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Nutrient and biogenic particulate distributions, primary productivity and nitrogen uptake in the Weddell-Scotia Sea marginal ice zone during winter

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ABSTRACT

During austral winter of 1988, we determined the distributions of inorganic nutrients (nitrate, silicic acid, phosphate, nitrite and ammonium) and particulate materials (chlorophyll, biogenic silica, particulate organic carbon and particulate organic nitrogen), as well as primary productivity and rates of nutrient (NO_3^- and NH_4^+) uptake in the upper 150 m of the marginal ice zone of the Weddell-Scotia Sea. Nutrient concentrations were high and particulate matter levels were low throughout the study area, but occasionally nutrient minima and particulate maxima occurred near the ice edge associated with warm-core eddies. Chlorophyll concentrations and primary productivity averaged 0.12 $\mu g\,l^{-1}$ and 32 mg C $m^{-2}\,d^{-1}$, respectively. Surface growth rates calculated from carbon uptake and total particulate organic carbon were very low (ca. 0.03 doublings d^{-1}), but living phytoplankton only comprised about 10% of the POC in the surface layer. Thus, mean phytoplankton growth rates appear to have been between 0.1 and 0.2 doublings d^{-1}. Although nitrate was about 40 times as abundant as ammonium, ammonium was consistently the preferred substrate of the plankton assemblages, accounting for over half of the nitrogen taken up. Paired samples from the same depth and vertically integrated *f*-ratios averaged 0.43. Both ammonium and nitrate were removed at rates that individually exceeded the apparent nitrogen demand of the phytoplankton, implying significant heterotrophic uptake of inorganic nitrogen.

1. Introduction

Seasonality at high latitudes is pronounced, with large variations in ice cover, vertical stability and incident irradiance. At its maximum extent sea ice covers 20 × 10^6 km², with advances of over 1500 km in certain areas (Zwally *et al.,* 1983). This marked seasonality has a strong influence on marine food webs, with organisms at many trophic levels exhibiting large variations in abundance and productivity. Life history strategies of polar organisms often involve some sort of resting stage (e.g.,

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phytoplankton encystment, zooplankton diapause) if they overwinter, and many larger organisms such as birds and marine mammals migrate to less harsh climates. Hence, during winter many heterotrophs enter a resting stage, depend on stored internal reserves, consume alternate food sources or migrate. In general, biological activity in polar oceans is thought to be at its lowest in winter, and primary productivity is considered to be negligble because of low incident irradiance levels, extensive ice cover and deep vertical mixing. However, there is little quantitative information available on the seasonal dynamics of polar oceans, and winter data are particularly lacking.

Marginal ice zones have been identified repeatedly as areas of elevated biomass and productivity, especially when compared with open water regions, which are beyond the effects of ice melt, or those covered by ice (e.g., Ainley *et al.,* 1986; Smith, 1987). However, ice-edge phytoplankton blooms have been thought to be associated only with seasonally retreating ice edges, when meltwater input is greatest and irradiance is near maximal. Recent results from the marginal ice zone of the Weddell Sea suggest that there are significant accumulations of phytoplankton biomass when the ice edge is nearly stationary in early autumn (Comiso *et al.,* 1990). Because of the likelihood of ice ablation at all times of the year (Muench *et al.,* 1990), it is possible that many organisms, functioning at a variety of trophic levels, are concentrated in the marginal ice zone throughout much of the year.

Vertical stability, which defines the time- and depth-integrated irradiance available for phytoplankton in open water, has repeatedly been implicated as the most important factor in the initiation and maintenance of ice-edge phytoplankton blooms in high latitude systems. Large accumulations of phytoplankton have been observed at the ice edges of the Bering Sea (Alexander and Niebauer, 1981), the Ross Sea (Smith and Nelson, 1985), the Greenland Sea (Smith *et al.,* 1987) and the Weddell-Scotia Seas (Nelson *et al.,* 1987, 1989). The major nutrients rarely appear to limit phytoplankton standing stocks in the Southern Ocean, although depletion of phosphate and nitrate to analytical detection limits has been observed in an ice-edge bloom in the Ross Sea (Nelson and Smith, 1986). Mitchell and Holm-Hansen (1991) argue that substantial nutrient fluxes are necessary to support "massive" (more than 10 μg chlorophyll *a* 1^{-1}) blooms and that biomass accumulation is inversely proportional to mixed layer depth. The factors responsible for the decline of ice-edge phytoplankton blooms are not well known, but include nutrient depletion (Niebauer and Alexander, 1985), grazing, sinking (Smetacek, 1985) and dispersal by vertical mixing (Smith and Nelson, 1985). A model based upon mixing depth, pigment-specific light attenuation and *in situ* photosynthetic parameters suggests that specific loss rates may be as high as 0.30–0.35 d^{-1} (Mitchell and Holm-Hansen, 1991), which implies that grazing and other loss processes may be important controls of phytoplankton in the Antarctic.

Ice-edge blooms appear to contribute about half of the annual primary productiv-

ity in the Southern Ocean. Nutrient depletion rates during summer led Jennings *et al.* (1984) to conclude that primary productivity in the Weddell Sea during spring and summer averaged at least 0.2 to 0.4 g C m^{-2} d^{-1}, or up to 4 times higher than estimates derived from ^{14}C-tracer measurements. Elevated rates of biogenic silica production within an ice-edge bloom and its accumulation in sediments also suggest that such blooms are quantitatively important in the Ross Sea (Nelson and Smith, 1986). Estimates of primary productivity indicate that about 40% of annual primary production of the Southern Ocean as a whole may be derived from ice-edge blooms (Smith and Nelson, 1986), and new production at the ice edge of the Weddell-Scotia Sea is at least 49 g C m^{-2} y^{-1} (Smith and Nelson, 1990). All of these estimates are based upon assumptions concerning the bloom's duration and intensity. Nonetheless, all of the data indicate that ice-edge productivity is high compared with that in pelagic polar systems, and that these blooms contribute a large portion of the total annual productivity of the Southern Ocean.

In order to understand the seasonally integrated importance of ice-edge blooms and the seasonal dynamics of the marginal ice zone of the Weddell-Scotia Sea region, we conducted a cruise to the ice edge during austral winter. The timing of the cruise was such that incident irradiance was low, but not zero, at the ice edge, and the ice was near its maximal extent. The objectives of this study were: (1) to determine the distributions of nutrients and biogenic particulate material, (2) to examine the important factors influencing the interactions between the nutrient fields and accumulations of phytoplankton, and (3) to measure growth, production and nutrient assimilation rates of phytoplankton populations. By comparing our winter data with previously available data from other seasons, we sought to define the seasonal patterns of ice-edge phytoplankton blooms in the Weddell-Scotia Sea and their contribution to annual carbon budgets of the Southern Ocean.

2. Methods

From June 9 to August 13, 1988, we sampled the marginal ice zone of the Weddell-Scotia Sea from the *R.V. Polar Duke* as part of the Antarctic Marine Ecosystem Research at the Ice-Edge Zone (AMERIEZ) program (Fig. 1). The cruise was divided into two legs, during which we conducted six transects normal to the ice edge along 35, 40, 44 and 48W. The transects at 40 and 48W were occupied on each leg, but there was no overlap in stations between the first and second 40W transects because of ice advance. A total of 144 stations were occupied with 54 on leg 1 and 90 on leg 2. Nutrient concentrations and particulate materials in the upper 150 m were determined at 123 stations, whereas measurements of carbon fixation and nitrogen uptake were made at 27 and 10 open-water stations, respectively.

