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The seasonal cycle of phytoplankton biomass and primary productivity in the Ross Sea, Antarctica

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Abstract

Phytoplankton standing stocks and carbon assimilation were measured during four cruises to the southern Ross Sea, Antarctica during 1996 and 1997 in order to assess the details of the seasonal cycle of biomass and productivity. The seasonal composite showed that phytoplankton biomass increased rapidly during the austral spring, and integrated chlorophyll reached a maximum during the summer (January 15) and decreased thereafter. Particulate matter ratios (carbon:nitrogen, carbon:chlorophyll) also showed distinct seasonal trends with summer minima. Carbon assimilation increased rapidly in the spring, and reached a maximum of $231 \text{ mmol C m}^{-2} \text{ d}^{-1}$, ca. four weeks earlier than the maximum observed biomass (during early December). It decreased rapidly thereafter, and in austral autumn when ice formed, it approached zero. The time of maximum growth rate coincided with the maximum in C-assimilation, and at 0.66 d^{-1} equaled predictions based on laboratory cultures. Growth rates over the entire growing season, however, were generally much less. Deck-board incubations suggested that photoinhibition occurred at the greatest photon flux densities, but in situ incubations revealed no such surface inhibition. We suggest that due to the nature of the irradiance field in the Antarctic, assemblages maintained in on-deck incubators received more light than those in situ, which resulted in photoinhibition. This in turn resulted in a 17% underestimate in on-deck productivity relative to in situ determinations. The phytoplankton bloom appeared to be initiated when vertical stability was imparted in austral spring, coincident with greater daily photon flux densities. Conversely, decreased productivity likely resulted from trace metal limitation, whereas biomass declines likely resulted from enhanced loss rates, such as aggregate formation and enhanced vertical flux of larger particles. The seasonal

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progression of productivity and biomass in the southern Ross Sea was similar to other areas in the ocean that experience blooms, and the cycling of carbon in this region is extensive, despite the fact that the growing season extends no more than five months. © 2000 Elsevier Science Ltd. All rights reserved.

1. Introduction

It is now recognized that the southern Ross Sea not only supports large concentrations of organic matter, but the turnover of carbon can be quite rapid and involve pathways that are quantitatively and qualitatively different than those in tropical and temperate waters. For example, observed chlorophyll and particulate organic carbon concentrations in the surface layer can exceed $15 \mu\text{g l}^{-1}$ and $85 \mu\text{mol l}^{-1}$, respectively (Smith et al., 1996), one to two orders of magnitude greater than open ocean areas like the equatorial Pacific (Barber et al., 1997b) and twice the maximum concentrations reported in the Peruvian upwelling system (Ryther et al., 1969) and the Bering Sea shelf (Ichikawa, 1982). Primary productivity is often dominated by *Phaeocystis antarctica* (Smith and Gordon, 1997), and export flux often consists of rapidly sinking colonial phytoplankton and aggregates (Lancelot et al., 1998; Asper and Smith, 1999). Standing stocks and grazing rates of zooplankton grazers (both micro- and mesozooplankton) are often low (Fabiano et al., 1997; Caron et al., 2000). Bacteria, although active, represent a much smaller fraction of euphotic zone biomass, and apparently do not contribute as significantly to carbon pathways as in tropical and temperate waters (Ducklow and Carlson, 1992; Karl, 1993). The seasonal cycle of phytoplankton in the Southern Ocean biomass and productivity also is characterized by large variations, and these variations remain poorly resolved despite the region's importance to marine carbon cycles (Sarmiento et al., 1998).

In recent years the large-scale distribution of phytoplankton in the Southern Ocean, obtained by satellites, has been used extensively not only to quantify the temporal and spatial variations of carbon transformations observed (Sullivan et al., 1993; Comiso et al., 1993; Arrigo and McClain, 1994; Arrigo et al., 1998a; Moore et al., 1999), but to understand the relationship of primary productivity with environmental forcing such as wind, sea ice, and irradiance (Banse, 1996). Satellites are unable to estimate phytoplankton abundance in areas of extensive cloud and/or ice cover, and hence are of relatively little use during extended periods in the Southern Ocean, such as austral spring. However, Smith and Gordon (1997) clearly showed that phytoplankton biomass during the ice-covered, early spring (mid-November) was large (chlorophyll concentrations $> 3 \mu\text{g l}^{-1}$), and thus growth must have been initiated during October. Austral spring contributes significantly to the annual production (Nelson et al., 1996), and Arrigo et al. (1998b) suggested that December production would reach $3.94 \text{ g C m}^{-2} \text{ d}^{-1}$. Previous observations have shown that phytoplankton biomass declines throughout the summer from the maximum in December (Arrigo and McClain, 1994; Smith et al., 1996; Asper and Smith, 1999).

The seasonal cycle of polar productivity is even more poorly known than that of biomass. Most studies of productivity have been confined to shorter, often ice-free periods. For example, Holm-Hansen and Mitchell (1991) found that productivity ranged from 0.12 to 2.12 g C m⁻² d⁻¹ in the period from December to March in the Antarctic Peninsula region. Smith et al. (1996) found summer (January) production in the Ross Sea averaged 2.63 g C m⁻² d⁻¹ in mid-January, and decreased to 0.78 g C m⁻² d⁻¹ in February. Open ocean rates are substantially lower. El-Sayed et al. (1983) found the mean productivity in the Ross Sea sector (off the continental shelf) to be 0.33 g C m⁻² d⁻¹, or about 56% that found at similar times on the continental shelf. Hence, both time and space variations confound the determination of seasonal production in the Antarctic.

Our objectives in this study were two-fold. First, we wanted to determine the seasonal cycle of productivity in the southern Ross Sea, and also to determine the seasonal cycle of phytoplankton biomass and rates of growth. Second, we wanted to use biomass and productivity information to elucidate the environmental controls of productivity in the region. It has been proposed that irradiance is the major limiting factor during the austral spring (Smith and Gordon, 1997), whereas during austral summer growth is limited by micronutrient availability (Sedwick and DiTullio, 1997). In addition, it is possible that both irradiance and iron co-limit growth (Sunda and Huntsman, 1997; Boyd et al., 1999). Changes in biomass also have been suggested to result from grazing (DiTullio and Smith, 1996) and enhanced sinking due to aggregate formation (Asper and Smith, 1999); furthermore, the relative importance of these loss processes appears to be largely controlled by the composition of the surface phytoplankton assemblage. A further objective of our study, therefore, was to understand better the mechanisms leading to the changes of biomass in the southern Ross Sea.

