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## Temporal and spatial patterns in the Ross Sea: Phytoplankton biomass, elemental composition, productivity and growth rates

Walker O. Smith Jr.,<sup>1</sup> David M. Nelson,<sup>2</sup> Giacomo R. DiTullio,<sup>1,3</sup> and Amy R. Leventer<sup>4,5</sup>

**Abstract.** The temporal and spatial patterns of phytoplankton biomass, productivity, and particulate matter composition in the Ross Sea were assessed during cruises in January 1990 and February 1992. Biomass and primary productivity in the southern Ross Sea were greatest during mid-January, with surface chlorophyll concentrations, particulate organic carbon levels, and integrated primary productivity averaging  $4.9 \mu\text{g L}^{-1}$ ,  $0.54 \text{ mg L}^{-1}$ , and  $2.63 \text{ g C m}^{-2} \text{ d}^{-1}$ , respectively. Comparable mean concentrations and rates for February were  $1.1 \mu\text{g L}^{-1}$ ,  $0.29 \text{ mg L}^{-1}$ , and  $0.78 \text{ g C m}^{-2} \text{ d}^{-1}$  (decreases of 76, 46, and 70%, respectively), indicative of the scale of temporal changes. A distinct south-north transition also was observed both in productivity and phytoplankton biomass, with the lowest values occurring in the northern Ross Sea. East-west gradients in phytoplankton biomass and composition occurred within the southern Ross Sea. The areal productivity of the Ross Sea ranged from  $0.15$  to  $2.85 \text{ g C m}^{-2} \text{ d}^{-1}$  and is among the highest found in the entire Antarctic. Carbon:chlorophyll ratios were uniformly high but were highest (150) in 1990 in the diatom-dominated western Ross Sea. Surface growth rates were modest, averaging less than  $0.2 \text{ day}^{-1}$  during both seasons. We hypothesize that the marked seasonality in the region provides an environment in which net growth rates, although slow, are maximized through low loss rates and which allows biomass to accumulate in the surface layer. Furthermore, the temporal variations are quantitatively similar to the observed spatial variations. Therefore the dominant determinant of phytoplankton biomass and productivity at any one point on the Ross Sea continental shelf is the stage of the seasonal growth cycle.

### 1. Introduction

Satellite images reveal that the Ross Sea is the site of the largest and most predictable phytoplankton blooms in the Southern Ocean [Comiso *et al.*, 1993; Sullivan *et al.*, 1993], and field studies have documented the substantial accumulations of particulate material [e.g., El-Sayed *et al.*, 1983; Smith and Nelson, 1985]. However, both satellite and field efforts are hindered by a lack of data that adequately resolve the temporal and spatial variations which are known to occur. Although Smith and Nelson [1985] suggested that meltwater released at a receding ice edge produces strong stratification in the presence of high concentrations of nutrients and thus stimulates extensive ice-edge blooms, few data exist over large areas to test adequately the role of ice on productivity and biomass accumulation. Studies in other regions have shown the importance of meteorological forcing of vertical mixing and the

resultant controls on phytoplankton growth in the marginal ice zone [Savidge *et al.*, 1995; Boyd *et al.*, 1995].

The Ross Sea continental shelf is also the site of extensive diatomaceous deposits [e.g., Ledford-Hoffman *et al.*, 1986]. The highest sedimentary biogenic silica concentrations (>40% by weight) occur in the southwestern portion near the coast, and levels an order of magnitude less (<5% by weight) occur in the northern shelf [Dunbar *et al.*, 1985]. An east-west gradient of similar magnitude is observed in the south, with the sediments decreasing to <5% opal in the southwestern Ross Sea. The causes of this spatial gradient are unknown. Gradients in surface productivity and phytoplankton composition, spatial variations in vertical flux and mineralization, and sedimentary resuspension and lateral transport all could influence the seabed composition.

The controls of phytoplankton biomass and growth in the Antarctic are also poorly known. It has been argued that irradiance controls phytoplankton growth and biomass on seasonal [Smith and Sakshaug, 1990] and short (e.g., days to weeks) time scales [Nelson and Smith, 1991]. However, it has also been suggested that iron can limit phytoplankton growth in the Southern Ocean as well as the occurrence of certain species [Martin *et al.*, 1990; de Baar *et al.*, 1990]. Grazing by microzooplankton has also been suggested to be an important factor in regulating phytoplankton biomass [Mitchell and Holm-Hansen, 1991], but little quantitative evidence is available to support this hypothesis. Given the high inorganic nutrient levels found throughout the Antarctic, it is unlikely that macronutrients play a significant role in controlling phytoplankton biomass. However, Sullivan *et al.* [1993] found large-scale correlations between chlorophyll and silicic acid concentrations (particularly in ice-free regions), which suggest that

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in some areas the role of nutrients may not be as unimportant as previously believed.

In 1990 and 1992 we conducted cruises to the continental shelf of the Ross Sea. Our objectives were (1) to quantify the horizontal gradients in phytoplankton biomass and productivity, (2) to measure the vertical flux of biogenic matter through the water column over 2 full years, (3) to measure the accumulation and regeneration rates of sedimentary material, and (4) to determine the nature and magnitude of the coupling between silica and carbon in both the water column and sediments. The cruises were conducted in January 1990 and February 1992, and seasonal trends were assessed by merging these data sets. Furthermore, the data collected during short-term field studies are linked by vertical flux information from moored, time-series sediment traps as well as the long-term (i.e., hundreds to thousands of years) sediment accumulation data [e.g., *DeMaster et al.*, 1992; *Nelson et al.*, this issue; *DeMaster et al.*, this issue]. This paper presents a description of the spatial and temporal variations of the surface layer processes in the Ross Sea.

## 2. Materials and Methods

Two cruises using the RV *Polar Duke* were conducted in the Ross Sea. The first was from January 12 to February 5, 1990, and the second was from February 5 to February 28, 1992. The general sampling pattern in both years was to sample transects perpendicular to the Victoria Land coast. In 1990 the transects were located at 76°30'S and at 72°30'S, whereas in 1992 those two transects as well as one at 75°S were sampled. Stations were occupied in heavy pack ice near the coast to open water (Figures 1a and 1b). On the basis of the temperature and salinity profiles, the southern transect (76° 30'S) was divided into three zones (I, II, and III) for further analysis of the spatial and temporal patterns of biomass and productivity in 1990 (Figures 1a and 1b). Too few samples were collected in 1992 to make a statistical treatment valid for that cruise.

