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# Growth dynamics of *Phaeocystis antarctica*-dominated plankton assemblages from the Ross Sea

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ABSTRACT: Large-volume experiments were conducted using natural seawater assemblages collected in the southern Ross Sea during austral spring 1994 and summer 1995 to assess the carbon and nitrogen exchanges among phytoplankton, bacteria and dissolved organic carbon pools, and to compare the elemental partitioning in these experimental enclosures with those observed *in situ*. Large concentrations of particulate matter were produced in these enclosures, which were at all times dominated by the colonial haptophyte *Phaeocystis antarctica*. Particulate organic carbon concentrations exceeded 200 µmol $l^{-1}$ at the end of the experiment. Bacterial carbon comprised only a small (<1%) fraction of the particulate carbon, but bacteria grew at 0.15 to 0.3 $d^{-1}$ and were not limited by bacteriovores. Nutrient levels decreased concomitantly with POC increases, and nitrate was reduced to undetectable levels. Dissolved organic carbon (DOC) levels remained low (less than 50 µM) while nutrients were present, but increased dramatically (to more than 200 µM) after nitrate was depleted. Growth rates calculated from changes in particulate matter concentrations were slightly below the predicted maximum based on temperature. Field studies, however, showed no depletion of nitrate, similar levels of particulate organic carbon to those found during exponential growth, low levels of DOC, and relatively low levels of bacterial biomass. It appears that *P. antarctica* in the Ross Sea does not produce large amounts of DOC during nutrient-replete growth; furthermore, because macronutrients are rarely, if ever, depleted where *P. antarctica* is dominant in the Ross Sea, it is likely that much of the carbon generated during its growth remains in the particulate pool.

KEY WORDS: Carbon · Antarctica · *Phaeocystis* · Phytoplankton · Bacteria · Dissolved organic · Particulate organic · Nitrogen

## INTRODUCTION

The Ross Sea is the site of the most spatially extensive phytoplankton bloom in the entire Southern Ocean (Sullivan et al. 1993, Arrigo & McClain 1994), and pigment concentrations of ca 15 µg $l^{-1}$ have been measured at the time of the biomass maximum (Smith et al. 1996). The bloom forms within the Ross Sea polynya early in the season (Smith & Gordon 1997), and peak biomass and production are reached by mid- to late December, soon after ice completely melts and/or is advected to the north. The bloom decreases in extent and magnitude throughout January, and in February chlorophyll levels are approximately 1 µg $l^{-1}$ or less (Arrigo & McClain 1994, Smith et al. 1996). The processes responsible for the bloom's decline are unknown, although active grazing and sinking of colonies and/or aggregates derived from *Phaeocystis* have been suggested to be quantitatively important loss processes from surface waters.

The colonial haptophyte *Phaeocystis antarctica* always dominates the phytoplankton in the center of the polynya, although other locations in the Ross Sea (such as near the coast of Victoria Land) also support large blooms of diatoms, especially later in the season (e.g. Smith & Nelson 1985). Particulate carbon concentrations increase by more than an order of magnitude within the *Phaeocystis* bloom, yet integrated stocks of

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dissolved organic carbon (DOC) levels change only slightly (Carlson et al. 1998). The limited DOC accumulation is surprising when compared to other systems. For example, *Phaeocystis* blooms in the North Sea generate large amounts of dissolved organic material, which ultimately result in large accumulations of emulsions which appear on European beaches after the bloom (Cadeé 1990, Lancelot et al. 1998). *Phaeocystis* also generates a substantial amount of extracellular polysaccharide mucus in its colonial matrix, and it has been suggested that large amounts of this material ultimately enter the DOC pool (Guillard & Hellebust 1971, Lancelot & Mathot 1987). Given the complex life history of *Phaeocystis* and the potential for unusual characteristics of its associated carbon dynamics (e.g. reutilization of the mucoid sheath in darkness to fuel respiration and the extracellular nature of the sheath; Lancelot & Mathot 1985), it is difficult to generalize about the interactions between the particulate and dissolved pools within *Phaeocystis* blooms.