Routine sampling at each station included vertical profiles of temperature, salinity, nutrients (NO$_3^-$, NO$_2^-$, NH$_4^+$, Si(OH)$_4$ and H$_3$PO$_4$), chlorophyll *a*, biogenic silica, and particulate organic carbon and nitrogen. Hydrographic structure, variabil-
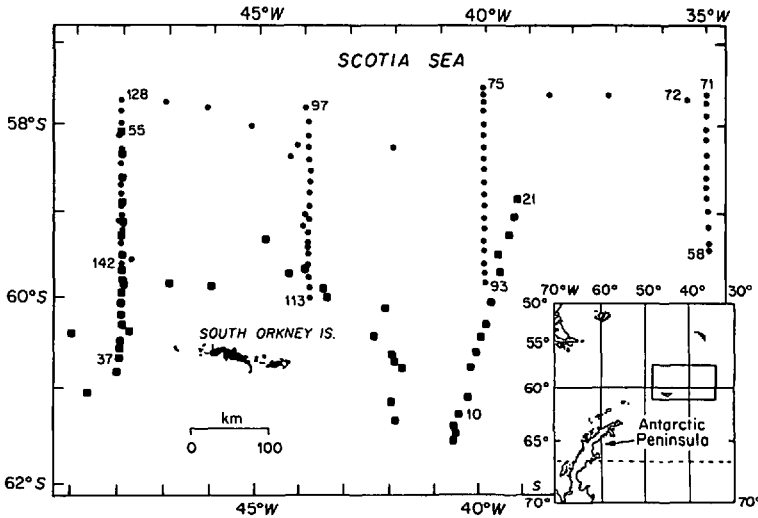
Figure 1. Map of station locations in the study area. Stations 1–55 were completed during leg 1 and stations 56–144 during leg 2.

ity and currents in the study area have been discussed by Muench *et al.* (1990). At each station 10-*l* seawater samples were collected from eight depths in the upper 150 m; the upper seven corresponded to the depths to which 100, 50, 30, 15, 5, 1, and 0.1% of surface irradiance penetrated. Optical depths were estimated from vertical irradiance profiles obtained with a Biospherical Instruments Inc. Model MER-1010 submersible spectroradiometer (Reynolds, pers. comm.). Water from stations which did not include irradiance profiles or those occupied at night was sampled from depths corresponding to the station completed most recently during the day. Each Niskin bottle was drained into a 20-*l* polypropylene carboy fitted with a spigot, and subsamples for individual analyses were drawn from each carboy.

Samples for nutrients were analyzed immediately after collection with a Technicon AutoAnalyzer II, using methods adapted from Atlas *et al.* (1971) for nitrate, nitrite, silicic acid and phosphate. Ammonium analyses were also performed on freshly collected samples, using automated modifications (Head, 1971; Whitledge *et al.*, 1981) of the method of Solorzano (1969). Chlorophyll *a* was determined by filtering 1.0 *l* through 25 mm Whatman GF/F glass fiber filters. The filters were placed on ice, sonicated in 90% acetone for 10 min, extracted for 10 min more and the extract's fluorescence determined before and after acidification on a Turner Designs Model 10 fluorometer, which had been calibrated with commercially purified chlorophyll *a* (Sigma Chemicals). Calibrations were done before each leg of the cruise.

Particulate organic carbon and nitrogen (POC and PON) concentrations were measured by filtering 1.05 *l* through precombusted (450°C for 3 h) 47 mm Whatman

GF/F glass fiber filters. Each filter was rinsed with 5–10 ml of 0.01 N HCl in filtered seawater to remove inorganic carbonates, placed in precombusted glass vials, dried at 60°C and analyzed on a Perkin-Elmer model 240B elemental analyzer. Corrections for background levels of carbon and nitrogen in filters and adsorption of dissolved organic matter were made by subtracting values from a second filter placed beneath the primary filter and processed identically. Samples (1.1 l) for analysis of biogenic particulate silica were collected by vacuum filtration onto 0.6 μm Nuclepore filters, dried at 60°C in covered plastic dishes, dissolved by NaOH digestion (Paasche, 1973) and analyzed for reactive silicate by the acid-molybdate method. Details and estimates of analytical precision for nutrient and particulate matter determinations are given in Nelson *et al.* (1989).

Primary productivity was measured by simulated *in situ* incubations. For these, 280 ml samples from the seven optical depths were incubated in polyethylene bottles wrapped with neutral density screens to reduce irradiance to that available at the depth sampled. Incubations lasted from dawn to dawn in on-deck incubators maintained at sea-surface temperatures with surface seawater (Smith and Nelson, 1990). Hourly rates given herein are simply divided by the total number of hours of incubation and underestimate the rate per hour of daylight. Samples were injected with ca. 40 μCi ^{14}C-NaHCO$_3$, incubated, filtered through a Whatman GF/F filter, and rinsed with a few ml of 0.1N HCl in seawater just prior to the completion of the filtration. Controls were samples which were treated identically but not incubated, and were used to correct for background and abiotic adsorption. All samples had 10 ml Ecolume (ICN) added to them and were counted after the cruise on a liquid scintillation counter. Counting efficiencies were determined using the Compton edge (H-number) method. Growth rates based on ^{14}C-fixation were calculated with Eppley's (1968) equation, using particulate carbon as an indicator of phytoplankton biomass.

Photosynthesis-irradiance (P-I) experiments were also conducted at a few stations in a "photosynthetron," using 2 ml samples in 20 ml glass vials and a 500 W quartz-halogen source (Lewis and Smith, 1983). Samples were incubated for 3 h at 32 irradiances determined by neutral density filters mounted on a blue acrylic filter to mimic *in situ* spectral irradiance. Neutral density screens were adjusted so that irradiance values were low, ranging from 0.5 to 480 μmol photons m^{-2} s^{-1}. About $\frac{1}{3}$ of the irradiance levels were subsaturating (i.e., 10 of 32 irradiances were ≤10 μmol photons m^{-2} s^{-1}) and over half of the intensities were ≤50 μmol photons m^{-2} s^{-1}. Temperature was maintained near ambient (±0.5°C) with two circulating water baths, and the data were normalized to chlorophyll and fitted to a three-parameter model (Platt *et al.,* 1980).

Nitrogen-uptake experiments were conducted with tracer (10% of ambient concentrations) additions of ^{15}N-labelled nitrate and ammonium. Incubations (6–9 h) were done in parallel with the ^{14}C-uptake measurements in 1-l screened bottles. Specific
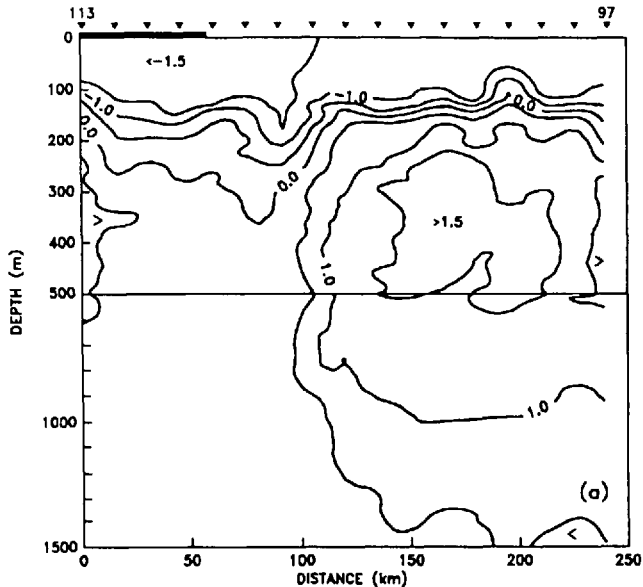
Figure 2. Hydrographic sections along a north-south transect through the marginal ice zone at 44W from July 31 to August 2, 1988; (a) temperature (°C), (b) salinity (psu), and (c) density (σ_t). The approximate position of the ice edge is shown at the top along with the station positions; the southernmost station is 113. CTD data from 10 m depth intervals were used in contouring. Note change in vertical scale at 500 m. Salinity and density data are after Muench *et al.* (1990).

and absolute uptake rates were calculated using initial particulate organic nitrogen (PON) concentrations (MacIssac *et al.,* 1985) because changes in PON during incubations were within analytical precision. Ammonium uptake rates were not corrected for isotope dilution (Glibert and Garside, 1984), but this correction would in all cases be <2% for the incubation times and label additions used. Ammonium relative preference indices (RPI) were computed from

$$\mathrm{RPI}_{\mathrm{NH_4^+}} = \frac{\rho_{\mathrm{NH_4^+}}/(\rho_{\mathrm{NO_3^-}} + \rho_{\mathrm{NH_4^+}})}{[\mathrm{NH_4^+}]/([\mathrm{NO_3^-}] + [\mathrm{NH_4^+}])}$$