Continuous depth profiles of temperature and salinity were collected at each station using a Neil Brown conductivity-temperature-depth (CTD) system, and density values were computed from these data. Downwelling irradiance was measured using an underwater quantum sensor, and the diffuse attenuation coefficient was calculated from these data or from the depth at which a secchi disk disappeared. Water samples were collected from the 50, 30, 15, 5, 1, and 0.1% isolumes, as well as the surface and other selected depths in the upper 150 m. Samples were collected using Niskin bottles with Teflon-coated closing springs mounted on a rosette. Subsamples were taken from the same bottles for nutrients, particulate matter concentrations, and rate determinations.

Chlorophyll *a* (hereafter referred to as chlorophyll) was measured fluorometrically on discrete samples collected throughout the water column. Samples (generally 280 mL) were filtered through 25-mm Glass Microfibre Filters (GF/F), placed in glass centrifuge tubes with 10 mL 90% acetone, sonicated on ice for 15 min, and extracted for 15 min more in the dark. The fluorescence was read on a Turner Designs Model 10 fluorometer before and after acidification. The fluorometer was calibrated before and after each cruise using commercially purified chlorophyll *a*. Particulate carbon and nitrogen concentrations were measured by filtering subsamples (500-1000 mL) through precombusted (450°C for 2 hours) GF/F filters which were rinsed with approximately 10 mL of 0.01N HCl in seawater. The

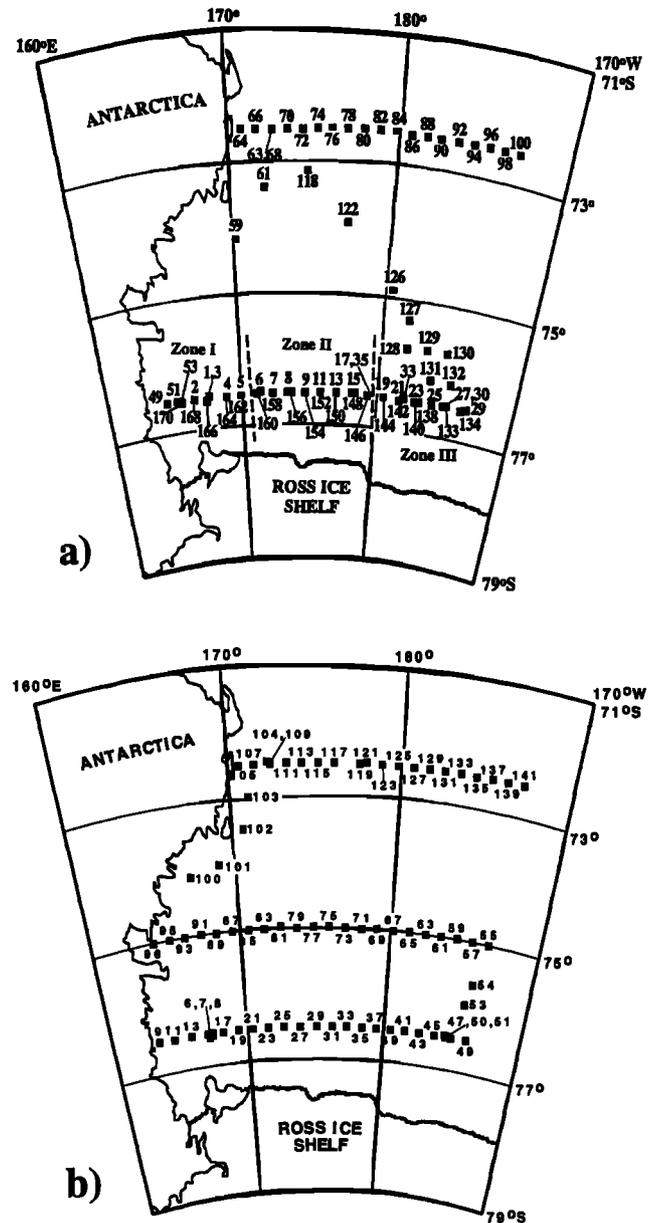


Figure 1. Maps showing station locations for all stations in which particulate matter concentrations and primary productivity were measured in (a) 1990 and (b) 1992.

samples were folded and placed in 10-ml precombusted glass vials, capped with precombusted aluminum foil, and dried at 60°C. Blanks were filters placed in series under the sample filter and therefore had seawater passed through them. All samples were analyzed on a Carlo-Erba Model 1180 elemental analyzer.

Biogenic silica was measured using the alkaline digestion technique of *Brzezinski and Nelson* [1989]. Subsamples were filtered through 0.6- $\mu$ m polycarbonate filters, placed in plastic petri dishes, and dried at 60°C. In the laboratory, samples were digested in 0.2 N NaOH at 100°C for 30 min, the pH was adjusted to 4.0, and the dissolved silicic acid was analyzed by standard colorimetric techniques. Samples for diatom enumeration were preserved in Lugol's solution, and all samples were counted using an inverted microscope. All elemental ratios were calculated by conducting a linear regression between two variables and

calculating the slope of the regression using Model II regression statistics [Laws and Archie, 1981].

Primary productivity was measured using simulated in situ techniques [Smith and Nelson, 1990]. Samples were collected at all times of the day from the seven isolumes and placed in 280-mL polycarbonate bottles; approximately 20  $\mu\text{Ci}$  of  $\text{NaH}^{14}\text{CO}_3$  was added to each, and they were placed in on-deck incubators through which surface seawater flowed. The incubator was equipped with troughs which were wrapped with plastic neutral density screening which reduced the irradiance to that of the corresponding isolume. The isolumes at or below 30% also had a blue filter to correct for light quality changes within the water column. Samples were generally incubated for 24 hours in order to include effects of diel solar cycles and diurnal rhythms and then were filtered through 25-mm GF/F filters, rinsed with approximately 5 mL of 0.01N HCl in seawater [Goldman and Dennett, 1985], and placed in scintillation vials with 10 mL Ecolume. The amount of added inorganic radioactivity in each sample was quantified by placing an aliquot (0.5 mL) of unacidified sample in a vial and adding scintillation fluor. All samples were counted on a liquid scintillation counter and corrected for quenching. Controls for all incubations were time-zero samples, which were treated identically except that they were filtered immediately after injection with radioisotope. Time-zero counts were generally less than 4% of the surface incorporation and averaged 21% of the values from the 0.1% isolume. All integrations were conducted from the surface to the base of the euphotic zone (depth of the 0.1% isolume), which varied from 20 to 125 m during the study. Photosynthetic incorporation into various cellular pools was assessed by conducting parallel  $^{14}\text{C}$  incubations and freezing the filters in liquid nitrogen. In the laboratory the filter was sequentially extracted using various solvents [DiTullio, 1993]. Growth rates were calculated from productivity and standing stocks of particulate carbon [Eppley, 1968].