Previous studies have suggested that *Phaeocystis* had antibiotic properties as a result of the formation of acrylic acid (Sieburth 1960, Davidson & Marchant 1992). However, studies confirming this suggestion have been difficult, as commercial acrylic acid preparations contain bactericidal compounds, and hence cannot be used in heterotrophic studies without purification. In addition, it has been found that *in situ* acrylic acid concentrations are too low to inhibit bacterial growth (Putt et al. 1994, Slezak et al. 1994). Recent work indicates that *Phaeocystis*, along with its extracellular matrix, seems to support active microbial growth which is responsible for much of the material being recycled in the upper 250 m of the water column (Putt et al. 1994, Brussard et al. 1996, Osinga et al. 1997). Wassmann et al. (1990) reported that as aggregates and intact colonies sank, motile unicells were released from the matrix, and the colonial matrices were then available for microbial degradation.

It is not clear what limits phytoplankton growth in the Ross Sea. Early in austral spring phytoplankton growth rates are ca 50% of the temperature-limited potential (Smith & Gordon 1997), but these reduced rates are likely due to low photon flux densities found under the ice. During the peak biomass and production period, growth rates are equal to the temperature-limited maximum (ca 0.5 $d^{-1}$; Smith & Gordon 1997). However, growth rates decrease markedly in January and February, and maximum light-saturated rates are only 0.1 to 0.2 $d^{-1}$ (Smith et al. 1996). Trace metals potentially might limit both growth rate and yield (Martin et al. 1990). Specifically, dissolved iron concentrations are extremely low in January (less than 0.2 nM), and iron addition experiments stimulated growth of all species during this period (Sedwick & DiTullio 1997). Nitrate concentrations decrease from 30 to ca 12 µM at the surface during the growing season, but only in rare, isolated locations in the Ross Sea (such as within intense, coastal diatom blooms; Smith & Nelson 1985) are nutrients reduced to levels which are at or below detection (e.g. nitrate concentrations less than 0.1 µM). Although grazing is substantial at some sites, there is no evidence that grazing losses can control overall phytoplankton biomass in the Ross Sea. Hence, one of the major oceanographic paradoxes is why macronutrients are *not* fully utilized, both throughout the Southern Ocean and in the Ross Sea in particular, and what limits the utilization of these nutrients *in situ*. Trace metals are the most likely explanation for the lack of nitrate utilization (and hence phytoplankton yield), but irradiance may limit growth rates, particularly early in spring (Smith & Gordon 1997).

Bacterial biomass and productivity in the Ross Sea are generally low, at least relative to phytoplankton. Bacterial biomass during the period of maximal phytoplankton biomass equaled only 3% of the total particulate organic matter, and bacterial productivity, while equal to that in other systems such as the North Atlantic or equatorial Pacific, was only 5% of the primary productivity (that determined on GF/F filters) (Carlson et al. 1998). Therefore the relationship between bacteria and phytoplankton (i.e. decreased importance of bacterial production in polar systems relative to phytoplankton) appears to be similar to that found in the rest of the Antarctic (Ducklow & Carlson 1992, Karl 1993, Lochte et al. 1997). Bacterial growth rates are ca 0.1 to 0.2 $d^{-1}$, but it is unknown to what degree substrate or nutrient limitation occurs *in situ* (Ducklow & Carlson 1992). Carlson et al. (1998) suggested that in November and December bacteria are limited by available labile substrate; it has also been suggested that iron might limit bacterial production (Pakulski et al. 1996), but few data are available to test this hypothesis. Bacterivory is common in waters of the Antarctic (Burkill et al. 1995, Becquevort 1997), but the extent to which grazing limits bacterial standing stocks is unknown, as is the nature of the temporal coupling between bacteria and their grazers.

The objective of this study was to quantify the various transformations of carbon and nitrogen within *Phaeocystis*-dominated phytoplankton assemblages under controlled conditions. We hypothesized that DOC production and flux would represent an important transformation, since extensive DOC formation and turnover has been observed in other systems dominated by *Phaeocystis* (Lancelot et al. 1998). We further hypothesized that bacteria would respond rapidly to this input by increasing their biomass and productivity. In order to study these transformations, we conducted large-volume experiments using natural

plankton communities (e.g. Sakshaug & Holm-Hansen 1986, Banse 1994) and followed the concentrations and transformations within the various inorganic and organic pools through time. In parallel, we conducted a field investigation in the Ross Sea in which the same pools were assessed to compare *in situ* patterns with the experimental enclosures.