2. Materials and methods

2.1. Oceanographic cruises

We conducted four cruises to the southern Ross Sea in 1996 and 1997 on the R.V.I.B. *Nathaniel B. Palmer* as part of the U.S. Southern Ocean JGOFS study (AESOPS, or Antarctic Environment Southern Ocean Process Study; Table 1; Fig. 1a–d). The first (NBP96-04A) sampled the very early spring period and was designed to investigate the causes of the initiation of phytoplankton growth in the spring. The second (NBP97-01) sampled during summer when phytoplankton biomass was large (albeit declining), and the third (NBP97-03) assessed the transition from late autumn to winter. The fourth cruise (NBP97-08) was conducted during the spring, the period of presumed most rapid growth and greatest productivity. Surface irradiance measurements as well as local meteorological conditions were recorded continuously from sensors mounted on the ship's mast. Photon flux densities were measured using a BioSpherical Instruments 4 π sensor, and data were binned and averaged at 1-min intervals.

Table 1

The sampling dates of the four cruises to the southern Ross Sea. Number of stations includes only those in which biomass or productivity were directly determined

Cruise	Sampling dates	Number of stations (biomass; productivity)
NBP96-04A	10/17–11/6/96	21; 14
NBP97-01	1/13–2/9/97	24; 20
NBP97-03	4/12–28/97	13; 12
NBP97-08	11/15–12/11/97	35; 34

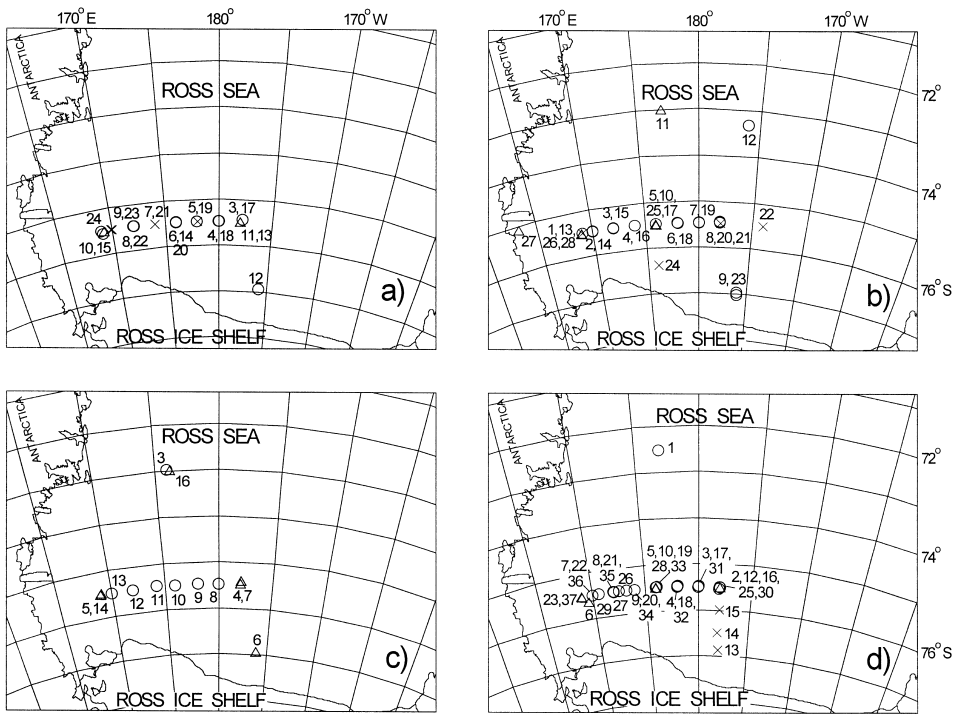


Fig. 1. Maps showing the locations of the stations sampled during (a) NBP96-04A, (b) NBP97-01, (c) NBP97-03, and (d) NBP97-08. (Δ) represents stations where biomass, on-deck and in situ productivity measurements were made, (\circ) represents stations with biomass and on-deck incubations, and (\times) represents stations with biomass only.

Much of the sampling occurred along $76^{\circ}30'S$ at a series of eight stations, each separated by ca. 60 km (Fig. 1a–d). Depths ranged from 324 to > 700 m. The Ross Sea polynya generally opens near the ice shelf in austral spring and extends northward to the area with reduced ice concentrations (Comiso et al., 1993), so that NBP96-04A

sampled across the polynya. Complete ice cover was observed during NBP97-03, and extensive concentrations of ice (broken, with occasional extensive open areas and substantial mesoscale variability) were noted during NBP96-4A and NBP97-08. In contrast, little ice, except the pack ice to the west, was encountered during NBP97-01 (Smith et al., 2000).

Profiles of temperature and salinity were collected throughout the water column using a CTD (SeaBird 911+) with dual sensors, and which also had a fluorometer (Chelsea Instruments) and an irradiance (PAR) sensor with a cosine collector (BioSpherical Instruments) interfaced with the CTD package. The CTD was mounted on a rosette of 24 10-l Niskin bottles to collect discrete samples for macronutrients and biomass (chlorophyll; particulate organic carbon and nitrogen) throughout the water column. The rosette frame was coated with an inert plastic resin to reduce trace metal contamination. Samples for productivity measurements were collected using a trace-metal-clean rosette mounted with Go-Flo[®] Niskin bottles (30-l capacity) (Hunter et al., 1996), which also had a PAR sensor mounted on the frame. The tops of all Go-Flo bottles were covered with plastic before and after deployment to reduce airborne contamination. Depths of collection were determined from the underwater irradiance data collected along the profile.

2.2. Analytical methods

Chlorophyll and macronutrient concentrations were quantified using standard JGOFS procedures (JGOFS, 1996). Chlorophyll samples were filtered through 25 mm Whatman GF/F filters under low (< 1/3 atm) vacuum, folded in half, and placed in centrifuge tubes with 7 ml 90% acetone. All samples were stored in the dark at –20°C for 24 h, and the extracted fluorescence read before and after acidification using a Turner Designs Model 10-AU fluorometer. Particulate carbon and nitrogen concentrations were determined by filtration through combusted (450°C for 2 h) Whatman GF/F filters under low vacuum. The filters were rinsed with a few ml of 0.01 N HCl in seawater to remove inorganic carbonates, after which they were placed in combusted glass tubes, capped with combusted aluminum foil, and dried at 60°C. All samples were returned to the laboratory and processed using a Carlo-Erba Model 252 elemental analyzer. Acetanilide was used as a standard.

Primary productivity was measured as carbon assimilation with both in situ and on-deck incubations. Samples were collected from depths spaced evenly within the euphotic zone and placed in tissue culture flasks (total volume 280 ml). They were immediately inoculated with ca. 20 μ Ci of trace-metal clean solution of NaH¹⁴CO₃ (pH 9.6), which was stored at 4°C in a Teflon bottle. Samples for in situ productivity determinations were placed in specially constructed Plexiglas holders that were then attached to a plastic-coated, 0.25" steel rope. The samples were returned to the depth of sampling for incubation. A 22.5 kg weight kept the line vertical, whereas the surface of the line was kept afloat by a large buoyant sphere, which was then connected to a spar-buoy with a navigational beacon. In addition to the samples, in situ PAR (photosynthetically active radiation) 4 π sensors (BioSpherical Instruments Inc.) with

internal recording devices were placed at selected depths to continuously record the irradiance within the water column. Generally four PAR sensors and samples from six depths were placed on each array. Samples were recovered after ca. 24 h. All samples were filtered through 25 mm GF/F filters under low vacuum. Filters were placed in scintillation vials with 0.1 ml 1 N HCl (to remove adsorbed inorganic ^{14}C and carbonates), and the radioisotope incorporation determined after another 24 h using liquid scintillation techniques. Values were corrected for abiotic absorption using time-zero controls. Total added radioactivity was measured by directly pipetting an unfiltered aliquot (0.1 ml) directly into 50 μl β -phenethylamine, to which fluor was directly added. All PAR data were down-loaded from each sensor immediately after each deployment.