### 3. Results

#### 3.1. Standing Stocks

A general pattern of vertical stratification was found during both cruises. A highly stratified region was found near the coast at  $76^\circ 30'\text{S}$  in each year, and little difference in the strength of this stratification was noted between the beginning and end of the 1990 cruise, a period of slightly more than 2 weeks (Figures 2a, 2b, and 2c). The coastal zone seemed to be constrained by a hydrographic front, and to the east the water column was much less stratified. This central area in turn graded into a region of slightly stronger

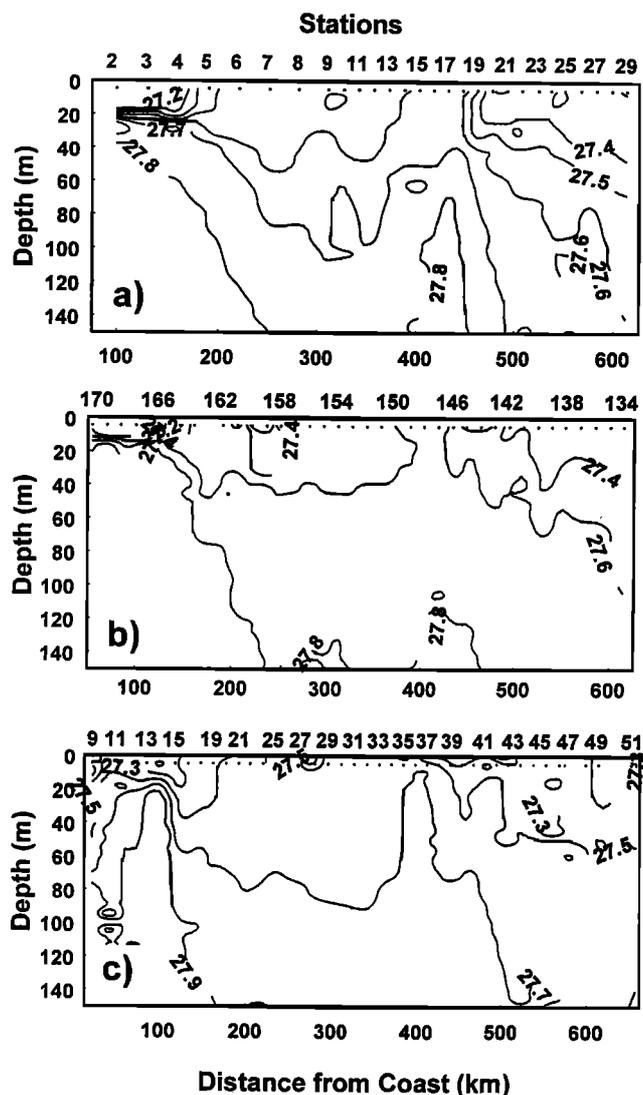


Figure 2. Vertical distribution of  $\sigma_t$  across three transects at  $76^\circ 30'\text{S}$  in the Ross Sea: (a) January 13-16, 1990; (b) February 1-4, 1990; (c) February 8-13, 1992.

stratification in the west. Mean mixed layer depths as well as average nitrate and silicic acid concentrations for these transects substantiate this pattern (Table 1). Stratification in the northern portion of the Ross Sea during both years was less pronounced than in the south (Figures 3a and 3b). Strong frontal structure was

Table 1. The Average Mixed Layer Depths and Surface Concentrations of Nitrate and Silicic Acid Within Transects in the Ross Sea in 1990 and 1992

Date	Transect	Mixed Layer Depth, m	Nitrate, $\mu\text{M}$	Silicic Acid, $\mu\text{M}$
Jan. 13-16, 1990	$76^\circ 30'\text{S}$	$32.5 \pm 13.4$	$15.4 \pm 6.10$	$52.7 \pm 16.5$
Jan. 31 to Feb. 5, 1990	$76^\circ 30'\text{S}$	$26.0 \pm 13.3$	$12.2 \pm 4.51$	$42.3 \pm 17.3$
Feb. 5-14, 1992	$76^\circ 30'\text{S}$	$37.1 \pm 28.2$	$16.5 \pm 4.00$	$64.2 \pm 12.2$
Jan. 22-28, 1990	$72^\circ 30'\text{S}$	$31.7 \pm 15.2$	$26.4 \pm 1.08$	$56.1 \pm 6.61$
Feb. 21-28, 1992	$72^\circ 30'\text{S}$	$45.5 \pm 19.6$	$25.0 \pm 5.61$	$58.7 \pm 7.97$

Standard deviation for each is also listed. Mixed layer depths are determined from a change in  $\sigma_t$  value of 0.1 unit.

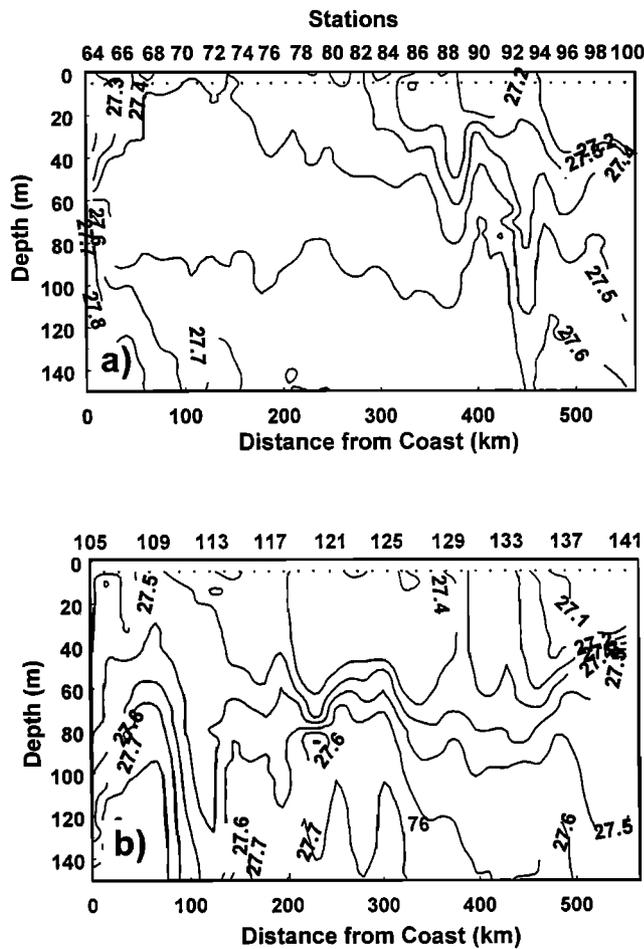


Figure 3. Vertical distribution of  $\sigma_t$  across two transects at 72°S in the Ross Sea: (a) January 23-26, 1990; (b) February 23-28, 1992.

not observed in the north, and mixed layers were similar to those found in the southwestern portion of the continental shelf (Table 1).