## MATERIALS AND METHODS

Experiments and observations were conducted from the RVIB 'Nathaniel B. Palmer' in the Ross Sea, Antarctica, from November 10 to December 8, 1994 (Cruise RSP$^2$-94) and December 17, 1995 to January 15, 1996 (Cruise RSP$^2$-95). The study area included open waters as well as those with varying concentrations of ice. Many of the stations were sampled along 76° 30' S during both cruises, and samples for experimental analysis were also collected along that transect (Fig. 1a, b). In 1994 this transect was occupied 2 times (November 13–17 and December 2–6), and in 1995–96 it was sampled 3 times (December 21–29, January 5–8, and January 8–12).

**Field observations.** Water samples were obtained from 24 ten-liter Niskin bottles mounted on a rosette which housed a Seabird 911 conductivity-temperature-depth (CTD) system and a BioSpherical Instruments Model 240 4π underwater irradiance sensor. Generally, duplicate water samples were taken from depths which corresponded to 100, 50, 30, 15, 5, 1, or 0.1% of surface PFD (photon flux density), as well as from depths spaced evenly below the 0.1% isolume to 150 m. The entire contents of 1 Niskin bottle from each depth were drained into polycarbonate carboys before subsampling for phytoplankton to ensure even distributions of particles. Subsamples for determination of ambient nutrient concentrations were taken from the carboys first, followed by those for determination of concentrations of chlorophyll *a*, particulate carbon and nitrogen, and phytoplankton taxonomy. The ambient concentrations of nutrients in the water samples were processed by a rapid-flow Alpkem autoanalyzer. Samples for DOC concentrations and bacterial biomass and productivity were collected directly from the duplicate Niskin bottle to minimize contamination.