(Glibert *et al.,* 1982) where $\rho_{\mathrm{NH_4^+}}$ and $\rho_{\mathrm{NO_3^-}}$ are the measured specific uptake rate of $\mathrm{NH_4^+}$ and $\mathrm{NO_3}^-$ and $[\mathrm{NH_4^+}]$ and $[\mathrm{NO_3^-}]$ are the measured ambient concentrations of nitrate and ammonium. We calculated *f*-ratios for paired samples from the same depth with

$$f = \rho_{\mathrm{NO_3^-}}/(\rho_{\mathrm{NO_3^-}} + \rho_{\mathrm{NH_4^+}})$$

(Eppley and Peterson, 1979) where $\rho_{\mathrm{NO_3^-}}$ and $\rho_{\mathrm{NH_4^+}}$ are the respective measured uptake rates (μmol liter^{-1} h^{-1}) for nitrate and ammonium. Vertically integrated values of uptake were also employed in *f*-ratio computations for uptake rates from the surface to the 0.1% isolume (Nelson and Smith, 1986; Smith and Nelson, 1990).
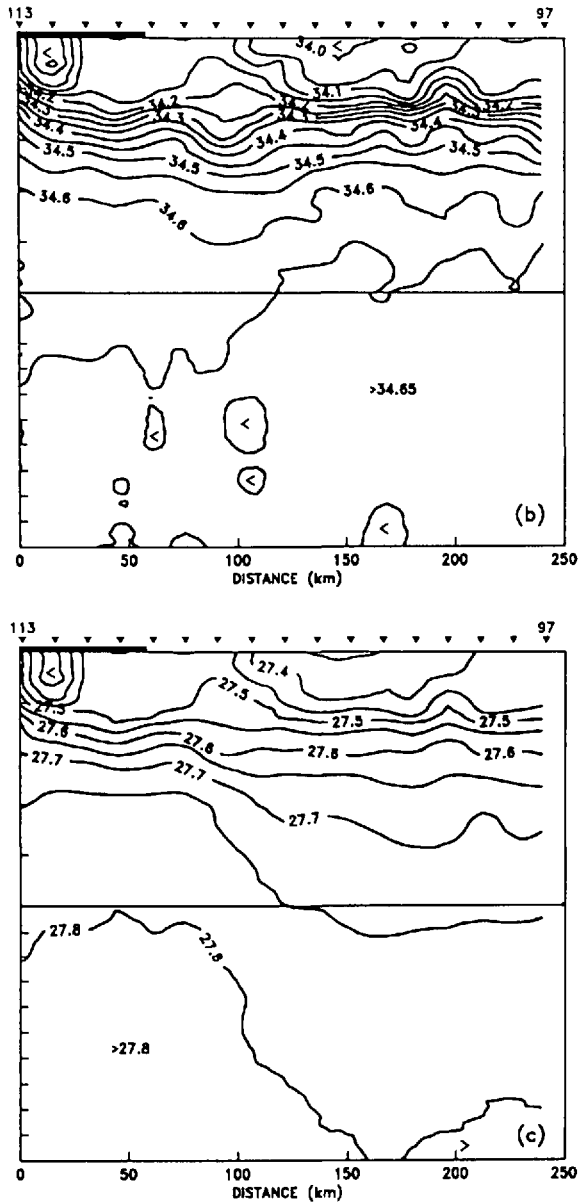
Figure 2. (Continued)

3. Results

In late June and early July the ice edge was typically south of 60S, but generally between 59 and 58S in late July and early August. Hence, our study was conducted during a period of significant ice advance. The position of the ice edge changed rapidly in response to prevailing winds, frequently advancing or retreating a degree of latitude in 3–5 d (ca. 22–37 km d^{-1}) during the latter part of the cruise. The
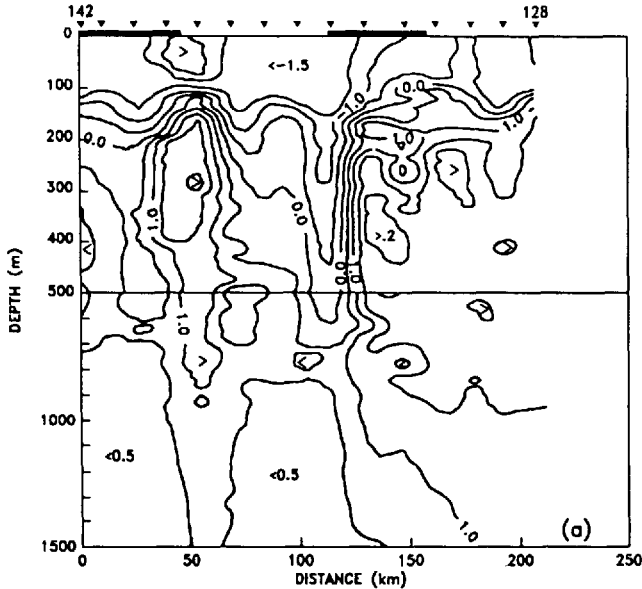
Figure 3. Hydrographic sections along a north-south transect through the marginal ice zone at 48W from August 8–11, 1988; (a) temperature (°C), (b) salinity (psu), and (c) density (σ_t). The approximate position of the ice edge is shown at the top along with the station positions; the southernmost station is 142. CTD data from 10 m depth intervals were used in contouring. Note change in vertical scale at 500 m. Salinity and density data are after Muench *et al.* (1990).

extreme northern position corresponded to surface water temperature $\approx -1°C$, and waters with reduced salinities were often evident near that isotherm (Muench *et al.*, 1990). The ice varied greatly from thin, young ice (e.g., grease, pancake and nilas) to thick, multiyear floes. The ice gradient from open water to heavy ($\geq 8/10^{ths}$) cover was highly variable, and in some cases ice in the marginal ice zone was banded rather than continuous.

The surface mixed layer was typically between 90 and 130 m deep, with temperatures ranging from $-0.5°$ to colder than $-1.5°$, except at a few of the most northern stations (Figs. 2 and 3). Salinities in the upper layers were 34.0 to 34.3 psu, and a weak north-south gradient (lower in the north) was present. Strong vertical gradients in temperature, salinity and density were present below the surface layer down to ca. 300–400 m (Muench *et al.*, 1990). The depth of the 0.1% isolume depth averaged 120 m, with relatively little spatial or temporal variation.

The hydrographic sections revealed complex structures consistent with the presence of warm core eddies (Fig. 3), and one such feature in the northwest portion of the study area was shown by drifter trajectory to be an anticyclonic eddy (Muench *et al.*, 1990). The temperatures of these features were warm ($> 1.0°$) and occurred in a sub-surface core from the base of the mixed layer to 500–1000 m (Fig. 3). Reduced
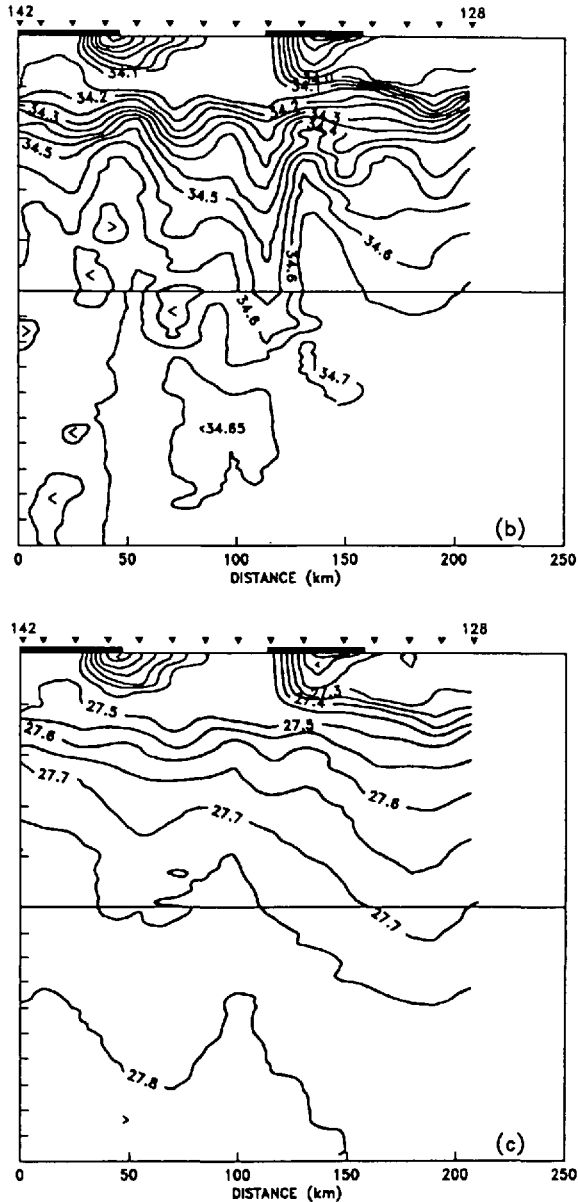
Figure 3. (Continued)