Phytoplankton biomass showed both temporal and spatial variations. The maximum chlorophyll concentrations in both years occurred within the southern transects and reached 11.8 and 4.8  $\mu\text{g L}^{-1}$  in 1990 and 1992, respectively, whereas maximum values for the northern transects in 1990 and 1992 were 3.7 and 2.4  $\mu\text{g L}^{-1}$ . Chlorophyll concentrations were greatest in mid-January in the southern sector and decreased markedly (76%) by mid-February (Figures 4a, 4b, and 4c). Chlorophyll concentrations were less in the northern section of the Ross Sea than in the south. The transect which was occupied at 75°S in 1992 was more similar to those at 76°30'S than those at 72°30'S (in terms of phytoplankton community composition), and the maximum chlorophyll concentration was 3.1  $\mu\text{g L}^{-1}$ .

Particulate carbon, particulate nitrogen, and biogenic silica distributions showed patterns similar to those of chlorophyll. When all data are analyzed, a clear temporal decrease in particulate carbon, particulate nitrogen, and biogenic silica concentrations becomes apparent (Table 2). Mean values of each within the transects also illustrate the south-north trend in phytoplankton biomass (Table 2). Differences also occurred within the southern transect and were greatest for biogenic silica, whose surface levels ranged from 27  $\mu\text{mol L}^{-1}$  in 1990 and 16  $\mu\text{mol L}^{-1}$  in 1992 near the coast to 3.5  $\mu\text{mol L}^{-1}$  in 1990 and 1.0  $\mu\text{mol L}^{-1}$  in 1992 in the south

central portion of the Ross Sea. Particulate carbon and nitrogen concentrations were also elevated within the coastal region (average surface concentrations of particulate organic carbon (POC) and particulate organic nitrogen (PON) equaled 590 and 110  $\mu\text{g L}^{-1}$  respectively, in 1990).

Diatoms reached their maximal abundance within the coastal region, and, in general, the abundance of diatoms closely paralleled the distribution of biogenic silica. The coastal region at 76°30'S in 1990 was dominated numerically by the centric diatoms *Fragilariopsis curta* and *F. cylindrus*. In regions east of the front, those two species were commonly found along with occasional large concentrations of *Chaetoceros* spp. High concentrations of the prymnesiophyte *Phaeocystis antarctica* were also observed in the areas east of the front but never to the west of the front. In the northern transect the same three diatoms (*P. curta*, *P. cylindrus*, and *Chaetoceros* spp.) were also numerically dominant, and *Corethron criophilum* was consistently observed.

### 3.2. Elemental Ratios

Elemental ratios of the particulate matter varied within and between transects, as well as seasonally (Table 3). Particulate

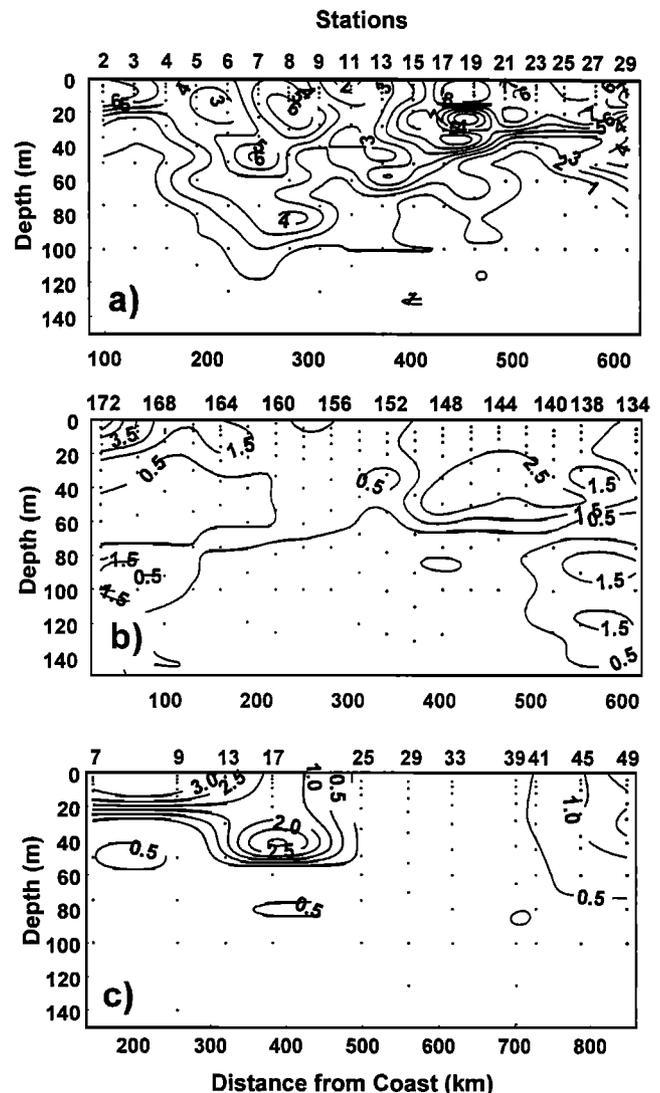


Figure 4. Vertical distribution of chlorophyll across three transects at 76°30'S in the Ross Sea: (a) January 13-16, 1990; (b) February 1-5, 1990; (c) February 6-11, 1992.

**Table 2.** The Average Concentrations and Standard Deviations at the Surface of Chlorophyll, Particulate Carbon, Particulate Nitrogen, and Biogenic Silica for Transects in the Ross Sea in 1990 and 1992

Date	Transect	Chlorophyll, $\mu\text{g L}^{-1}$	Particulate Carbon, $\mu\text{mol L}^{-1}$	Particulate Nitrogen, $\mu\text{mol L}^{-1}$	Biogenic Silica, $\mu\text{mol L}^{-1}$
Jan. 13-16, 1990	76°30'S	4.87 ± 2.09 <sup>a</sup> (n = 22)	535 ± 148 <sup>a</sup> (n = 17)	97.3 ± 27.8 <sup>a</sup> (n = 17)	9.83 ± 8.6 <sup>a</sup> (n = 16)
Jan. 31 to Feb. 5, 1990	76°30'S	1.75 ± 0.74 (n = 17)	353 ± 129 (n = 17)	68.1 ± 20.0 (n = 17)	9.19 ± 6.0 (n = 17)
Feb. 5-14, 1992	76°30'S	1.12 ± 0.87 (n = 19)	288 ± 141 <sup>b</sup> (n = 19)	60.1 ± 26.4 <sup>b</sup> (n = 16)	4.63 ± 4.04 (n = 15)
Jan. 22-28, 1990	72°30'S	0.89 ± 0.49 (n = 20)	170 ± 73.8 (n = 20)	35.5 ± 16.3 (n = 20)	3.44 ± 1.9 (n = 20)
Feb. 21-28, 1992	72°30'S	0.59 ± 0.62 (n = 11)	110 ± 54.6 (n = 9)	22.5 ± 10.7 (n = 9)	3.83 ± 1.52 (n = 7)

Here *n* is the number of samples.