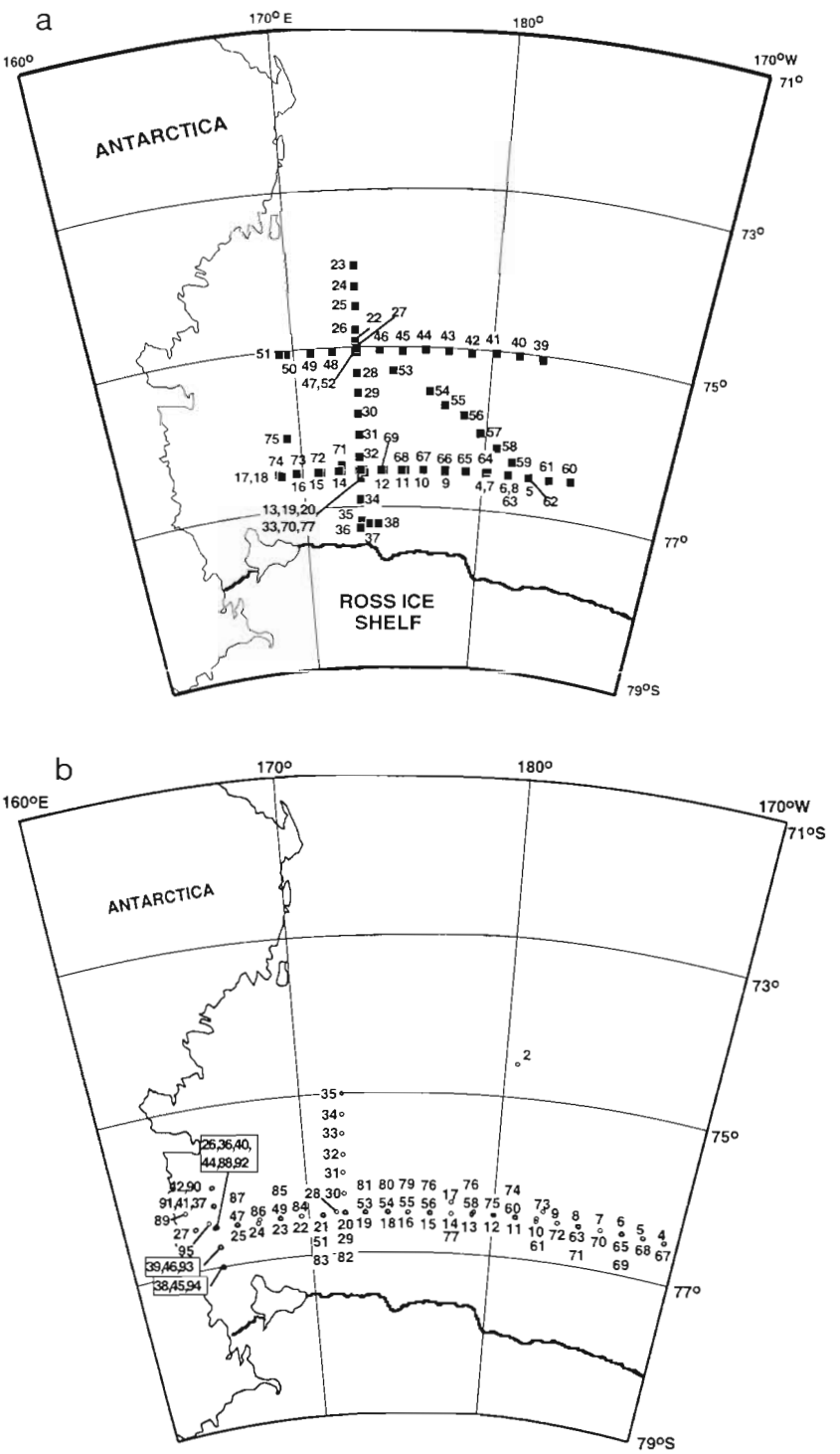


Fig. 1. Station locations and sites of experimental enclosure sampling during (a) spring 1994 and (b) summer 1995–1996 studies

Chlorophyll *a* concentrations were determined fluorometrically. Small volumes (<250 ml) were filtered through Whatman 25 mm GF/F filters, placed in 10 ml 90% acetone, sonicated on ice in the dark for 15 min, extracted for an additional 15 min, and the resultant fluorescence measured on a Turner Designs fluorometer both before and after acidification. The fluorometer was calibrated with commercially purified chlorophyll *a* (Sigma). Particulate organic nitrogen and carbon concentrations were assessed by filtering known volumes through 25 mm combusted (2 h at 450°C) GF/F filters. The filters were rinsed with small amounts (ca 5 to 10 ml) of 0.01 N HCl in filtered seawater to remove inorganic carbonates, placed in combusted glass vials, capped with combusted aluminum foil, and dried at 60°C. All samples were analyzed by high temperature pyrolysis on a Carlo-Erba Model EA-1108 elemental analyzer.

DOC samples were collected via gravity filtration through an in-line, combusted GF/F filter into a combusted glass vial. The in-line filters were attached directly to the Niskin or incubation bottle via a short piece of acid washed silicone tubing. Low vacuum filtration (<100 mm Hg) with combusted glass filter towers was used to collect DOC during the first enclosure experiment. The first 25 ml were collected for analysis. Possible artifacts such as elevated DOC release could have occurred by being drawn under vacuum, and in subsequent experiments DOC was collected by in-line filtration. All DOC samples were analyzed by the high temperature combustion method using a homemade instrument as described in Carlson et al. (1998). Ultra-high-purity $O_2$ was used as a carrier gas and flowed through the machine at 175 ml $min^{-1}$. One hundred µl of sample were injected manually into a quartz combustion tube (490 × 13 mm) packed with platinum gauze (Ionics), 7% platinum on alumina catalyst (Dymatec), Sulfix (Wako Pure Chemical Industries, Inc.) and CuO wire (Leeman Labs), and heated to 740°C. Sulfix was used for the removal of halides and the CuO wire was used to convert CO to $CO_2$. After passing through the combustion furnace, the carrier gas passed through several water traps and a copper halide trap before entering the LiCor 6252 $CO_2$ analyzer, where the signal was integrated with chromatographic software (Dynamax Macintegrator I, Version 1.3; Rainin Inst.). The resultant purified $CO_2$ was detected with a LiCor 6252 $CO_2$ analyzer.