surface salinities overlying the structures were consistent with ice melting due to the elevated temperatures. The structures appeared to have been "pinched off" at pycnocline depths as the surface water cooled and freshened, and upper mixed layer temperatures did not reflect the warm, deeper temperatures as strongly. The
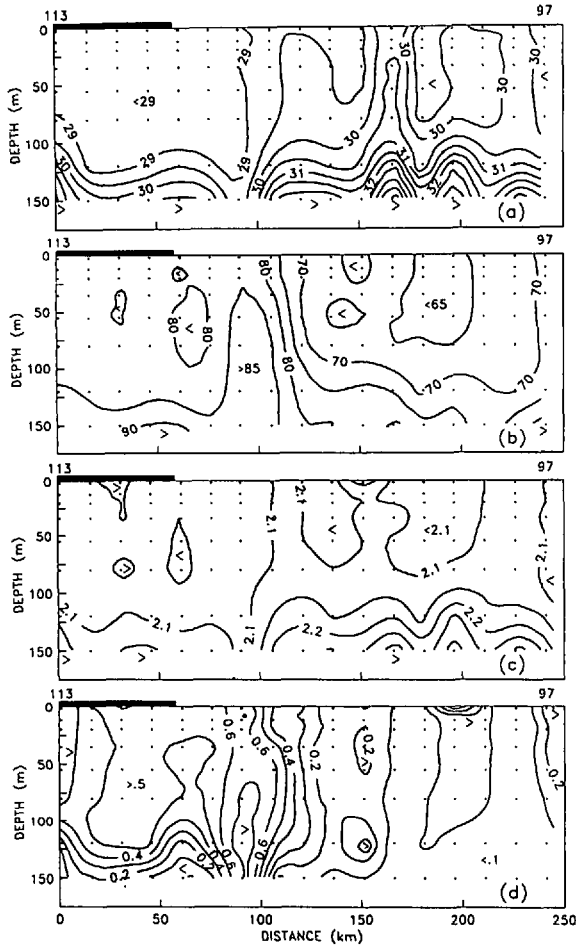
Figure 4. Concentrations of inorganic nutrients along the transect at 44W depicted in Figure 2; (a) nitrate, (b) silicic acid, (c) phosphate, and (d) ammonium. Dots represent sample depths; all concentrations in μM.

subsurface core water in these eddies appeared to have originated from the Polar Front (Muench *et al.*, 1990).

Nutrient concentrations in the upper 150 m were high, with values approaching their seasonal maxima for this region. Nitrate, silicic acid and phosphate rarely fell below 28, 60 and 2 μM, except at the most northerly stations or in meltwater features (Figs. 4a, b, c and 5a, b, c). Spatial variations of these three nutrients in the surface mixed layer were small relative to other seasons and ice-edge regions (e.g., Nelson *et al.*, 1987, 1989). Nutrient concentrations were typically highest at depth and under the pack ice with minima in meltwater lenses or around biomass maxima. Nutrient gradients were greatest near the top of the pycnocline and in meltwater regions, near
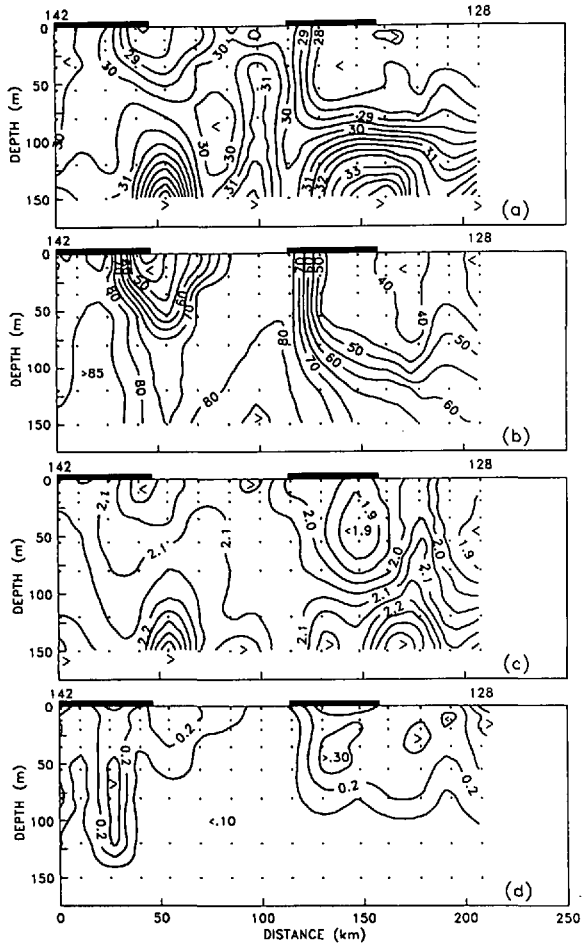
Figure 5. Concentrations of inorganic nutrients along the transect at 48W depicted in Figure 3; (a) nitrate, (b) silicic acid, (c) phosphate, and (d) ammonium. Dots represent sample depths; concentrations are μM.

water mass boundaries or inside warm core eddies (Figs. 3 and 5). Ammonium concentrations were more variable than those of the other nutrients, with tenfold differences within some sections, and often appeared to be highly structured with discrete maxima (Figs. 4d and 5d). Levels of ammonium were highest at the beginning of the cruise (maximum values > 1 μM).

Phytoplankton biomass, as indicated by chlorophyll and biogenic silica, was low compared to other seasons (Table 1) and showed little variation in the surface layer (Figs. 6 and 7). The close correspondence between chlorophyll and biogenic silica maxima implies that diatoms were a significant component of the phytoplankton. Biogenic particles displayed slight, near-surface maxima within 100 km of the ice

Table 1. Mean values of particulate parameters in four marginal ice zones in the Southern Ocean from the four seasons.

Parameter	Ross Sea (1–2/83)* summer	Weddell-Scotia Sea (11/83)** spring	Weddell-Scotia Sea (7–8/88)*** winter	Weddell Sea (3/86)**** autumn
Chlorophyll (μg l^{-1})	2.9	4.0	0.12	0.38
Particulate carbon (μmol l^{-1})	33.2	10.6	5.2	3.6
Particulate nitrogen (μmol l^{-1})	5.6	1.5	0.51	0.46
Biogenic silica (μmol l^{-1})	21.7	1.4	0.26	1.6
Carbon:chlorophyll[+] (mass ratio)	138	32	530	114
Carbon:nitrogen[+] (mole ratio)	5.9	7.1	10.2	7.8
Silica:carbon[+] (mole ratio)	0.65	0.13	0.05	0.44

*Nelson and Smith (1986).
**Nelson *et al.* (1987).
***Present study. Data include all values in top 150 m from ice-free stations.
****Nelson *et al.* (1989).
[+]Ratio of mean values.

edge, but the position of the maxima relative to the ice edge varied considerably. Particulate organic carbon and nitrogen, which include detritus, autotrophs and heterotrophs, showed similar maxima, as well as additional accumulations near the ice edge (Fig. 6b, c). Density minima and biomass maxima coincided closely seaward of the ice edge, consistent with other observations in ice-edge systems (Smith and Nelson, 1985; Nelson *et al.,* 1987).

Maximum chlorophyll concentrations were 0.33 μg l^{-1}, whereas those below the mixed layer and under the pack ice were generally <0.10 μg l^{-1} (Figs. 6a and 7a), suggesting that the ice edge was a region of phytoplankton growth. The low chlorophyll concentrations we observed are typical of values reported for austral winter in Bransfield Strait (Brightman and Smith, 1989), whereas in Antarctic coastal waters during spring and summer chlorophyll concentrations may reach 25 μg l^{-1} or more (e.g., Holm-Hansen and Mitchell, 1991). However, most chlorophyll concentrations in pelagic regions of the Southern Ocean have a mean value <0.5 μg l^{-1}. Our mean values of chlorophyll in winter were over three and thirty times lower than previous AMERIEZ cruises in fall (Nelson *et al.,* 1989) and spring (Nelson *et al.,* 1987), respectively (Table 1). The presence and persistence of small accumulations of biomass indicates that even in winter conditions are favorable in the marginal ice zone for phytoplankton growth and accumulation, albeit at low rates.