<sup>a</sup>Significantly different from February, 1992 section at 76°30'S ( $p < 0.001$ )

<sup>b</sup>Significantly different from February, 1992 section at 72°30'S ( $p < 0.001$ )

carbon:chlorophyll mass ratios averaged 126 and 183 for the entire southern transect in 1990 and 1992, respectively, whereas for the northern transect they were 228 and 150 in the 2 years. Within the southern transect, the highest ratios in 1990 (150; Table 3) were observed closest to the coast where diatoms dominated and the lowest ratios (111) in the central section where *Phaeocystis* often was prevalent. The number of data points in 1992 was less, and therefore the trends could not be analyzed with confidence. The northern section's ratios were closer to those of the coastal zone, consistent with the dominance of diatoms in that area.

Particulate carbon:nitrogen ratios were much less variable than the carbon:chlorophyll ratios (Table 3), ranging from 5.0 to 7.9 (compared to the Redfield ratio of 6.6). The lowest C:N ratios observed were in the coastal, diatom-dominated waters, and the highest were encountered in the northern section in 1990. In general, C:N ratios were greater later in the season. Molar carbon:biogenic silica ratios were lowest in the water dominated by diatoms near the coast and averaged 2.4 in 1990 and highest in waters with lower biogenic silica concentrations (Table 3). These ratios increased in the southern region away from the coast, presumably reflecting the increased relative contribution of diatoms to particulate matter composition. The POC:BSi mole ratios in the northern section averaged 4.3 and 3.7 in the 2 years.

### 3.3. Rate Processes

The productivity in the Ross Sea was high and ranged from 0.15 to 2.85  $\text{g C m}^{-2} \text{d}^{-1}$ . In 1990, integrated euphotic zone primary productivity averaged 0.98  $\text{g C m}^{-2} \text{d}^{-1}$  for the entire Ross Sea ( $n = 69$ ; standard error = 0.063; minimum 0.23  $\text{g C m}^{-2} \text{d}^{-1}$ ; maximum 2.82  $\text{g C m}^{-2} \text{d}^{-1}$ ). Productivity for the first occupation of the southern transect averaged 2.63  $\text{g C m}^{-2} \text{d}^{-1}$ , whereas the second occupation of this transect productivity averaged 1.14  $\text{g C m}^{-2} \text{d}^{-1}$  (Table 4). The first occupation was significantly greater than any other ( $p < 0.001$ ). Because of the limited number of measurements in each zone (approximately 4 each zone), no attempt was made to distinguish within transect variations. The northern section had a mean daily productivity of 0.82  $\text{g C m}^{-2} \text{d}^{-1}$ . In 1992, integrated euphotic zone productivity for the entire cruise averaged 0.71  $\text{g C}$

$\text{m}^{-2} \text{d}^{-1}$  ( $n = 45$ ; standard error = 0.085; minimum 0.15  $\text{g C m}^{-2} \text{d}^{-1}$ ; maximum 2.56  $\text{g C m}^{-2} \text{d}^{-1}$ ), which is significantly less than the overall productivity in 1990 ( $p < 0.02$ ). The mean productivities on the 76°30', 75°, and 72°30'S transects were 0.78, 0.86, and 0.51  $\text{g C m}^{-2} \text{d}^{-1}$ , respectively (Table 4). Rates of carbon fixation within the water column were similar between the 2 years (Figure 5), but because the chlorophyll concentrations were greater in 1990 than in 1992, chlorophyll-specific productivity was greater in 1992 (approximately 1.0 and 2.0  $\text{mg C (mg chl)}^{-1} \text{h}^{-1}$ ; Figure 6a). Maximum growth rates were also low (generally  $< 0.2 \text{ day}^{-1}$ ; Figure 6b) and were less than 30% of the maximal temperature-limited growth rate [Eppley, 1972].

Carbon allocation patterns in 1992 indicated that much of the photosynthate (on average 38.7%) remained as low molecular weight compounds at the end of the 24-hour incubations (Figure 7). The next most important intracellular pool was protein (average of 29.9% of the total photosynthate), and there was an approximately equal allocation between polysaccharides and lipids (Figure 7). We hypothesized that low molecular weight allocation would be related to growth rate of the assemblage, but no relationship was found between the two. Also, little change in the carbon fixation partitioning was noted with depth. The gross patterns of photosynthate allocation also were similar between the southern and northern transects, despite differences in overall productivity, biomass, species composition, and growth rates.

## 4. Discussion

The continental shelf of the Ross Sea has been suggested to be the site of the largest and most predictable phytoplankton bloom in the entire Southern Ocean [Comiso et al., 1993; Sullivan et al., 1993]. Our results confirm the large-scale patterns observed from satellites, but they also distinguish the spatial and temporal variations which occur. For example, a large change was noted in biomass and productivity in the southern Ross Sea over a period of approximately 28 days, with chlorophyll concentrations decreasing by 76% and productivity decreasing 70%. Spatial differences in biomass also were observed between the northern portion of the continental shelf and the southern portion, with

Table 3. Compositional Ratios (RAT) of Particulate Matter Within the Transects in the Ross Sea

Date and Transect	Carbon:Chlorophyll, w/w				Carbon:Nitrogen, w/w				Carbon:Silica mol/mol			
	RAT	N	r	r	RAT	INT	N	r	RAT	INT	N	r
76°30'S, 1990	126	140	0.77	0.77	5.85	40.0	383	0.91	4.20	17.4	334	0.62
Zone I	150	108	0.83	0.83	4.95	59.8	91	0.96	2.42	9.78	72	0.87
Zone II	111	156	0.75	0.75	7.03	23.5	199	0.85	9.28	19.0	180	0.40
Zone III	116	121	0.79	0.79	6.22	31.2	93	0.90	4.36	7.70	82	0.75
76°30'S, 1992	183	144	0.87	0.87	5.63	-8.28	122	0.95	2.65	12.2	93	0.82
72°30'S, 1990	228	52.3	0.73	0.73	7.91	35.1	163	0.83	4.25	4.20	178	0.71
72°30'S, 1992	150	44.6	0.94	0.94	5.38	-5.50	61	0.97	3.72	-2.90	35	0.88

INT is intercept, N is number of samples analyzed, and r is the correlation coefficient. All elemental ratios were determined by Model II regression. All regressions are significant at  $p < 0.01$ . Ratios are calculated as weight to weight (w/w).

