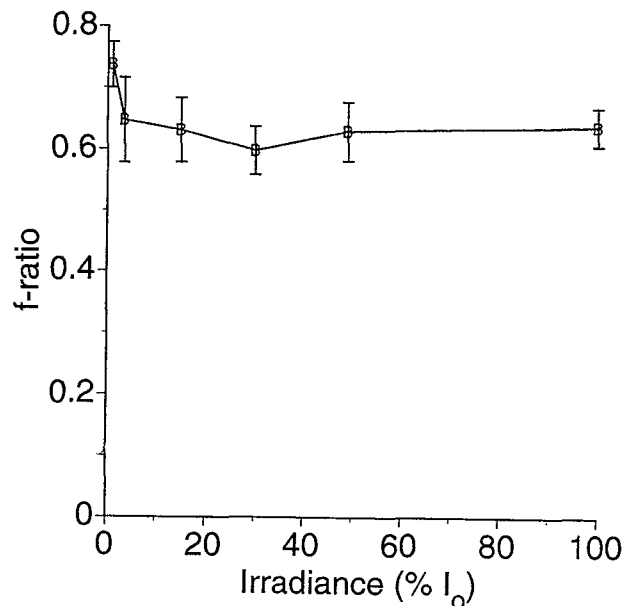


Fig. 6. Irradiance versus the *f*-ratio during the 7th KARP cruise in January 1994.

nificant difference in the *f*-ratio between the MIZ and offshore stations.

C:N Production Ratio

The *C:N* production ratios ranged between 0.76 and 5.83 (mean = 2.61) in molar terms, which is significantly lower than the traditional Redfield ratio of 6.7:1 (Table 1). These values ranged between

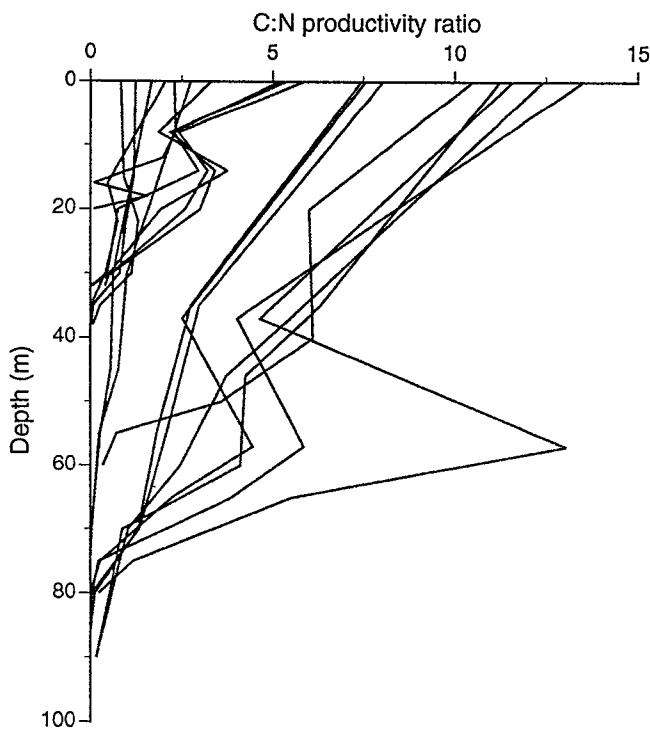


Fig. 7. Vertical profiles of the C:N productivity ratio during the 7th KARP cruise in January 1994.

extremely low (below 1) at the MIZ and relatively high (close to normal) at offshore stations. Productivity stations can be divided into two groups according to the vertical profile of the C:N productivity ratio (Fig. 7). The ratios were high at the surface and at stations with deep euphotic depths, and low at depths and stations with shallow euphotic depths.

Discussion

There were significant differences in primary production, C:N productivity ratio and the f-ratio between the ice edge zone and offshore areas. This coincides with the differences in vertical structures of temperature and salinity, which determine the density field and hence the stability of water column.

The spatial distribution of primary production indicates differences in the timing of spring bloom; low close to the MIZ and increased progressing towards the offshore as the stabilized water column ages, then declined in the offshore area as the nutri-

ent concentration decreased and the vertical mixing increased. It is also evident in the distribution of phytoplankton biomass and the similar pattern is also observed in bacterial biomass and secondary production (Kang *et al.* 1995). Wilson *et al.* (1986) concluded that the phytoplankton bloom in the receding ice edge zone in the western Ross Sea was seeded by algae released from melting ice, and that ice-edge bloom can have a substantial impact on the biogeochemical cycles and food web dynamics of the Southern Ocean.

Relatively low values of chlorophyll normalized photosynthesis (P^b) compared to other regions of the ocean could be due to the increase in mixing depth, which in combination with low ambient irradiance, decreases the average light intensity experienced by water column phytoplankton (e.g., Nelson and Smith 1991). Smith & Nelson (1990) reported average primary productivity in the Weddell Sea MIZ in spring to be $490 \text{ mg C m}^{-2} \text{ d}^{-1}$, which is at the lower end of our results.

The high f-ratio in the study area was also reported by Smith & Nelson (1990; the average f-ratio of 0.52) in this area during the austral spring. The reason for high f-ratio could be due partly to high nitrate utilization rate at high ambient nitrate concentrations and also partly to low grazing activity, because it takes time for the zooplankton biomass to build up in response to the increased production and/or biomass of phytoplankton.

The unusually low values of C:N productivity ratio, especially near the MIZ, indicates the unbalanced growth of phytoplankton. Smith & Harrison (1991) pointed out the uncoupling of C and N cycles in the surface layers of the Weddell Sea and the Ross Sea, especially at low irradiance. Treguer & Jacques (1992) speculated that the release of nitrogen-rich dissolved organic matter from the particulate pool soon after production and bacterial uptake of inorganic nitrogen in concert with dissolved organic carbon might be involved for such an imbalance. Other reasons could be the different response of carbon and nitrogen metabolism to the variation of temperature and light regimes. Contrary to the equatorial Pacific where there is an intense vertical mixing and

the uptake of nitrogenous nutrients (especially that of nitrate) is low compared to the uptake of carbon, the MIZ of the Antarctic Ocean exhibits high uptake rate of nitrogenous nutrients due to high nitrate concentration and due to the stability of water column which is favorable for the development of nitrogen utilization enzyme system (shift-up; Dugdale and Wilkerson 1992). Another possibility is the luxurious uptake of nitrate at high ambient nitrate concentration by the dominant species *Phaeocystis antarctica* (Fryxell and Kendrick 1988; Kang and Fryxell 1993), which may have a large internal storage pool of nitrogen. However, this imbalance could be temporary and spatially limited near the MIZ where the changes in hydrographic regime is highly dynamic.

In the offshore region of the southern ocean, where the productivity is low, a hypothesis for iron or other trace metal limitation has been proposed (Martin *et al.* 1990b), and some investigators tested this hypothesis, even though the experiments were not conducted *in situ* but in enclosed incubation bottles (Buma *et al.* 1991). However, this hypothesis may not be applied to the MIZ, because this area is close to the landmass and there could be plenty of trace metal input available for the phytoplankton community in the melting water. de Baar *et al.* (1995) suggest that iron may be acquired as the Antarctic Circumpolar Current crosses shallow topographic features, but the time required for diffusion of such bottom material is too long to support the observed patterns. The mystery of missing flux (Honjo 1990) needs to be investigated in future researches.

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