Particulate organic carbon and nitrogen concentrations were low (averaging 5.2 and 0.51 μmol l^{-1}, respectively) when compared with those found at the Weddell-Scotia Sea ice edge in spring (Nelson *et al.,* 1987), but similar to those observed in autumn in the Weddell Sea (Nelson *et al.,* 1989; Table 1). Concentrations of biogenic silica were >0.3 μmol l^{-1} within biomass maxima and <0.2 μmol l^{-1} below the
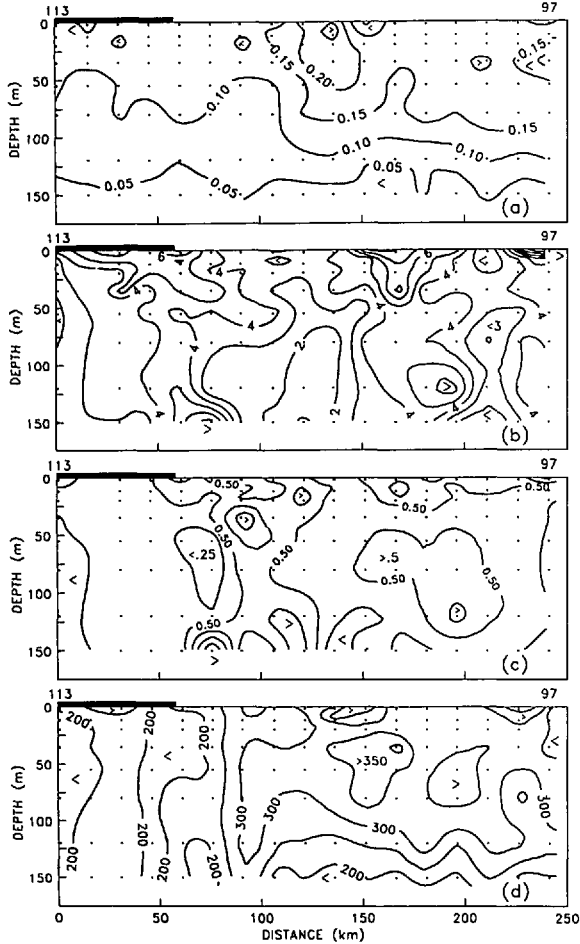
Figure 6. Distributions of particulate matter along the transect at 44W depicted in Figure 2; (a) chlorophyll ($\mu g\, l^{-1}$), (b) particulate organic carbon ($\mu mol\, l^{-1}$), (c) particulate organic nitrogen ($\mu mol\, l^{-1}$), and (d) biogenic silica ($nmol\, l^{-1}$).

mixed layer and beneath pack ice cover (Figs. 6d and 7b). Biogenic silica levels were about five times less than those observed in ice-edge systems in the Weddell-Scotia Sea during other seasons (Table 1).

Incident photosynthetically active radiation was low during our study, averaging 3.6 (± 2.8) and 7.2 (± 5.8) mol photons $m^{-2}\, d^{-1}$ on legs 1 and 2, respectively (Lizotte *et al.*, 1989, R. Reynolds pers. comm.). Maximum instantaneous irradiances above the sea surface exceeded 1200 μmol photons $m^{-2}\, s^{-1}$ during a few clear days, but most days were overcast, and fluxes averaged 138 and 225 μmol photons $m^{-2}\, s^{-1}$ (R. Reynolds, pers. comm.). The photoperiod increased from 7.1 to 8.6 h during the cruise.
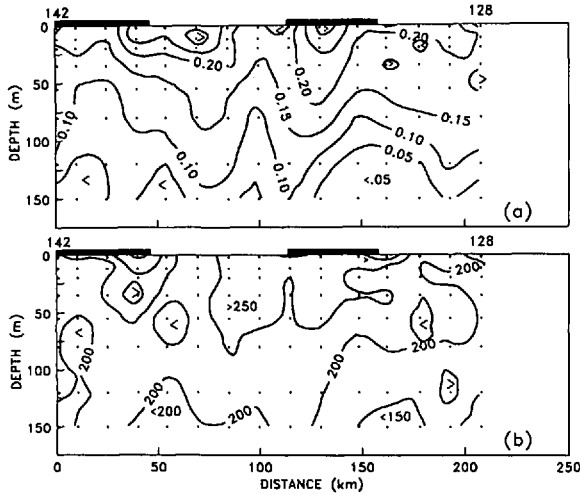
Figure 7. Distributions of particulate matter along the transect at 48W depicted in Figure 3; (a) chlorophyll ($\mu g\, l^{-1}$), and (b) biogenic silica (nmol l^{-1}).

Primary productivity was low throughout the study (Table 2). The mean integrated productivity was 32 mg C m^{-2} d^{-1} and ranged from 10 to 86 mg C m^{-2} d^{-1} in ice-free waters. Productivity estimated from photosynthesis-irradiance parameters was similar to that estimated from simulated *in situ* incubations and averaged 26 mg C m^{-2} d^{-1}. The highest rates of carbon fixation were observed at the surface (mean of 0.045 mg C m^{-3} h^{-1}; Fig. 8). Chlorophyll concentrations at stations where productivity measurements were completed averaged 0.15 $\mu g\, l^{-1}$, and chlorophyll-specific productivity averaged 0.30 mg C (mg chl)$^{-1}$ h^{-1} at the surface. Growth rates at the 50% isolume were very low and averaged 0.026 doublings d^{-1} ($n = 18$), or only 0.014 doublings d^{-1} ($n = 17$) if the high value at station 55 is excluded (Table 2). The 50% isolume was chosen because populations incubated at that irradiance should be near light saturation and for direct comparison with previous results (Smith and Nelson, 1990). Regression analyses showed that chlorophyll and daily irradiance explained only 18% and 23% of the variance in primary productivity values.

Photosynthetic parameters obtained from photosynthesis-irradiance (P-I) experiments revealed no significant variation with depth above the 1% isolume (Table 3). Because of low temperatures and low biomass, the P-I results from individual experiments were relatively variable. Standard deviations for the three primary parameter estimates averaged 25%, 19% and 182%, respectively, for the maximum photosynthetic rate in the absence of photoinhibition (P_s^B, mg C (mg chl)$^{-1}$ h^{-1}), the initial slope (α, mg C (mg chl)$^{-1}$ h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$), and β (mg C (mg chl)$^{-1}$ h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$), an indicator of the degree of photoinhibition at high irradiances. Nevertheless, parameter values were fairly consistent between stations and depths. In several instances one experiment contributed most of the variance to the depth-averaged values of certain parameters (e.g., a high I_b of

Table 2. Integrated primary productivity, surface chlorophyll-specific productivity and phyto-
plankton growth rates during austral winter, 1988. Data are from simulated in situ
incubations and integrations were from the surface of the 0.1% irradiance level. Growth
rates were based on 24 h incubations at the 50% isolume. ND = no data.

Station number	Primary productivity (mg C m^{-2} d^{-1})	Chlorophyll-specific productivity (mg C (mg chl)$^{-1}$ h^{-1})	Growth rate (doublings d^{-1})
13	16.4	0.49	0.009
21	57.4	0.35	0.006
22	23.4	0.13	0.007
23	38.8	0.25	ND
25	16.7	0.17	ND
35	18.1	0.24	ND
44	17.7	0.41	0.014
47	34.2	0.46	0.034
51	50.3	0.75	0.017
55	86.4	0.70	0.237
69	31.0	0.35	0.010
71	9.9	0.13	0.002
73	15.7	0.23	0.007
76	16.2	0.17	0.010
78	14.9	0.22	0.010
80	20.1	0.16	0.007
94	36.6	0.10	ND
96	25.3	0.24	0.018
99	33.1	0.32	0.045
102	24.5	0.20	0.011
104	29.1	0.15	0.018
107	14.2	0.18	0.014
123	81.1	0.34	ND
128	50.6	0.45	ND
131	33.1	0.22	ND
134	31.0	0.37	ND
137	40.7	0.40	ND
Mean	32.1	0.30	0.026

28,571 μmol photons m^{-2} s^{-1} for the 15% isolume at St. 131). Maximum photosyn-
thetic rates in the absence of photoinhibition (P_s^B) and the maximum realized
assimilation numbers (P_m^B) averaged 0.28 and 0.23 mg C (mg chl)$^{-1}$ h^{-1}, respectively,
which is similar to the mean surface value for chlorophyll-specific productivity given
above. The mean photosynthetic efficiency (α) for all experiments was 0.056 mg C
(mg chl)$^{-1}$ h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$. Photoadaptive indices (I_k) and optimal
irradiances (I_m) were highest at the surface, but averaged only 9.8 and 60 μmol
photons m^{-2} s^{-1}, respectively, for all depths, indicating that the populations were
highly shade-adapted. Photoinhibition was not evident in the mean productivity

Table 3. Means ($\pm$ standard deviations) of parameters for photosynthesis-irradiance experiments from three optical depths (expressed as a percentage of surface incident irradiance, I_o, and the corresponding absolute depth in meters). Data ($n = 9$) are from stations 128, 131 and 134 along 48W. Definition of parameters and their units are given in methods.