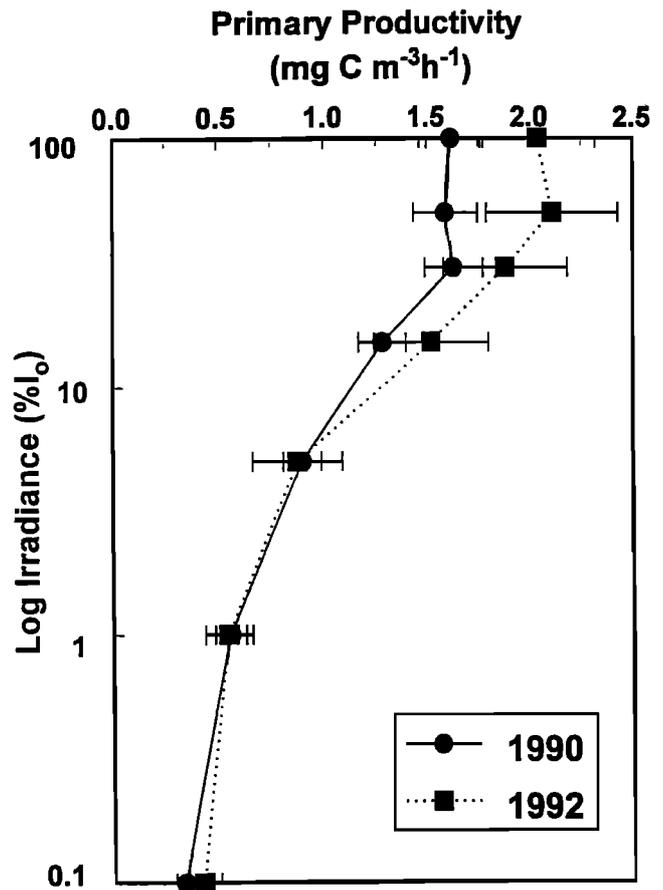


Figure 5. Vertical distribution of average euphotic zone primary productivity in 1990 and 1992. The average depths of the 0.1% isolume in 1990 and 1992 were 60 and 41 m, respectively. The bars represent standard errors.

biomass in the north on average only 23-37% of that in the south in 1990 and 38-83% in 1992 (depending on the variable compared). Similarly, primary productivity in the north was 72 and 65% of the productivity in the southern transect during 1990 and 1992, respectively, when the two transects closest in time of sampling are compared. Such temporal and spatial trends in productivity and biomass were not totally unexpected, based on patterns of ice retreat. Zwally *et al.* [1983] and Comiso *et al.* [1993] clearly demonstrated that the Ross Sea ice cover retreats in two directions. The first is from the south, where the Ross Sea polynya along the Ross Ice Shelf expands rapidly to the north in November and December. The second is from the northern extent of the ice, which gradually retreats toward the continental shelf. The result is that the southern section we studied (76°30'S) becomes largely ice-free (except in the far western portions near the Victoria Land coast) in December, whereas the northern section (72°30'S) does not become ice-free until mid-January (we confirmed this general pattern in 1990 and 1992 from the ship). Hence biomass has less time to accumulate, and overall productivity is therefore less.

We assumed that the temporal patterns we observed resulted from changes which occur throughout the Ross Sea in a predictable manner and were not attributable to interannual variations, but few data exist to adequately test this assumption. However, ice-retreat patterns are very consistent between years, suggesting only small interannual variations in physical forcing of

**Table 4.** Summary of Primary Productivity Data (Means and Standard Deviations) from Transects in 1990 and 1992

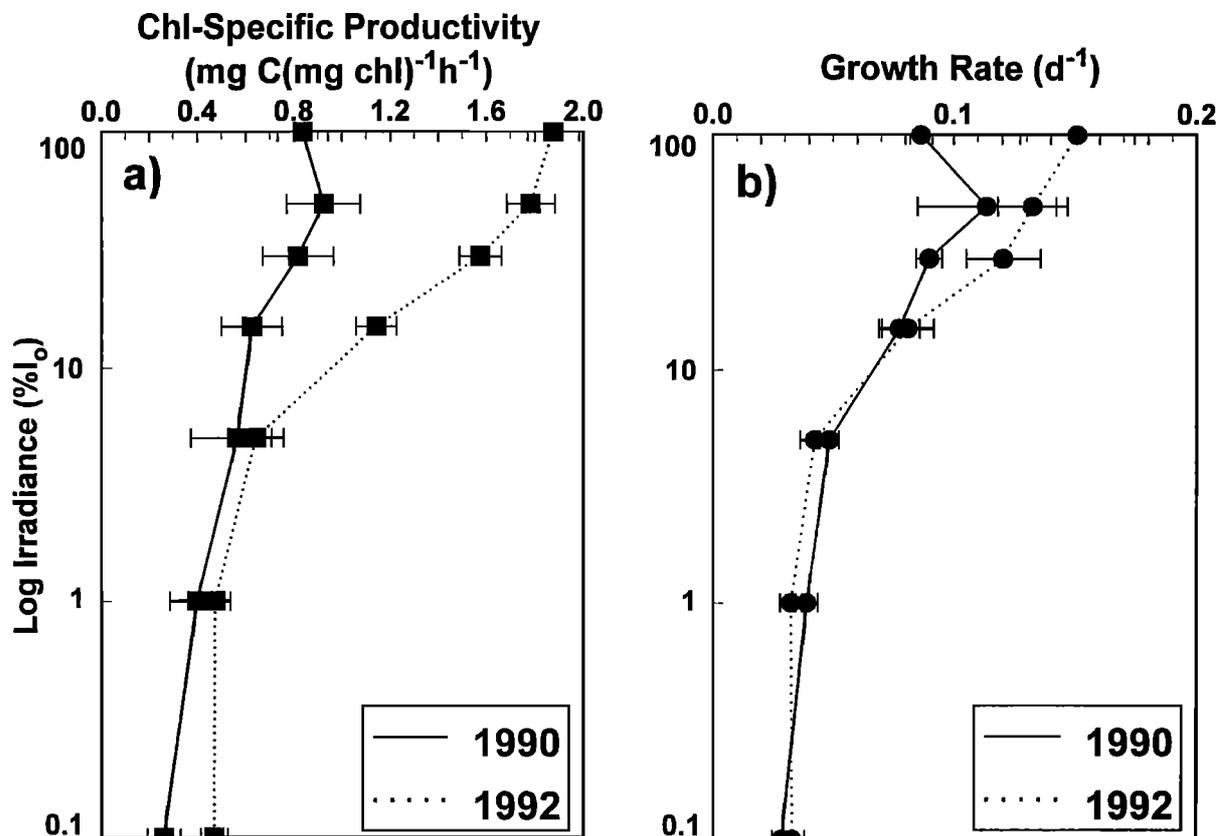
Date	Transect	Primary Productivity, g C m <sup>-2</sup> d <sup>-1</sup>
Jan. 13-16, 1990	76°30'S	2.63 ± 1.43 ( <i>n</i> = 22)*
Jan. 31 to Feb. 5, 1990	76°30'S	1.14 ± 0.61 ( <i>n</i> = 19)
Feb. 5-14, 1992	76°30'S	0.78 ± 0.65 ( <i>n</i> = 19)
Feb. 15-19, 1992	75°S	0.86 ± 0.65 ( <i>n</i> = 11)
Jan. 22-28, 1990	72°30'S	0.82 ± 0.61 ( <i>n</i> = 14)
Feb. 21-28, 1992	72°30'S	0.51 ± 0.36 ( <i>n</i> = 14)

Here *n* = number the number of stations.