Parallel incubations were conducted in on-deck incubators. The incubators were constructed of clear Plexiglas with lids to help reduce freezing, and all but one covered with neutral density screens that reduced irradiance to 50, 23, 16, 7, 5 and 2% of the surface value. These reductions were repeatedly checked using a hand-held quantum meter. Samples were collected from the depths which corresponded to these isolumes. All sample collection, incubation, filtration and quantification procedures were the same as those used for the in situ incubations. Chlorophyll concentrations were measured from all trace-metal-clean casts as well.

2.3. Data analysis

All data from on-deck incubations were processed using the procedures described by Barber et al. (1997a), since the largest source of error in estimates of primary productivity occurs in assigning depths (Barber et al., 1997b). We used the observed chlorophyll distributions to model the in situ irradiance attenuation after Morel (1988), and then recalculated the productivity-irradiance profiles, which in turn allowed accurate estimates of integrated production of the water column. All productivity data (actual observations and modeled values) are available via <http://www1.who.edu/jg/dir/jgofs/southern/>. Growth rates were calculated from productivity (ΔC) and particulate carbon concentrations (POC) using

$$\mu = \frac{1}{t} \ln \left[\frac{[\text{POC}] + \Delta\text{C}}{[\text{POC}]} \right]. \quad (1)$$

Mixed-layer depths were determined from the σ_t values calculated from the 1-m averaged data from the CTD casts. The mixed layer was defined by a change of 0.01 σ_t unit from the stable, surface value.

The data from the four cruises were merged to form a seasonal composite in order to investigate the temporal patterns in phytoplankton processes. We recognize that such a treatment is influenced by both spatial variations within the study region, as well as interannual variations between the two years. However, we believe the seasonal composite generated represents a robust representation of the patterns and processes which occur in the southern Ross Sea (see Discussion).

3. Results

Phytoplankton biomass followed the expected cycle for polar systems (Cushing, 1981; Smith and Sakshaug, 1990); that is, it increased to a single maximum that was roughly in phase with solar radiation. Mixed layers ranged from nearly 500 m in early spring to < 5 m within the melting pack ice during summer. Weekly means within each cruise show that mixed-layer depths exhibit a minimum in summer and increase in autumn (Table 2). Nitrate concentrations decreased as biomass increased, with surface concentrations prior to active phytoplankton growth equaling 31.2 μM , and the lowest weekly averages reaching 11.3 μM (Table 2). Interestingly, autumn nitrate concentrations were less than those observed at 150 m, despite the low phytoplankton biomass present.

Early spring biomass was extremely low, with surface concentrations of chlorophyll averaging $0.11 \pm 0.06 \mu\text{g l}^{-1}$ during the first week of NBP96-4A (October 17–24). Chlorophyll concentrations increased markedly in November and December (Table 2; Fig. 2a), and on December 12 the maximum observed surface value was reached (14.1 $\mu\text{g l}^{-1}$). The maximum integrated (through 100 m) chlorophyll concentration occurred (377 mg m^{-2}) on January 15. Similarly, particulate organic carbon values also increased rapidly in spring (euphotic zone values ranged from 0.95 to 108 $\mu\text{mol l}^{-1}$; Fig. 2b). Particulate nitrogen (PN) values also increased concomitantly, reaching 566 mmol m^{-2} in early January (Table 2). A second-order polynomial trend line generated from the C/N ratio of surface particulate organic matter predicted minimal values on January 3. The minimum observed value of 5.24 mol/mol occurred on December 9, and the maximum during the austral autumn/winter when PN concentrations were lowest (Fig. 2c). Particulate carbon/chlorophyll ratios were lowest in late spring (Table 2), with the observed minimum of 24.8 occurring on November 20. The minimum predicted from a second-order polynomial regression would occur on November 26 (Fig. 2d). Values increased markedly during the autumn cruise, with a maximum weekly mean of 1150 (Table 2).

Primary productivity measured by on-deck incubations also increased rapidly in austral spring (Table 2, Fig. 3a), concurrent with the integrated daily photon flux density (Fig. 4). Maximum productivity values were observed on December 6 and equaled 231 $\text{mmol C m}^{-2} \text{d}^{-1}$. Minimum values were recorded during the autumn cruise (0.82 $\text{mmol C m}^{-2} \text{d}^{-1}$). Maximum in situ productivity values equaled 240 $\text{mmol C m}^{-2} \text{d}^{-1}$ on December 12. Integrated daily irradiance varied by three orders of magnitude among the cruises, with minima in daily PAR occurring during the autumn–winter cruise. Photoperiods reached 24 h on October 20 and did not decrease until after the summer cruise (mid-February). During the autumn cruise photoperiods decreased from more than 8 h to less than 4 (Fig. 4). Productivity was weakly correlated with daily irradiance when data from all cruises are pooled ($\text{PP} = 0.498\text{PAR} + 11.8$; $R = 0.536$, $n = 83$, $p < 0.001$), but there was a large amount of variability in this relationship for individual cruises as well as the entire series. A similar, significant relationship was found between the mean irradiance in the water column (daily PAR divided by the depth of the mixed layer) and primary productivity, but this relationship had even more scatter ($R^2 = 0.236$). $P_{\text{opt}}^{\text{B}}$ (the maximum

Table 2
Weekly averages and standard deviations of physical, chemical, and biological variables within the Ross Sea. Z_{mix} = mixed layer depth; Z_{cr} = critical depth; POC = particulate organic carbon; PON = particulate organic nitrogen; PP = primary productivity. Water column values integrated through 100 m. Productivity means represent the means of on-deck incubations only. Critical depths calculated after Nelson and Smith (1991)