Extensive conditioning of the combustion tube was essential to minimize the machine blank. After conditioning, the system blank was assessed with low carbon waters (LCW) that had been referenced against blank water provided by Jonathan Sharp for the 1994 DOC intercomparison program. The system response was standardized daily with a 4-point calibration curve of glucose solution in LCW. Deep Sargasso seawater (>2000 m) served as a reference standard. Analyzing LCW and deep seawater reference several times a day allowed us to assess the machine's stability from run-to-run and day-to-day. Samples were acidified with 85% $H_3PO_4$ (10 µl per 10 ml sample) and purged of inorganic carbon with $CO_2$-free oxygen for at least 10 min immediately prior to injection.

Bacterial abundance and biovolume were determined microscopically. Samples were preserved with particle-free 25% glutaraldehyde (final concentration 1%) and stored at 4°C for less then 48 h until slide preparation. Samples were filtered through 0.2 µm black polycarbonate filters and stained with acridine orange (final concentration 0.005%) according to Hobbie et al. (1977). Biovolumes were estimated using a Zeiss Axiophot epifluorescence microscope and a video image analysis system (Carlson & Ducklow 1996). A carbon conversion factor of 120 fg $\mu m^{-3}$ was used to convert bacterial biovolume to cellular carbon for consistency with Carlson et al. (1998). Bacterial production was estimated from the incorporation of $^3$H-thymidine (TdR) using 20 nM exogenous TdR. In 1994 TdR incorporation assays were harvested by filtration onto 0.45 µm filters, whereas in 1995 we followed the procedures of Smith & Azam (1992). Samples were incubated at −1.5°C in the dark for 3 to 12 h before processing. A conversion factor of $1.5 \times 10^{18}$ cells $mol^{-1}$ of TdR was used to derive carbon-based production rates (Ducklow & Carlson 1992).

**Large-volume experiments.** Large-volume experiments were conducted in acid-washed polycarbonate carboys which contained ca 25 l seawater. Results from 3 experiments (GCE94-1, GCE94-2, and GCE95-1) are reported herein. Water samples were collected either from multiple 10 l Niskin bottles closed at the same depth (GCE94-1 and GCE94-2) or from 30 l Niskin bottles (GCE95-1). Water for the 3 experiments was collected from 20, 2 and 15 m, respectively. In addition, the water used in GCE94-2 was diluted with unfiltered deep (200 m) water to reduce the initial inoculum biomass. No attempt was made to sample using trace-metal clean techniques. The carboys were incubated on-deck in a deep, Plexiglas chamber through which surface seawater flowed to maintain surface seawater temperatures. Subsamples were collected throughout the experiment, although in order to minimize wall effects the remaining volume was never allowed to decrease below 10 l.

Growth rates from these experiments were calculated using an exponential growth equation. Subsamples for $^{14}$C incorporation into phytoplankton were collected into 280 ml acid-washed polycarbonate bottles. All samples were inoculated with 20 µCi of $H^{14}CO_3$ and incubated for 24 h under the same irradiance con-

ditions as the experimental enclosure. Samples were filtered under low vacuum through GF/F filters and placed in scintillation vials to which 0.2 ml 1.0 N HCl were added. Tests showed no significant filtration artifacts were introduced when filtration volumes and pressures were kept low. After another 24 h scintillation fluor (Ecolume, ICN) was added and the samples counted on a Beckman scintillation counter. All counts were corrected for quenching using an external standard correction.