\*Significantly different (*p* < 0.001) from both Jan. 31 to Feb. 5 and Feb. 5-14 transect, as well as the 72°30'S transects

biological processes [Zwally *et al.*, 1983]. Similar distributions and magnitudes of phytoplankton biomass at 76°30'S have been observed for cruises at the same time of year [Smith and Nelson, 1985; W. O. Smith, unpublished data, 1994], and Arrigo and Weiss [1996] found that pigment levels in the southern Ross Sea observed from satellite were similar among years, although the timing of the maximum varied over approximately 3 weeks. The available data on surface layer biological processes suggest that the magnitude of interannual variations is much less than those induced by the annual temporal patterns [Arrigo and Weiss; 1996], and hence the use of both years' data to elucidate the temporal patterns will not introduce a large bias.

Our results suggest that the temporal patterns are of similar magnitude to the spatial differences in the Ross Sea, consistent with the findings of Comiso *et al.* [1993]. The general temporal pattern we observed was a maximum in productivity and biomass in mid-January (the earliest we sampled in our program) and a substantial decrease thereafter. Chlorophyll decreased rapidly in late January, with mean concentrations being less than half those observed 2 weeks earlier (Table 2). In contrast, biogenic silica concentrations did not decrease as quickly (Table 2). This pattern is consistent with the vertical flux pattern along 76°30'S [DeMaster *et al.*, 1992]. That is, flux in the eastern portion of the southern transect reached its annual maximum earlier in the year



**Figure 6.** Vertical distributions of (a) average chlorophyll-specific productivity and (b) growth rates in the euphotic zone in 1990 and 1992, respectively. The bars represent standard errors.

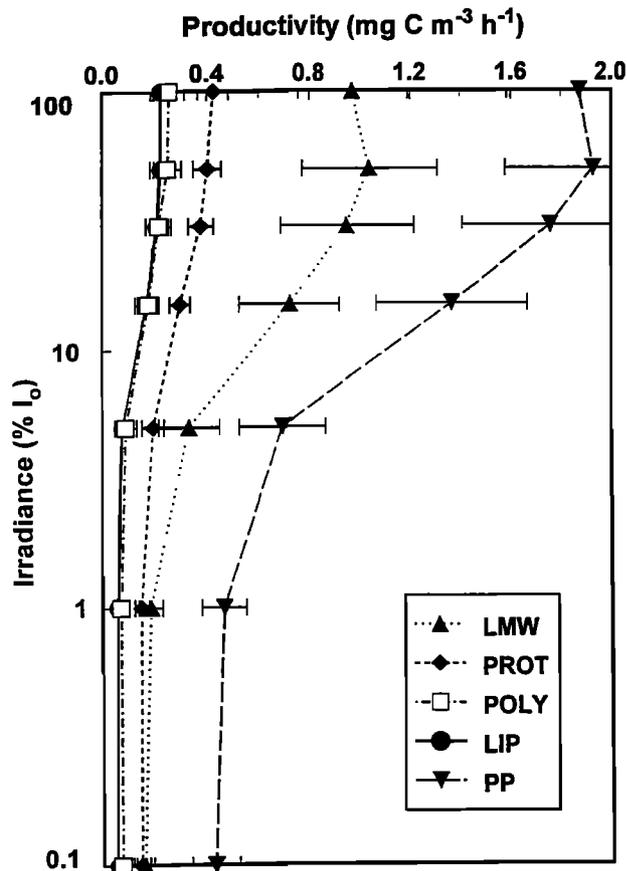


Figure 7. The average productivity and allocation of photosynthate into various intracellular carbon pools at various isolums throughout the euphotic zone. PROT, protein; LMW, low molecular weight compounds; POLY, polysaccharides; LIP, lipids; PP, total productivity. The bars represent standard errors.

than the flux in the western portion. The composition of the flux was also greatly different, with the flux in the west being dominated by fecal pellets and the flux in the east being dominated by cellular debris and organic aggregates. It is likely that diatoms were removed largely by herbivorous grazing, which was decoupled in time with production, whereas nondiatomaceous phytoplankton (i.e., *Phaeocystis*) were removed by aggregation and passive sinking, thereby decoupling removal of carbon and silica from the surface layer. High relative fluxes of phaeophorbides (with respect to total phaeopigments) into free-floating sediment traps in the western portion of the study area and of phaeophytin in the eastern section support this hypothesis [DiTullio and Smith, this issue].

The elemental composition of the phytoplankton varied spatially and temporally as well (Table 3). Using regression analyses, the slope of the regression is taken as the ratio of elemental material which resulted from growth, and the intercept can be interpreted as an estimate of detrital contribution. We recognize the impact that detrital material can have on the determination of elemental ratios [Banse, 1977], and by including large numbers of samples we hoped to derive a mean ratio that resulted from phytoplankton growth. Microscopic analysis did not suggest a large detrital component in this or other studies in the region [Wilson et al., 1986]. Within the 76°30'S transect, large differences were noted in the carbon:chlorophyll and carbon:silica ratios, which in turn correlated with the differences in the

dominant assemblages in the zones. Diatom-dominated waters near the coast had the highest C:CHL ratio in mid-January (150), whereas in waters dominated by *Phaeocystis* the ratio approached 116. The C:CHL ratio increased in February and approached 183. This suggests that the assemblages were adapting through time and adjusting their carbon:chlorophyll ratio as a function of in situ environmental conditions. It has also been shown that for some species the C:CHL ratio is influenced by growth rate [e.g., Tang, 1996]. Regardless of the cause(s), the extreme carbon:chlorophyll ratio is a characteristic feature of the phytoplankton of the Ross Sea.