Week	Dates	Z_{mix} (m)	Z_{cr} (m)	Nitrate* (μM)	Chlorophyll (mg m^{-2})	POC (mmol m^{-2})	PON (mmol m^{-2})	POC/CHL ^a (wt/wt)	PP (mmol C $\text{m}^{-2} \text{d}^{-1}$)
<i>NBP96-4A</i>									
1	Oct. 17–23	173 ± 154 (6)	381 ± 127	31.2 ± 0.14	10.1 ± 4.06	146 ± 21.0	14.6 ± 3.10	231 ± 127	6.90 ± 2.75 (6)
2	Oct. 24–30	150 ± 148 (5)	291 ± 66	30.8 ± 0.15	18.9 ± 10.3	202 ± 51.9	25.9 ± 10.5	150 ± 78.9	23.5 ± 20.6 (5)
3	Oct. 30–Nov. 6	46 ± 15 (3)	258 ± 131	30.5 ± 0.38	49.4 ± 47.7	442 ± 263	54.3 ± 43.8	140 ± 58.0	73.8 ± 16.2 (3)
<i>NBP97-01</i>									
1	Jan. 13–19	20 ± 8 (8)	88 ± 54	11.3 ± 3.64	377 ± 115	4900 ± 1940	566 ± 179	177 ± 40.5	61.7 ± 35.0 (8)
2	Jan. 20–26	22 ± 11 (4)	99 ± 66	17.3 ± 8.52	162 ± 133	2990 ± 1680	374 ± 203	267 ± 90.5	42.8 ± 9.77 (4)
3	Jan. 26–Feb. 1	31 ± 12 (8)	75 ± 43	11.6 ± 3.69	233 ± 98.5	4190 ± 1650	498 ± 169	274 ± 60.6	48.4 ± 10.4 (8)
4	Feb. 2–9	26 ± 11 (8)	105 ± 62	12.5 ± 3.61	145 ± 66.0	1940 ± 1540	264 ± 205	351 ± 218	55.7 ± 41.4 (3)
<i>NBP97-03</i>									
1	Apr. 14–20	196 ± 97 (3)	24 ± 30	26.6 ± 1.76	4.09 ± 1.35	223 ± 44.5	21.8 ± 3.07	830 ± 112	1.53 ± 0.900 (2)
2	Apr. 21–28	155 ± 78 (8)	2.8 ± 1.7	26.7 ± 0.98	2.38 ± 0.52	247 ± 24.8	21.2 ± 3.47	1150 ± 317	1.06 ± 0.145 (8)
<i>NBP97-08</i>									
1	Nov. 15–21	47 ± 23 (7)	403 ± 244	29.7 ± 0.50	76.5 ± 50.7	616 ± 307	104 ± 59.6	94.5 ± 52.4	68.8 ± 37.0 (7)
2	Nov. 22–28	18 ± 6 (12)	212 ± 100	28.2 ± 1.36	120 ± 104	1010 ± 559	149 ± 81.2	136 ± 39.0	78.3 ± 29.2 (9)
3	Nov. 29–Dec. 5	30 ± 10 (9)	315 ± 251	25.8 ± 2.61	145 ± 79.5	1040 ± 589	160 ± 115	140 ± 92.9	122 ± 49.7 (9)
4	Dec. 5–11	20 ± 7 (9)	171 ± 128	22.6 ± 4.82	228 ± 167	1960 ± 1270	302 ± 182	187 ± 81.4	125 ± 79.5 (9)

^aSurface value.

chlorophyll-specific productivity within the water column) increased even more rapidly than chlorophyll or productivity, and tripled from 0.62 to $1.92 \text{ mg C (mg chl)}^{-1} \text{ h}^{-1}$ within 13 days in early spring (Fig. 3b), suggesting photoacclimation to the increasingly favorable irradiance field. The actual acclimation may have occurred much more rapidly (Abbott et al., 2000), but the temporal resolution of the discrete samples collected prohibit a clear definition of the time required. Maximum $P_{\text{opt}}^{\text{B}}$ values were found on November 18 ($3.41 \text{ mg C (mg chl)}^{-1} \text{ h}^{-1}$).

In situ measurements of productivity generally were greater than those obtained from on-deck incubations. This difference appeared to result from photoinhibition

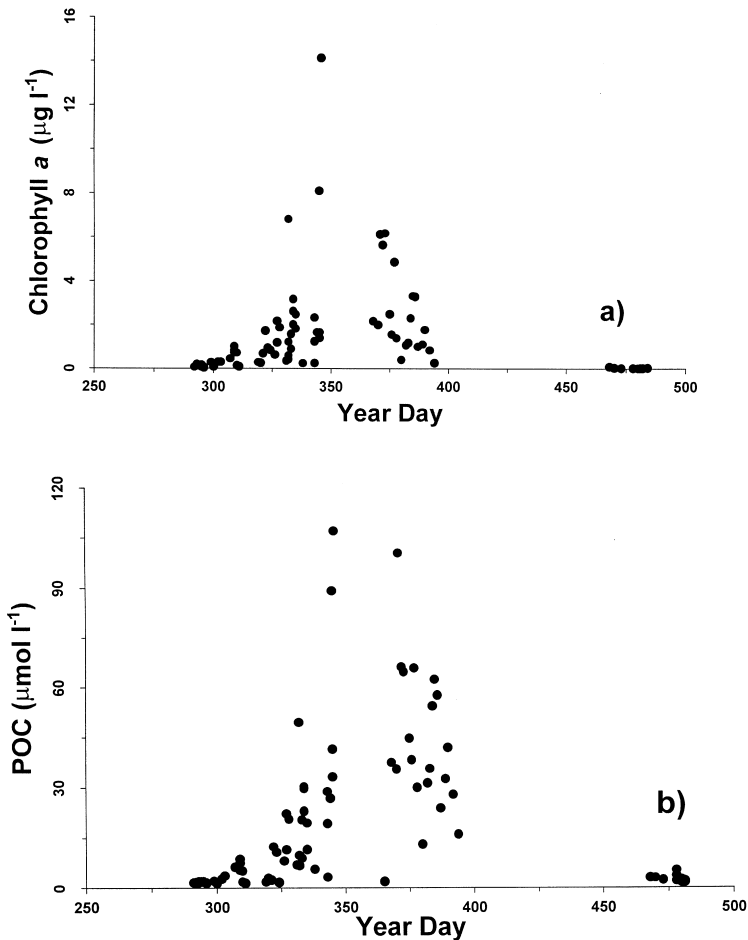


Fig. 2. Temporal changes in near surface concentrations of (a) chlorophyll, (b) particulate organic carbon, (c) carbon:nitrogen ratio in particulate organic matter, and (d) particulate organic carbon:chlorophyll ratio. The lines in (c) and (d) are second-order polynomial fits. Data represent a composite of those collected during the four cruises and less than 30 m in 1996–1997.