$\% I_o$ depth (m)	P_s^B	α	β ($\times 10^{-3}$)	P_m^B	I_k	I_b	I_m
100	0.42	0.044	0.72	0.33	20.8	3496	120
(0 m)	(0.18)	(0.062)	(0.98)	(0.29)	(30.2)	(4561)	(142)
15	0.17	0.064	0.25	0.15	4.0	10500	26
(35 m)	(0.08)	(0.051)	(0.38)	(0.05)	(2.3)	(15688)	(20)
1	0.25	0.060	0.17	0.22	4.9	2167	30
(80 m)	(0.06)	(0.033)	(0.11)	(0.06)	(3.2)	(1791)	(14)
All I_z	0.28	0.056	0.38	0.23	9.8	5387	60
	(0.14)	(0.042)	(0.55)	(0.16)	(16.3)	(8567)	(81)

profile (Fig. 8), and would rarely be significant in a well-mixed surface layer even atthe higher irradiances of clear days, as indicated by the relatively high values for the photoinhibition index (I_b).

Nitrate accounted for ca. 40% of the nitrogen consumed by the plankton assemblage (Table 4). Vertically integrated rates of NO_3^- uptake averaged 1.47 (± 0.77)
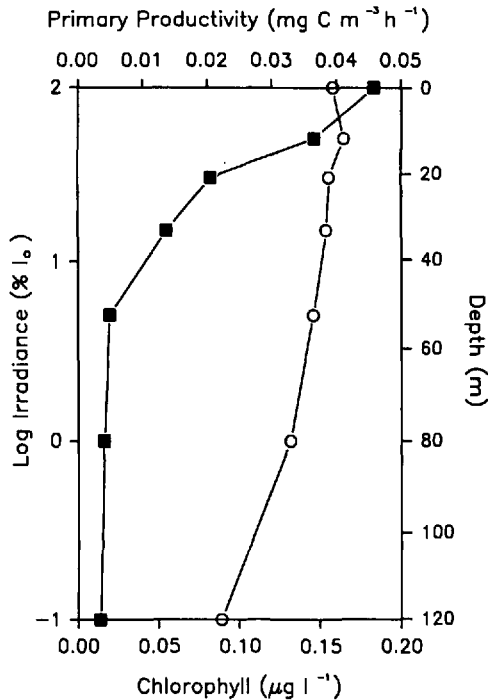

Figure 8. Profiles of mean chlorophyll (circles) and primary productivity (squares) for optical depths and the associated absolute depths during austral winter. Standard deviations averaged 36% and 91% of the mean values plotted, respectively.

Table 4. Specific (V) and absolute (ρ) uptake rates for ammonium and nitrate and the associated f-ratios. Specific uptake rates were from the 50% isolume. Absolute uptake rates represent euphotic zone integrations; f-ratios were derived from integrated values. ND = no data.

Station number	$V_{NH_4^+}$ $(10^{-3}\,h^{-1})$	$V_{NO_3^-}$ $(10^{-3}\,h^{-1})$	$\rho_{NH_4^+}$ (mmol m^{-2} d^{-1})	$\rho_{NO_3^-}$ (mmol m^{-2} d^{-1})	f-ratio
22	0.74	0.39	0.66	0.29	0.31
51	1.62	0.56	1.04	1.80	0.63
55	1.49	0.64	0.97	1.10	0.53
71	5.65	0.87	ND	0.73	—
83	2.01	2.31	1.23	1.53	0.56
96	ND	1.24	ND	2.02	—
104	10.1	1.54	ND	0.85	—
123	1.35	ND	ND	ND	—
128	8.39	1.54	9.70	2.46	0.20
137	2.86	2.58	4.47	2.44	0.35
Mean	3.80	1.30	3.01	1.47	0.43
±s.d.	3.42	0.77	3.56	0.77	0.17

mmol m^{-2} d^{-1}, whereas the mean uptake rate for NH$_4^+$ was higher and more variable (3.01 ± 3.56 mmol m^{-2} d^{-1}). Mean NH$_4^+$ concentrations were greatest at the surface, and below the 0.1% isolume ammonium levels were only a third of surface values (Fig. 9). By contrast, nitrate levels were high and almost invariant with depth. Vertically integrated f-ratios (from stations with paired uptake profiles) varied from 0.20 to 0.63 and averaged 0.43 (± 0.17) (Table 4). Paired uptake samples from the same station and depth yielded the same mean f-ratio of 0.43 (± 0.22), and although there was considerable variability, the highest f-ratios occurred at the lowest ammonium concentrations at depth (Fig. 10a). Consequently, there appeared to be an increase in f-ratio with depth (Table 5). Based on ammonium relative preference indices (Fig. 10b), ammonium also was the preferred nitrogen substrate, and this was true at all depths (Table 5). Hence, ammonium appeared to be the major component of planktonic nitrogenous nutrition during our study.

4. Discussion

The largest seasonal signal in environmental conditions for the three AMERIEZ cruises was in incident irradiance and photoperiod. Irradiance levels averaged 25.7, 16.0 and 5.5 mol photons m^{-2} d^{-1}, respectively, for spring, autumn and winter, with photoperiods of ca. 18, 14 and 8 hours. Other physical and chemical conditions in the marginal ice zone did not differ as greatly. Stratification was strongest and most uniform in autumn, spatially variable in spring and relatively weak in winter (mixed layer depths averaged ca. 35, 70 and 100 m during these seasons). Nitrogen concentrations were always high, with abundant nitrate (>21 μM) and a minor (generally <1 μM) surface-layer maximum in ammonium (Fig. 9; see also Smith and
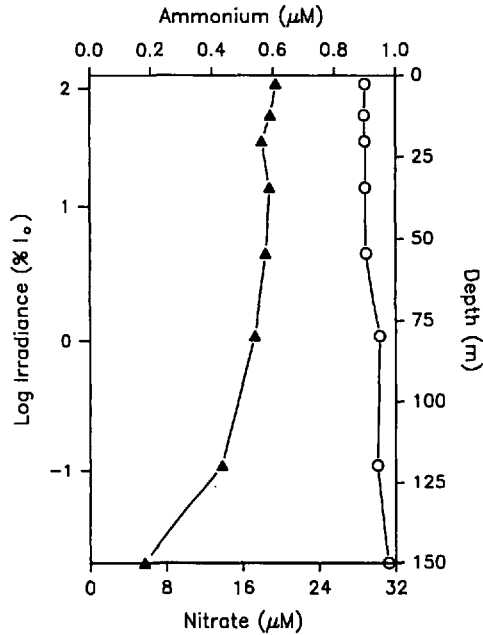
Figure 9. Profiles for mean nitrate (circles) and ammonium (triangles) concentrations for all stations in the study area. Standard deviations averaged 4% and 81% of the mean values plotted, respectively.

Nelson, 1990). Therefore, irradiance availability, which is largely a function of season, weather, and mixing rates and depths, appears to be the dominant environmental factor regulating phytoplankton biomass accumulation and productivity in the Weddell/Scotia Sea marginal ice zones.

a. Nutrient and biomass distributions. Physical processes appear to have had the largest impact on nutrient distributions (Figs. 4, 5). Near the middle of our sections there often was a north-south gradient (particularly for silicic acid, which decreased over 10 μM in ca. 20 km) delineating the Weddell-Scotia Confluence as defined by the Scotia Front. However, this front was not as well defined by temperature or salinity as it was in 1983 or 1988 (Muench *et al.,* 1990). The silicic acid gradient coincided with the maximum surface temperature gradient and the Confluence, as indicated by the $-1.5°C$ surface isotherm.