DiTullio and Smith [this issue] used high-performance liquid chromatography (HPLC)-derived pigments to differentiate taxonomic dominance at stations in the southern transect and found that at stations dominated by 19'-hexanoyloxyfucoxanthin, a pigment found in *Phaeocystis*, the carbon:chlorophyll ratio was 92. Similarly, for stations with large concentrations of fucoxanthin (and not 19'-hexanoyloxyfucoxanthin), and therefore dominated by diatoms, the C:CHL ratio was 210. Finally, a pigment-labeling experiment at a station dominated by diatoms resulted in a C:CHL ratio of 134. This method [Redalje and Laws, 1981; Goericke and Welschmeyer, 1992] provides a direct measurement of the C:CHL ratio, unbiased by the presence of detritus. All of these results suggest that diatoms, particularly those near the coast, have a higher, and in some cases much higher, C:CHL ratio than other species in the Antarctic and that these ratios in the Ross Sea are much greater than those found in other areas of the ocean [e.g., Bannister and Laws, 1983]. It is interesting to note that the laboratory results of Durban [1977] showed that at low temperatures, C:CHL ratios of *Thalassiosira nordenskiöldii* increased, an effect opposite to that of irradiance, whereas Verity [1981] found in *Leptocylindrus danicus* that the C:CHL ratio increased at both low temperatures and irradiances. This suggests that the in situ effects of temperature and irradiance (and their interaction) might be controlled by species composition. It is possible that the effects of temperature are quantitatively more important than those of irradiance, but much more work is needed to verify this suggestion.

The carbon:biogenic silica ratios we observed (from 2.4 in the diatom-dominated coastal zone to 4.25 in the northern region) were similar to those reported by Smith and Nelson [1985] for the coastal region (1.6, computed as an average of all ratios rather than a Model II regression). Other reported Antarctic C:Si ratios were 2.3 from the western Weddell Sea in austral autumn [Nelson et al., 1989] and 7.7 from the Weddell-Scotia Sea ice edge in austral spring 1983 [Nelson et al., 1987]. Our values encompass the ratios observed elsewhere in the Southern Ocean; furthermore, they suggest that the diatom assemblages near the coast have extremely low C:Si ratios. Due to the low number of samples, it is difficult to resolve the temporal patterns in this ratio. Ratios in the northern transect were slightly higher than those near the coast in the south but not as high as the ratio found in the eastern portion of the southern transect, where non-diatomaceous species were more common.

Despite the substantial productivity observed, particularly during the mid-January occupation of the southern transect, growth rates were relatively low (Figure 6b). Eppley's [1972] equation for growth under optimal conditions predicts a maximal growth rate at 0°C of 0.85 doublings d<sup>-1</sup> (equal to an instantaneous growth rate of 0.59 day<sup>-1</sup>). We found growth rates up to 0.2 day<sup>-1</sup> at the surface, where nutrients were replete and irradiance near optimal. On the basis of protein incorporation [DiTullio, 1993], the relative growth rate in 1992 averaged 43% of  $\mu_{max}$  which suggests an average growth rate of 0.25 day<sup>-1</sup>. Hence both

estimates of growth rates are similar. A variety of studies throughout the Southern Ocean also have found growth rates well below the temperature-limited maximum [Smith and Sakshaug, 1990]. For example, Nelson and Smith [1986] found maximal carbon-based growth rates in the diatom-dominated coastal waters to range from 0.043 to 0.23 doublings  $d^{-1}$ . Similarly, studies in the marginal ice zone of the Weddell Sea in spring 1983 measured growth rates up to 0.75 doublings  $d^{-1}$  but with the mean equaling 0.30 doublings  $d^{-1}$  (0.32 doublings  $d^{-1}$  when corrected for detrital influence) [Smith and Nelson, 1990]. In autumn, 1986 growth rates reached 0.38 doublings  $d^{-1}$  but averaged 0.14 doublings  $d^{-1}$  [Smith and Nelson, 1990].

A number of factors can reduce growth rates. For example, micronutrient limitation has been suggested to be important in some areas, but iron additions on the Ross Sea continental shelf have not resulted in substantial increases in growth [Martin et al., 1990]. Specifically, two Fe-addition experiments from water collected along 76°30'S showed no increase in either growth or yield [Martin et al., 1990]. Irradiance also can limit growth in a variety of ways. For example, deep vertical mixing can effectively limit the total irradiance an assemblage receives over 24 hours and hence reduce daily growth. Ice and extreme solar angles can limit the amount of radiation entering the water column, reducing in situ growth. Finally, or in combination with other factors, high concentrations of algal biomass can attenuate irradiance rapidly, thereby shading phytoplankton at the lower isolumens.

Underestimates of growth rates due to detrital and nonalgal organic matter undoubtedly occurred, but bacterial or microzooplanktonic carbon in polar waters is rarely great enough to underestimate algal carbon by a factor of two or more. Cota et al. [1990] estimated that bacteria account for approximately 5% of the total particulate carbon pool, and Garrison and Buck [1991] suggested that microzooplankton account for a similar amount of carbon. Furthermore, DiTullio and Smith [this issue] used a pigment labeling technique [Goericke and Welschmeyer, 1992] to measure growth rates at a few stations, and measured growth rates were similar to those estimated from carbon turnover. It remains unclear if Eppley's [1972] equation adequately resolves growth at extremely low temperatures, and if it does, then it is uncertain what factor(s) might be causing reduced growth rates in the Ross Sea.

Much of the carbon produced during photosynthesis remained in the low molecular weight fraction (Figure 7). The relative constancy of the incorporation patterns was surprising, in that even at very low light levels the allocation patterns were not markedly altered. It is likely that the relative allocation patterns were invariant due to the relatively low growth rates found throughout the water column. We found that approximately 31% of the total production appeared in the protein fraction. DiTullio and Laws [1986] found from 31 to 48% of the  $^{14}C$  incorporation went into protein in tropical waters, and Laws et al. [1985] found protein to account for 41-47% of the total carbon fixation after 24 hours in tropical waters.

The primary productivity of the Ross Sea is substantial during mid to late summer, despite the fact that biomass was decreasing markedly. The early January average (the first occupation of the southern transect in 1990; Table 4) of 2.63  $g\ C\ m^{-2}\ d^{-1}$  is greater than the maximum observed during intensive upwelling in the equatorial Pacific [Barber et al., 1996] and is greater than the long-term mean for the coastal upwelling system off Peru [Chavez and Barber, 1987]. Clearly, it is a productive system on short time scales (e.g., weeks to months). The productivity of the system remains low, however, over longer timescales (e.g., months to a year) due to the long periods of negligible productivity [Nelson et

al., this issue]. The pulsed nature of the production processes, as well as the altered coupling to grazing losses [Frost, 1991] and bacterial utilization of organic matter [Cota et al., 1990; Karl, 1993], in turn results in extreme pulses of organic matter delivered to depth [von Bodungen et al., 1986; Fischer et al., 1988; Wefer et al., 1988; Bathmann et al., 1991]. Hence both the quantitative and qualitative aspects of the Antarctic carbon cycle and its biological processes are different from those in other areas of the ocean. Understanding the surface layer carbon dynamics and the coupling to deeper waters in the Ross Sea, the most productive subregion in the Southern Ocean, may provide insights into the structure of biogeochemical cycles of the entire Antarctic.

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