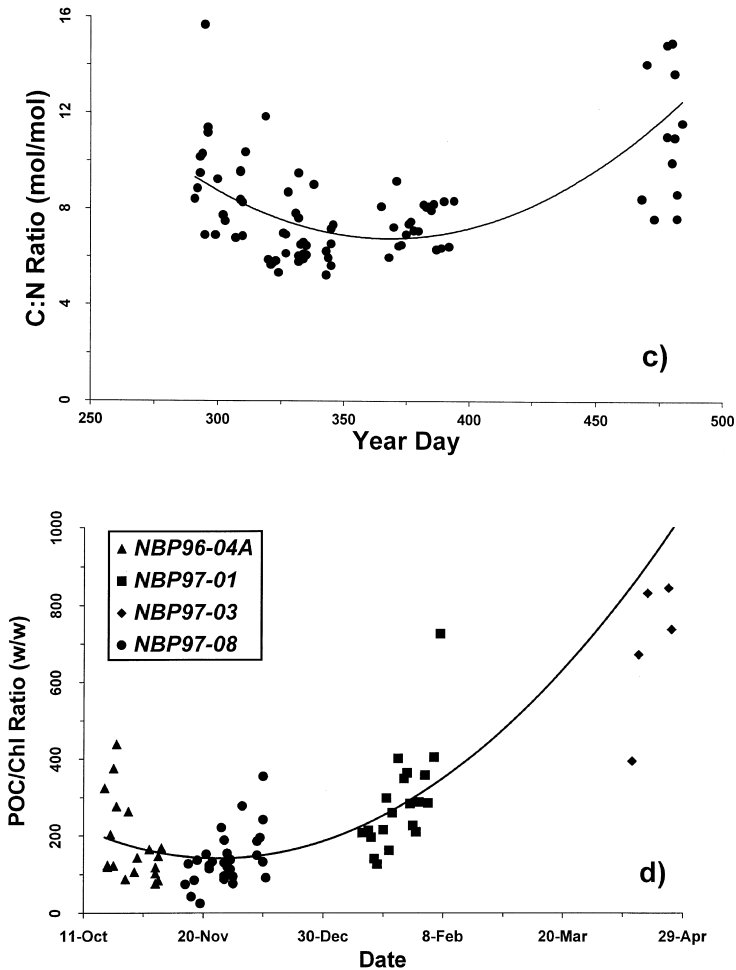


Fig. 2 (continued)

that on-deck incubations experienced at the highest irradiance levels (Fig. 5). The mean underestimate (determined by regression) of integrated productivity obtained by on-deck incubations relative to the in situ measurements incubated at the same irradiance percentage was 17%. These underestimates varied temporally as well, with the greatest underestimates occurring during the summer when photoinhibition was most pronounced, and the least during the late autumn.

Growth rates of surface assemblages, calculated from Eq. (1), were maximal in austral spring (Fig. 6), with the maximum rate (0.66 h^{-1}) occurring on November 17. Mean surface growth rates during early (October 18–30) and late spring (November 15–22) averaged 0.11 and 0.47 h^{-1} , respectively. The four greatest growth rates observed occurred within a four-day period from November 19–23. Growth rates during the summer cruise were extremely low, and averaged 0.059 h^{-1} , despite the

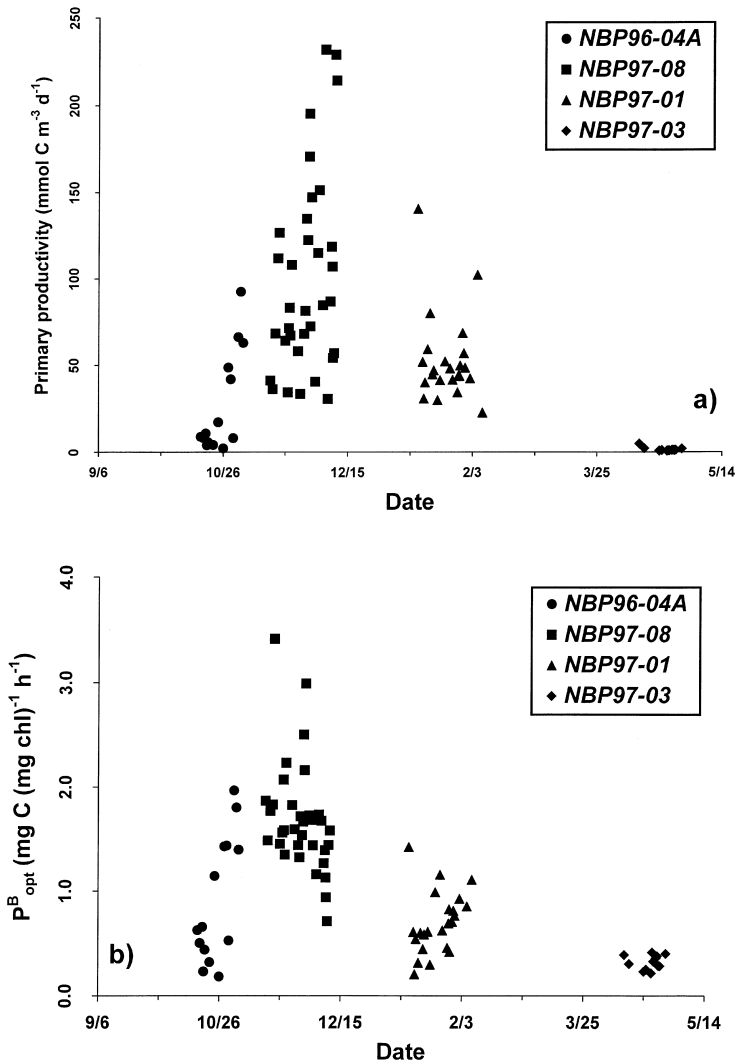


Fig. 3. Temporal changes observed in the Ross Sea in (a) integrated primary productivity and (b) chlorophyll-normalized maximum photosynthetic rates. Rates are determined from on-deck incubations.

favorable irradiance fields and macronutrient concentrations. That is, under conditions that are seemingly favorable for phytoplankton growth (vertical stratification, little wind mixing, large amounts of macronutrients, no ice, and large amounts of incident irradiance), phytoplankton growth in summer was close to zero. In contrast, during early spring when ice was present, irradiance was lower, and the mixed layers were deeper, growth rates were two orders of magnitude greater.

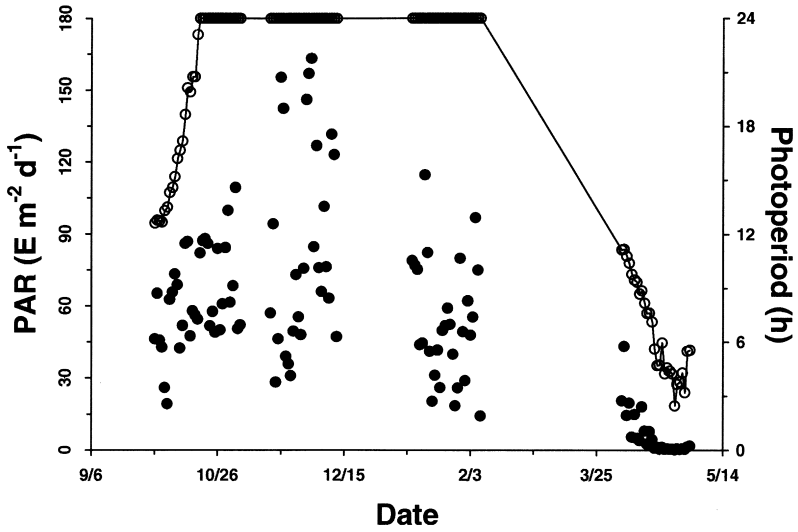


Fig. 4. Temporal changes in the observed ship-board integrated daily irradiance levels and measured photoperiods.