Anticyclonic warm-core eddies associated with the Scotia Front resulted in marked perturbations in the temperature and nutrient fields. The eddies were usually characterized by an upper layer of enhanced stability overlying a warm core which extended to depths in excess of 700 m. The upper layers of these features often had lowered salinities, reflecting the introduction of meltwater from ice which had become trappd in the eddy circulation. Concentrations of the three major nutrients displayed minima in the surface meltwater lenses (Fig. 5). Based on the low silicic
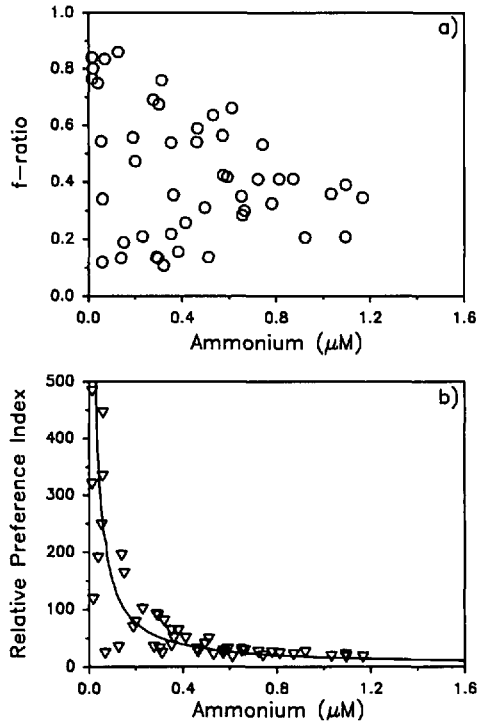
Figure 10. Relationships between (a) *f*-ratio and (b) relative preference index and ammonium concentration for paired samples from the same depth. The solid line in (b) is the ammonium RPI calculated for various ammonium levels and assuming a constant nitrate concentration (30 μM) and constant uptake rate (0.001 h^{-1}) for both nitrate and ammonium.

acid concentrations within these lenses, the source waters are likely to have originated north of the Scotia Front.

Biological effects on nutrient fields were also evident, but they appear to be minor. In areas of enhanced vertical stability, small accumulations of particulate material were observed, corresponding to decreased nutrient concentrations. Similar relation-

Table 5. Mean ($\pm$ standard deviation) for *f*-ratios and ammonium relative preference indices (RPI) as a function of irradiance.

Irradiance (%)	*f*-ratio	RPI
100	0.36 ($\pm$0.17)	35.4 ($\pm$16.5)
50	0.29 ($\pm$0.14)	67.1 ($\pm$54.1)
30	0.30 ($\pm$0.09)	46.4 ($\pm$28.0)
15	0.40 ($\pm$0.16)	122.8 ($\pm$151.7)
5	0.52 ($\pm$0.24)	136.5 ($\pm$135.7)
1	0.54 ($\pm$0.27)	66.4 ($\pm$63.9)
0.1	0.57 ($\pm$0.19)	119.2 ($\pm$166.1)

ships between the particulate and nutrient fields were observed during the spring and autumn AMERIEZ cruises, although each exhibited much more pronounced particle maxima and nutrient minima (Nelson *et al.,* 1987, 1989). Although winter appears to be the seasonal minimum of phytoplankton growth and activity, autotrophic activity did not cease entirely, and the productivity created small modifications in the nutrient distributions.

Modest accumulations of nitrite (not shown) and ammonium (Fig. 4d and 5d) were found at several locations in the mixed layer. Neither form of nitrogen is thermodynamically stable in well-oxygenated seawater, and their presence is an indication of recent decomposition of organic material and/or excretion by living organisms. At some stations there were elevated concentrations of both nitrite and ammonium (up to 0.35 and 0.55 μM, respectively) associated with local minima in chlorophyll concentrations, which suggests that these were regions of enhanced heterotrophic activities.

Distributions of POC and PON were frequently, but not always, related to hydrographic structure. Vertically uniform, slightly elevated concentrations of POC and PON were observed in regions with little density stratification, and in these regions levels of chlorophyll and biogenic silica, more specific indicators of autotrophic biomass (Nelson *et al.,* 1987), were low (Fig. 6). Small increases in chlorophyll and biogenic silica concentrations were limited to areas where mixed layers were <100 m; these areas were not necessarily coincident with the observed ice-edge location. We hypothesize that ice ablation released particulate and dissolved materials continuously, with the largest quantity released at the ice edge. In winter particulate material is enriched with detrital and heterotrophic components relative to autotrophic ones, and hence the chlorophyll and biogenic silica concentrations were low with respect to POC and PON. The distribution of ammonium, which is higher near the ice edge and generated via degradation of organic nitrogen (Fig. 4d), also supports this hypothesis. Therefore, the position of the ice edge, which is controlled by physical processes, is crucial both directly and indirectly in determining the spatial distribution of biogenic particulate material.

b. Particulate matter composition. The compositional ratios of the particulate matter differed considerably from those observed in previous studies in the Southern Ocean (Table 1). The mean carbon:chlorophyll ratio (530) was much higher than reported for other areas of the Southern Ocean (Smith and Sakshaug, 1990). The regression between particulate organic carbon (POC) and chlorophyll (Chl) was

$$POC = 57.1\ (\pm 28.9) + 47.2\ (\pm 30.1)\ Chl$$

and had a relatively large positive intercept for carbon which suggests that microheterotrophs and detritus comprised a significant fraction of the particulate organic material (Banse, 1977). The slope of the regression was close to the value found in

regions dominated by phytoplankton. If we assume that the slope of the regression gives an accurate representation of carbon in intact phytoplankton cells, then ca. 90% of the total POC was not associated with phytoplankton (i.e., mean chlorophyll of 0.12 μg l^{-1} × C/Chl ratio of 50 = 6 mg C m^{-3} or 0.5 μmol C l^{-1}, which is 10% of the mean POC concentration). A comparison of our POC values integrated to 100 m and microscopic estimates of carbon associated with living organisms by Garrison *et al.* (1991) suggests that about 94% of the carbon was nonliving. Their data also indicated that the biomass of heterotrophic organisms was usually larger than autotrophs. Furthermore, the molar ratio of carbon to nitrogen in our study was 10.2, which is higher than in most marine systems (e.g., Parsons *et al.,* 1984), but is again indicative of the large contribution of detritus to the POC pool. The silica:carbon ratio (0.05) was half the value which is typical for most cultured diatoms (Brezinski, 1985). Other studies have found ratios 2–10 times higher (Nelson and Smith, 1986; Nelson *et al.,* 1987, 1989), which again suggests that the influence of non-diatomaceous carbon was substantial. Leynaert *et al.* (1991) reported a mean Si:C ratio of 0.03 for surface waters near the ice edge of the southern Scotia Sea during spring, 1988. Hence, there appears to be a great deal of variability in particulate matter composition between seasons and locations in the Antarctic. This variability may reflect differences in methodology, species composition and physiological state among different ice edge studies, as well as large compositional changes which occur at one location throughout the year in response to changes in environmental conditions.

c. Primary productivity. Productivity averaged 32 mg C m^{-2} d^{-1} in winter, much less than the means for AMERIEZ cruises in autumn and spring, respectively (126 and 489 mg C m^{-2} d^{-1}; Table 2, Smith and Nelson, 1990). Hence, productivity seems to parallel seasonal trends in irradiance and particulate matter, but these correlates explained only about 20% of the variation in production estimates during this cruise. Our average productivity estimates for ice edge in winter are considerably greater than the estimated productivity of 3–11 mg C m^{-2} d^{-1} from simulated *in situ* measurements for an area west of the Antarctic Peninsula during June and July, 1987 (Brightman and Smith, 1989); however, incident irradiance was even lower in their study. Previous ice-edge studies in the Weddell Sea found productivity to range from 104 to 410 mg C m^{-2} d^{-1} in February and March (El-Sayed and Taguchi, 1981) and to average 300 mg C m^{-2} d^{-1} in October–November (Marra and Boardman, 1984). Although lower than in other seasons, the winter productivity values indicate that there is potential for phytoplankton growth at the ice edge during the period of minimum irradiance levels and greatest mixed layer depths.

Winter phytoplankton exhibited photosynthetic parameters characteristic of shade-adpated populations and displayed no significant vertical variations above the 1% isolume (Table 3). The results suggest that phytoplankton were acclimated to low

ambient light levels and that vertical mixing rates exceeded rates of photoadaptation to a particular light environment. Our mean photosynthetic efficiency (α), which describes the light-limited portion of the P-I response, was 0.056 μg C (μg chl)$^{-1}$ h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$. That value is relatively high but well within the range of values reported for polar phytoplankton (e.g., Harrison and Platt, 1986; Brightman and Smith, 1989, Holm-Hansen and Mitchell, 1991). The photoadaptive index (I_k) and maximum assimilation numbers (P_m^B) averaged 10 μmol photons m^{-2} s^{-1} and 0.23 μg C (μg chl)$^{-1}$ h^{-1}, respectively. These latter parameter estimates are lower than most observations on phytoplankton, but are similar to bottom ice algae that grow under conditions of chronically low light and temperature (Cota and Smith, 1991), and our mean cholorophyll-specific productivity at the surface (0.30 μg C (μg chl)$^{-1}$ h^{-1}) (Fig. 8).