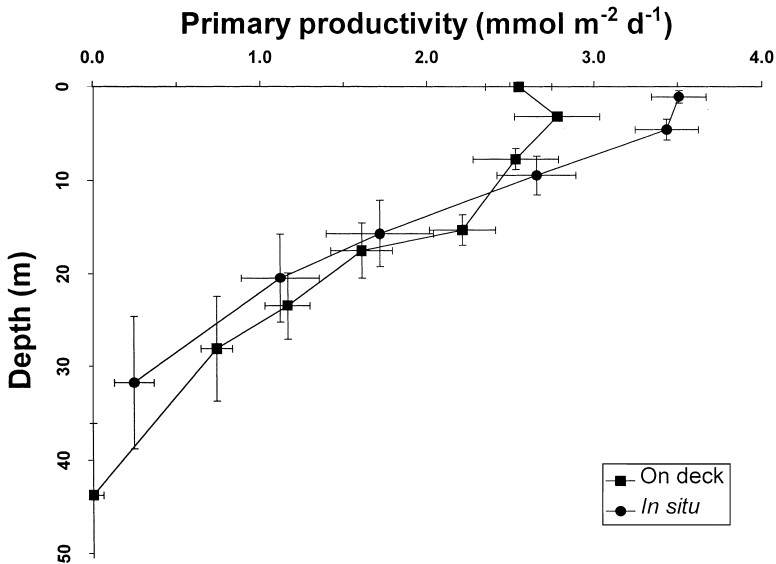


Fig. 5. Primary productivity as a function of depth in the on-deck and the in situ incubations during NPB97-01.

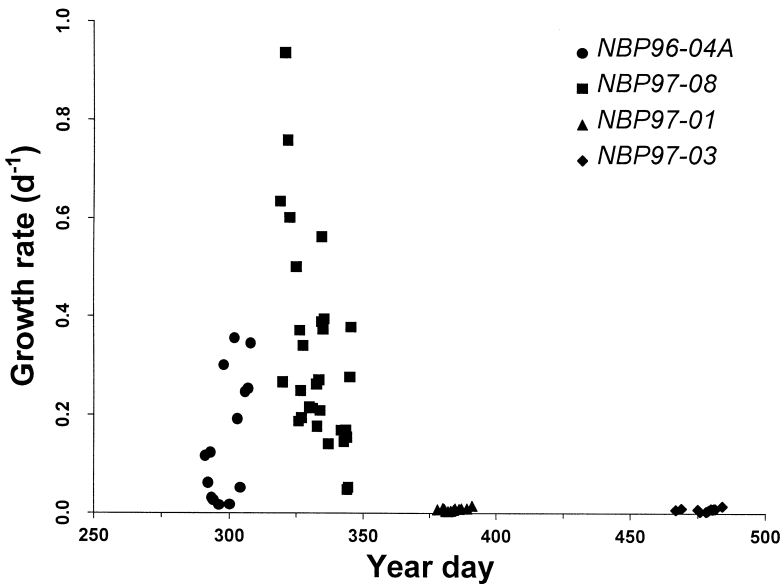


Fig. 6. Temporal changes in the growth rates of surface phytoplankton calculated from Eq. (1).

4. Discussion

Studies designed to understand the temporal variations in phytoplankton standing stocks and carbon transformations of the Southern Ocean have been difficult to complete, as many of the open-ocean regions within the seasonal ice zone cannot be monitored continuously using ships. Additionally, within any single region there exists variations of phytoplankton biomass in space, which often are related to specific physical conditions such as ice cover or winds (Veth et al., 1992; Arrigo et al., 1998). Finally, studies that attempt to contrast results from different years may be influenced by interannual variations. Interannual variations in physical conditions (e.g. wind and ice; Gloersen and Campbell, 1991; Stammerjohn and Smith, 1997; Arrigo et al., 1998a) are well documented, and variations in higher trophic level biomass and reproductive success also have been observed (e.g., Fraser et al., 1992; Knox, 1994; Loeb et al., 1997). Such interannual variations of phytoplankton biomass and production have not been documented as thoroughly, although sub-Antarctic variations have been assessed (Clarke and Leakey, 1996). Given the interannual variability in the ice cover in the Ross Sea, it might be expected that biomass and production might vary substantially among years (Smith et al., 1988).

However, despite the potential influence of both spatial and interannual variations on obscuring seasonal trends, we believe that the influences were of much smaller magnitude than the temporal changes, and that the seasonal composite is an accurate representation of the temporal variations in the southern Ross Sea. Within a single

transect at any one time in the Southern Ross Sea, it is usual to find marked variations among stations (e.g., Figs. 2,3,4 and 6), but by averaging all values for a single transect (Table 2), the mean condition for that time period is approximated. The fact that *all* of the variables averaged in Table 2 provide a coherent temporal progression leads us to believe that the trend observed is in fact real. The influence of interannual variations, on the other hand, is more difficult to assess, since few data are available from other years for comparison. We know that ice conditions and taxonomic distributions during the two years were different (Mathot et al., in preparation), but it appears that the average biomass and productivity found during late spring are not dramatically different from those that would be predicted from early spring and summer conditions (Table 2). It has been suggested that systems that are strongly physically forced (such as coastal upwellings and the Southern Ocean) are less variable in the relationship between forcing functions and phytoplankton responses than those that are biologically controlled (e.g., oligotrophic gyres; Barber and Smith, 1981). These data support this hypothesis; that is, once physical conditions become favorable for the onset of a bloom, then the progression from initial growth, acclimation, rapid growth, biomass accumulation, and growth and biomass decline are relatively tightly coupled. Such a scenario is also suggested by the data of Arrigo et al. (1998a).

Waters of the southern Ross Sea are striking for the seasonal variations that they exhibit with regard to phytoplankton biomass and productivity. Previous studies, as well as recent satellite images, have established this region as the site of the Antarctic's most spatially extensive phytoplankton bloom (Sullivan et al., 1993; Comiso et al., 1993; Smith et al., 1996; Arrigo et al., 1998b), and its peak concentrations of biogenic material rival those of highly eutrophic coastal systems (Smith and Nelson, 1985; Lancelot and Mathot, 1985; Platt and Sathyendranath, 1988). However, the details of the entire seasonal cycle until this time have been poorly resolved. Our seasonal composite shows that the Ross Sea is characterized by a unimodal peak in both primary productivity and phytoplankton biomass, although the timing of the maximum is different for each. That is, biomass was maximal in early January, whereas productivity was greatest approximately 29 days earlier (Table 2; Figs. 2 and 3). Additionally, the maximum observed chlorophyll-specific photosynthetic rate was observed ca. 3 weeks prior to the integrated productivity maxima. The rapid increase in P_{opt}^B reflected the increase in carbon assimilation early in the season and the temporal delay in biomass accumulation. These lags suggest a distinct cascade of events within the assemblage that enable phytoplankton to maximize its growth. First, the photophysiological status of the phytoplankton is optimized (as evidenced by the low C/Chl ratios in austral spring, as well as the photoacclimation to enhanced photon flux densities; Fig. 3b), allowing for rapid growth per unit biomass to occur under in situ irradiance and nutrient conditions. Second, water-column productivity becomes maximal under optimal photophysiological state (created by adaptation to increased vertical stratification). Finally, productivity ultimately decreases due to limitation by an environmental factor. Biomass increases as productivity becomes maximal because loss rates are low at this time, and then decline when losses become greater. As such, we suggest that growth is limited by one factor, whereas biomass is limited by a completely different and independent process.

We further suggest that the factor limiting phytoplankton productivity and growth during late spring and summer is trace-metal availability. A number of studies conducted in different years found a strong growth response by Ross Sea phytoplankton during early summer upon addition of trace amounts (≈ 1 nM) of iron (Sedwick and DiTullio, 1997; Fitzwater et al., 2000; Coale et al., in preparation), and a similar response has been found in other parts of the Southern Ocean (e.g., Buma et al., 1991; de Baar et al., 1995; Boyd et al., 1999). In addition, Olson et al. (2000) found that the variable fluorescence of single cells measured during pump-probe flow cytometry experiments (a sensitive measure of the limitation of cells by environmental factors) was low in unenriched controls but increased significantly to near maximal levels upon iron addition. Irradiance clearly did not limit phytoplankton growth in the surface mixed layer, as mean photon flux densities in late spring and early summer were always greater than those required to saturate photosynthesis (Hiscock et al., in preparation). Macronutrient concentrations also remained elevated throughout the study (greater than measured half-saturation constants; Smith and Harrison, 1991) and could not have contributed to growth rate reductions. Hence, it appears that the most likely cause for the reduction in productivity during late December was the depletion of iron.

In contrast, during early spring productivity was likely limited by irradiance. During this period (prior to November) the absolute amount of irradiance impinging on the surface was increasing, but the solar angle remained extreme for much of the day (despite the fact that the photoperiod had reached 24 h by this time). In addition, the early spring was characterized by substantial amounts of ice cover (Smith et al., 2000), which decreased rapidly in November. A 1-m thick slab of ice can attenuate up to 98% of surface irradiance (Marra and Boardman, 1984; Smith and Sakshaug, 1990); therefore, its presence can greatly influence the amount of irradiance present within the water column. During NBP96-04A, NBP97-01 and NBP97-08, the mixed-layer depths were always less than the calculated critical depths (Nelson and Smith, 1991; Table 2), although the influence of ice was not included in these Z_{cr} estimates. The mean water-column irradiance [calculated after Riley (1957), although the effects of ice cannot be expressly included] within the mixed layer also increased rapidly during the spring and was much greater in the upper 25 m than required to drive positive photosynthesis. Productivity in on-deck measurements during austral autumn was greater than zero, but because the ice present would further attenuate irradiance, it is likely that these are significant overestimates (despite the very low values measured; Fig. 3a). However, it is impossible to quantify precisely the effect of ice on water column productivity in our study, but it is likely that even in early spring, irradiance was sufficient to support phytoplankton growth, albeit not at maximum rates.

The biomass of phytoplankton did not reach its maximum until some 29 days after the productivity maximum (Figs. 2 and 3). We interpret this to mean that although phytoplankton growth and productivity had declined due to micronutrient limitation, the biomass (the balance between growth and losses) continued to slowly increase until loss processes exceeded growth, causing biomass to decrease. Loss processes operative in the Ross Sea include zooplankton grazing and ingestion (and subsequent

enhanced vertical flux of fecal material), increased sinking of large colonies of phytoplankton due to micronutrient limitation, production of large particles via aggregation and accelerated vertical flux, increased rates of viral lysis of phytoplankton cells (and enhanced rates of sinking of detrital material), and losses due to increased vertical mixing. We cannot effectively discriminate among all of these processes, but believe some are more likely explanations for the observed decreases in biomass than others. For example, grazing appears to be a function of phytoplankton community composition (e.g. Verity and Smetacek, 1996). As large portions of the southern Ross Sea are dominated by *Phaeocystis antarctica*, and because *P. antarctica* in the Ross Sea has extremely low losses as a result of microzooplankton grazing (Caron et al., 2000), losses due to zooplankton ingestion appear to be small. However, in other regions *Phaeocystis* has been reported to be effectively removed by mesozooplankton (e.g. Holm-Hansen and Huntley, 1984; Estep et al., 1990; Haberman, 1998), and we cannot discount the potential for removal by larger zooplankton in the Ross Sea. However, Dunbar et al. (1998) found the contribution of fecal pellets to the organic matter collected in sediment traps in areas dominated by *Phaeocystis* was small, suggesting that *Phaeocystis* in large part was not being grazed by mesozooplankton. No data are available on the rates of viral lysis on *Phaeocystis* in the Ross Sea, although viruses have been shown to infect *P. pouchetii* (Jacobsen et al., 1966). Mixed-layer depths (and hence mixing losses) are not significantly greater throughout summer or between summer and late spring (Table 2), although at specific locations (e.g. 76°30'S, 176°E) the mixed layer did deepen somewhat during late summer. The broad temporal trend, however, suggests that physical dispersion of the bloom alone did not account for the decline in biomass.

Asper and Smith (1999) found that vertical flux rates, as measured by short-term deployments of floating sediment traps, increased in summer relative to spring, and suggested that loss processes exhibited a temporal signal that was substantially uncoupled from phytoplankton productivity and biomass accumulation. They further suggested that this resulted from the temporal pattern of aggregate formation and enhanced vertical flux of the larger particles, and camera studies showed the abundance and sinking rates of aggregates (> 0.5 mm) increased during periods of enhanced flux (Asper et al., unpublished). They did not, however, rule out simple enhanced sinking rates of colonies of *P. antarctica*, since these particles were smaller than the camera's resolution, and our data likewise cannot preclude that possibility.

The in situ measurements of primary productivity were quantitatively different from the on-deck measurements both in the absolute rates and the vertical distribution of carbon incorporation. Comparison of paired productivity values showed in situ measurements were ca. 17% greater than the estimates derived from on-deck incubations, which we attribute to the strong photoinhibition in on-deck samples at the isolumens with high photon flux densities (Fig. 5). We suggest that the light environment that samples experience in on-deck incubators is significantly different than that in situ, since the surface irradiance includes a strong contribution of reflected and low angle light (for example, from the ship's deck, as well as surrounding snow and ice) (Barber et al., 1997b). Measurements of PAR using a cosine collector showed the photon flux densities measured by a 4π sensor were ca. 45% greater

(Reynolds and Mitchell, unpublished), but that the temporal patterns were consistent between the two types of sensors. Hence the in situ irradiance was quantitatively less than on deck, and this reduction led to the reduction of photoinhibition and increased measured rates of photosynthesis. We also made some paired comparisons between samples with the spectral quality changed (by using blue filters) and those with only the quantity changed (by neutral density filters), and no significant difference was observed (data not shown). Hence it appears in turbid, eutrophic regions such as the Ross Sea, light quality effects are of less importance than light quantity effects, in contrast to the results of oligotrophic tropical regions (Laws et al., 1991).