The majority of polar phytoplankton studies have been conducted during seasons other than winter. The one previous data set collected during winter concentrated on the P-I responses of surface populations and employed a much different range of irradiances (10–2000 μmol photons m^{-2} s^{-1}), but values for α, I_k and P_m^B were 0.026 μg C (μg chl)$^{-1}$ h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$, 54 μmol photons m^{-2} s^{-1} and 1.16 μg C (μg chl)$^{-1}$ h^{-1}, respectively (Brightman and Smith, 1989). During spring Holm-Hansen and Mitchell (1991) calculated mean values of 0.06 μg C (μg chl)$^{-1}$ h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$, 18 μmol photons m^{-2} s^{-1} and 1.1 μg C (μg chl)$^{-1}$ h^{-1}, respectively, for α, I_k and P_m^B, based on *in situ* productivity profiles west of the Antarctic Peninsula. In contrast to our results, Lizotte *et al.* (1989) reported substantially different P-I responses during the winter AMERIEZ cruise. Their phytoplankton data also show no vertical variations in photosynthetic parameters within the upper 120 m, but they found mean values for α, I_k and P_m^B of 0.01 μg C (μg chl)$^{-1}$ h^{-1} [μmol photons m^{-2} s^{-1}]$^{-1}$, 75 μmol photons m^{-2} s^{-1} and 0.86 μg C (μg chl)$^{-1}$ h^{-1}, respectively, for a station with heavy ($>8/10^{ths}$) ice cover where phytoplankton might be expected to be even more shade adapted. If this response were characteristic of the marginal ice zone populations, then photosynthesis of phytoplankton would approach saturation only briefly at local noon in the top few m of ice-free waters, given the low irradiance levels observed during the cruise. Conversely, our P-I data suggest that the phytoplankton were adapted more closely to the "average" irradiance of the well-mixed surface layer. Irradiance profiles, which were collected about local noon (Reynolds, pers. comm.), yield an average depth of about 35 m for an irradiance of 10 μmol photons m^{-2} s^{-1}, similar to the mean photoadaptive index we observed (Table 3). Our use of a white light source with a blue filter may account for part of the discrepancy between the studies. Our mean optimal irradiance I_m was 60 μmol photons m^{-2} s^{-1} (Table 3), indicating that maximal photosynthesis was achieved only in the top 10–15 m. Furthermore, our P-I experiments revealed that photoinhibition was not severe up to 480 μmol photons m^{-2} s^{-1}; similarly productivity measurements exhibited no evidence for photoinhibi-

tion at surface irradiances (Fig. 8), suggesting that photoinhibition was unlikely to reduce productivity during winter.

During winter ammonium was, on average, the main source of inorganic nitrogen taken up by the plankton assemblage (Table 4), despite the fact that nitrate was about 40 times more concentrated (Fig. 9). Previous studies have clearly shown that nitrate was the dominant nitrogen source in ice-edge systems, but ammonium was often the main nitrogen source in polar waters away from the ice edge (Smith and Nelson, 1990). There was considerable variation in vertically integrated f-ratios between stations in our study (Table 4) and within stations for paired samples (Fig. 10a), but the mean f-ratio increased near the bottom of the euphotic zone (Table 5). Average ammonium concentrations decreased almost monotonically with depth (Fig. 9), and this variation in substrate availability may have contributed to the increased f-ratios at depth. The relationship between the f-ratio and ammonium concentration exhibited a large amount of variability, although the general trend showed that the highest f-ratios occurred at the lowest ammonium concentrations (Fig. 10a). The ammonium relative preference index (RPI; Glibert et $al.,$ 1982) varied inversely with ammonium availability (Fig. 10b), similar to the finding in spring (Smith and Nelson, 1990). There was no systematic variation of RPI with depth (Table 5). The interpretation of such indices is complicated, however, because it is a function of four variables (Paasche, 1988; Dortch, 1990). For example, if the rates of ammonium and nitrate uptake were constant (e.g., saturated by irradiance and substrate) and nitrate concentrations did not vary, then the major component of variation in the ammonium RPI would be produced by changes in concentrations of ammonium, even though these concentration changes had no effect on the uptake rate of either ammonium or nitrate. In fact, under these conditions (constant uptake of ammonium and nitrate), the ammonium-RPI as a function of ammonium concentration would be similar to the results we obtained (Fig. 10b). Therefore, RPI values do not appear to be reliable expressions of physiological nitrogen preferences of the plankton of the marginal ice zone.

In contrast to the low carbon fixation rates, specific and absolute rates of nitrogen uptake were similar to rates from other seasons (Table 4). Computations of new production are made difficult by the presence of detritus (Harrison, 1981), which varies seasonally in the marginal ice zone, and when uptake of inorganic nitrogen is decoupled from that of carbon. Nitrogen uptake by polar plankton is less dependent on irradiance than is carbon uptake, and dark uptake of nitrogen (particularly ammonium) is often a large fraction of that observed in light (Smith and Harrison, 1991). Indeed, bacteria are responsible for a large percentage of ammonium uptake in a variety of systems (e.g., Wheeler and Kirchman, 1986). The relative proportions of inorganic and organic nitrogen utilized by bacteria may depend upon the "quality" (i.e., the C/N ratio) of organic substrates available (Goldman et $al.,$ 1987).

Our data suggest that heterotrophic uptake of nitrogen was indeed substantial.

The mean vertically integrated rate of nitrate uptake (1.47 mmol m^{-2} d^{-1}, Table 4) was 2 to 4 times the estimated total nitrogen requirement of the phytoplankton, based upon an average ^{14}C-productivity (32 mg C m^{-2} d^{-1}) and a typical range of C:N ratios for Antarctic phytoplankton (from 5 to 8; e.g., Copin-Montegut and Copin-Montegut, 1978; Jennings *et al.,* 1984; Nelson and Smith, 1986). In a mid-summer ice-edge phytoplankton bloom in the Ross Sea, where independent evidence showed that a very high fraction of the POC was present as living phytoplankton, the ratio of vertically integrated carbon productivity to total nitrogen (nitrate plus ammonium) uptake closely matched the POC:PON ratio of the suspended particulate matter (Nelson and Smith, 1986). These two ratios also agreed closely during early bloom conditions near the Weddell-Scotia Sea ice edge in spring, but nitrogen uptake exceeded autotrophic requirements in the Weddell Sea marginal ice zone in late summer/early autumn (Smith and Nelson, 1990). This implies that heterotrophic uptake of nitrogen is highly significant during winter in the Weddell-Scotia Seas. Bacteria can use nitrate as a nitrogen source (Horrigan *et al.,* 1988), but in general nitrate uptake is attributed to phytoplankton in most systems (Laws, 1991). In autumn, chlorophyll levels were considerably lower than those in the spring and summer, and organic detritus was a significant component of the POC (Nelson *et al.,* 1989). The seasonal trend just described is consistent with the hypothesis that as the relative contribution of phytoplankton carbon to total POC diminishes, the ratio of autotrophic to heterotrophic nitrogen uptake also diminishes. To a first-order approximation, this would imply that the biomass and activity of heterotrophic plankton are much less variable seasonally than is the case for phytoplankton, and that heterotrophic metabolism is the dominant process in the nitrogen cycle of the surface layer, essentially by default, in winter when uptake by phytoplankton is at its annual minimum due to limitation by low irradiance. Although the spatial distribution of bacterial productivity was similar to that of phytoplankton during spring and autumn, bacterial biomass did not show large seasonal or spatial variations in the marginal ice zone (Cota *et al.,* 1990), implying that the seasonal pattern we have just hypothesized may be correct in its main features. If this crude picture of the relative seasonal importance of heterotrophic activity is even approximately correct, then heterotrophic organisms (most likely bacteria) would have the largest influence on elemental cycling and particulate matter composition in winter.

5. Summary

1. The marginal ice zone in winter was found to be an area of measurable phytoplankton productivity and nutrient uptake, albeit at low rates.

2. The distribution and composition of particulate matter were closely linked to physical processes such as eddy generation, which in turn controlled the rates of ice ablation and input of particulate and dissolved matter from ice.

3. Primary productivity was low and appeared to be limited by available irradiance, which is lowest during this season.

4. Ammonium provided about half of the plankton's nitrogen demand during the winter season, in contrast to results of other seasons, when nitrate was the main nitrogen source being exploited.

5. Based on carbon and nitrogen uptake ratios, it appears that nitrogen cycling by heterotrophs predominates over autotrophic processes in winter.

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