Growth rates during the cruises varied dramatically (Fig. 6). However, because the calculations involve the use of POC for estimating phytoplankton biomass, the estimates potentially may seriously underestimate actual growth. During the spring period microscopically derived POC concentrations were similar to those measured by direct chemical means, but during summer algal POC can be overestimated by up to 60% due to contributions of detritus and heterotrophic material (Mathot, personal communication). Thus the mean μ could be underestimated by ca. 240% (the mean summer rate was 0.059 d^{-1} , which increases to 0.14 d^{-1} if algal POC was overestimated by 60%). Regardless of the magnitude of the underestimate, summer growth rates remain extremely low even with this potential bias. Modest rates were observed in early spring (mean growth rate of surface samples was 0.14 d^{-1}) compared to the temperature-limited rate of 0.52 h^{-1} (Eppley, 1972). Late spring growth rates were greater and averaged 0.27 d^{-1} during the spring cruise. Maximum growth rates were observed during NBP97-08, with growth at two stations in November exceeding the maximum predicted by the Eppley (1972) equation (Stations 403 and 404 where $\mu_{\text{surface}} = 0.66$ and 0.57 d^{-1} , respectively). Conversely, the growth rates observed in austral summer were surprisingly low (mean = 0.059 d^{-1}). Few data are available to provide a quantitative description of temperature-limited growth below 2°C (the lower limit of the data available to Eppley), and it is impossible to know if the maximum rates observed are overestimates due to unbalanced growth or if they represent realistic and attainable growth rates. Smith et al. (1999) found diatom growth rates (determined by ^{32}Si uptake rates) were always low in the Ross Sea ($< 0.2 \text{ h}^{-1}$), whereas carbon-based growth rates for entire assemblages occasionally approached 0.5 h^{-1} . Clearly, both environmental factors and community composition can influence net growth rates in Antarctic waters, and our results show the extreme variability that can occur within a restricted region and over short time scales. They also suggest that a better understanding of the maximum attainable growth rate is needed to improve our predictive capability in the event of future increases in surface layer temperatures.

A seasonal study was conducted in the Bransfield Strait region by Mitchell and Holm-Hansen (1991), who attempted to relate quantitatively the local mixing regime with phytoplankton biomass and growth. The AESOPS results provide a much more comprehensive data set with which to test these relationships. We found significant chlorophyll concentrations ($> 0.5 \mu\text{g l}^{-1}$) were not observed in mixed layers greater than 50 m (with the exception of one station), similar to the suggestion of Sakshaug and Holm-Hansen (1984). Furthermore, surface chlorophyll concentrations

were inversely related to mixed layer depths (Fig. 7; $CHL = 77.2z_m^{-1.31}$; $R = 0.722$; $p < 0.001$). The implication of this correlation is that biomass accumulates when stratification occurs, not only because the in situ environment is optimized for phytoplankton growth, but because phytoplankton biomass can in turn accumulate when vertical-mixing losses are minimized. Trace-metal limitation occurs after phytoplankton demand exceeds the supply of additional iron. Conversely, deep mixing will disrupt stratification and reduce growth while replenishing trace metals to the euphotic zone. Only those processes which can supply micronutrients and re-establish vertical stratification (e.g., ice ablation, mesoscale eddies and their associated vertical transports) can provide a semi-continuous, optimal environment for phytoplankton growth. Martin et al. (1990) and Sedwick and DiTullio (1997) suggested ice melt provided iron, which in turn stimulates water column productivity, but surface layers always show very low iron concentrations (Fitzwater et al., 2000). As such, the role of ice ablation in trace metal stimulation of phytoplankton remains equivocal.

The Ross Sea is the Antarctic's most productive sea (Arrigo et al., 1998b), and our results confirm and extend this general conclusion. Phytoplankton photosynthesis, productivity, growth and biomass accumulation in the southern portion respond rapidly to the modest vertical stratification and increasing surface solar radiation found in early spring, and the bloom is initiated. This bloom initiation appears to occur in early October (Smith and Gordon, 1997; Arrigo et al., 1998a), which is earlier than most, if not all, ice-covered waters in the Antarctic, but the reason for this rapid

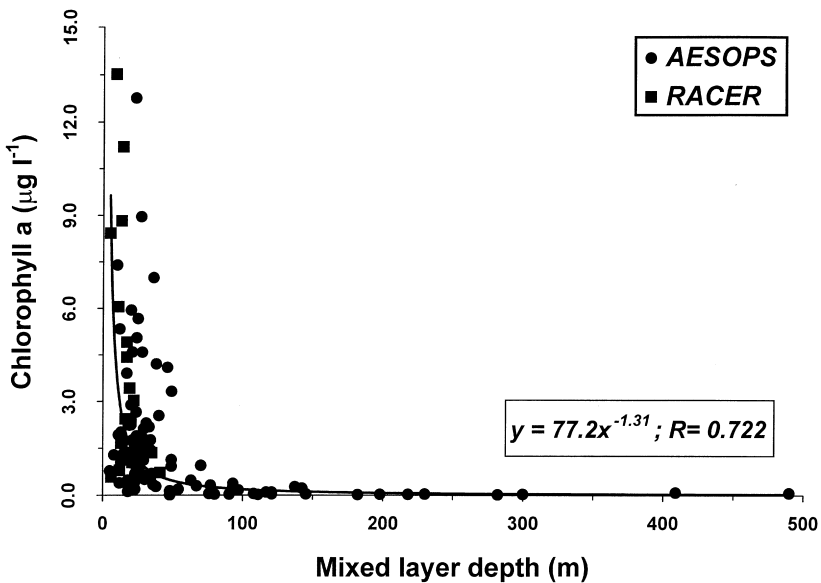


Fig. 7. Variations of chlorophyll concentration as a function of mixed layer depth. RACER data from Mitchell and Holm-Hansen (1991).

onset of growth relative to other areas of the Southern Ocean is unclear. Rapid growth occurs at sub-zero temperatures until early December (coincidentally the time of complete ice retreat), at which time productivity rapidly decreases, most likely due to trace-metal limitation. Biomass remains high, and declines more slowly, as loss processes are only weakly coupled to phytoplankton productivity and biomass. Virtually no autotrophic activity occurs in late autumn. Although the seasonal cycle of growth, biomass accumulation and decline is limited to at most five months, carbon transformations during this period are substantial and are unlike many other areas of the world's oceans (e.g. Karl, 1993). As such, the Ross Sea can serve as a model to which to compare all other highly productive, continental shelf areas in the Southern Ocean.

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