## RESULTS

### Large-volume experiments

#### GCE94-1

The first large-volume experiment (GCE94-1) was initiated early in the 1994 cruise (seawater collected on November 14 from Stn 7) and followed for 19 d. *Phaeocystis antarctica* dominated the phytoplankton assemblage throughout the experiment. Nitrate and phosphate declined rapidly, with the maximal rate of decrease between Days 5 and 9 (Fig. 2a). Nitrate declined to less than 0.5 µM by Day 10, whereas phosphate concentrations remained above 0.3 µM. Silicic acid decreased by 6 µM in the first 10 d, and ammonium levels remained low throughout the experiment. Chlorophyll (chl) levels initially declined, but increased to ca 9.6 µg $l^{-1}$ on Day 10, after which they again decreased. Particulate matter concentrations increased dramatically (from 9.4 to 123 µmol $l^{-1}$ by Day 10; Fig. 2b); furthermore, they continued to increase after nitrate depletion and reached 240 µM at the end of the experiment. Particulate organic nitrogen (PON) levels reached ca 21 µmol $l^{-1}$ at the time of nitrate depletion and did not increase significantly thereafter. Bacteria grew exponentially throughout the experiment. The initial ambient bacterial biomass was low, and biomass increased at a net rate of 0.25 ± 0.03 $d^{-1}$ ($R^2$ = 0.92; n = 11) over 13 d to a peak biomass of 0.85 µmol C $l^{-1}$. Bacterial production was not determined during this experiment.

DOC was initially near the background level for the region (ca 42 µM), but by Day 10 nearly doubled to 80.6 µM (Fig. 2c). DOC concentrations continued to increase after nutrient depletion in a manner similar to POC, and by the end of the experiment reached 261 µM. Increases in POC and DOC were highly correlated throughout the experiment (n = 13; $R^2$ = 0.83; $p < 0.01$). To emphasize the partitioning of organic carbon between the particulate and dissolved phases, we calculated the ratio of the recently produced DOC ($DOC_R$) to total labile organic carbon [$TOC_R$ = (DOC – 42 µM) + POC]. This ratio initially was 0.18 (i.e. most of the recently produced organic material was in the particulate pool), but increased slightly during exponential growth, so that the average ratio for the experiment after Day 3 was 0.35. DOC as a percentage of TOC initially equaled 0.83 and decreased to 0.40 by Day 10, when it slightly increased until the end of the experiment.

Ratios of various properties also varied in a systematic manner (Fig. 2d). For example, the POC/PON ratio ranged from 3.3 to 5.4 (mol/mol) through Day 10, but increased to 7.9 (mol/mol; 9.2 g/g) by the end of the experiment. Carbon:chlorophyll ratios were initially 42.3 and averaged 160 during the first 10 d, but increased to 732 at the experiment's end. Nitrogen:chlorophyll ratios were 6.7 at the experiment's start, ca 45 during exponential growth, and 27.3 on Day 10 (the onset of non-detectable nitrate concentrations). Nitrate:phosphate ratios were ca 13.5 initially and decreased to 3.0 by Day 9, whereas Si:$NO_3$ ratios were 2.6 at the start of the experiment. The bacterial contribution to the particulate carbon pool was at all times <1%.

Phytoplankton growth rates were calculated from changes in particulate matter concentrations, decreases in nitrate concentrations, and from $^{14}C$-assimilation measurements combined with particulate matter determinations (Eppley 1967; Table 1). The greatest calculated daily growth rate resulted from the disappearance of nitrate during exponential growth (0.69 $d^{-1}$), although the growth rate based on the initial and Day 14 nitrate concentrations equaled 0.42 $d^{-1}$. Growth rates derived from particulate matter changes and $^{14}C$-isotope incorporation were less than the long-term nitrate-based growth rate (ca 0.26 and 0.35 $d^{-1}$,

Table 1. Phytoplankton growth rates ($d^{-1}$) during exponential growth calculated from changes in nitrate and particulate matter concentrations and an exponential growth equation. Temperature-limited growth rate calculated from the equation of Eppley (1972) using the ambient seawater temperature (–1.8°C). $^{14}C$-based rates represent mean during exponential growth

| Variable used to derive growth rate | GCE94-1[a] | GCE94-2[b] | GCE95-1[c] |
|---|---|---|---|
| Change in nitrate concentration | 0.49 | 0.09 | 0.22 |
| Change in POC concentration | 0.26 | 0.26 | 0.14 |
| Change in PON concentration | 0.27 | 0.24 | 0.14 |
| Change in chlorophyll concentration | 0.13 | 0.02 | –0.02 |
| POC concentration with $^{14}C$ incorporation | 0.35 | 0.26 | No data |
| Temperature | 0.52 | 0.52 | 0.52 |

[a]Rates calculated from net changes from Days 0 to 10; [b]calculated from net changes from Days 0 to 7; [c]calculated from net changes from Days 0 to 9

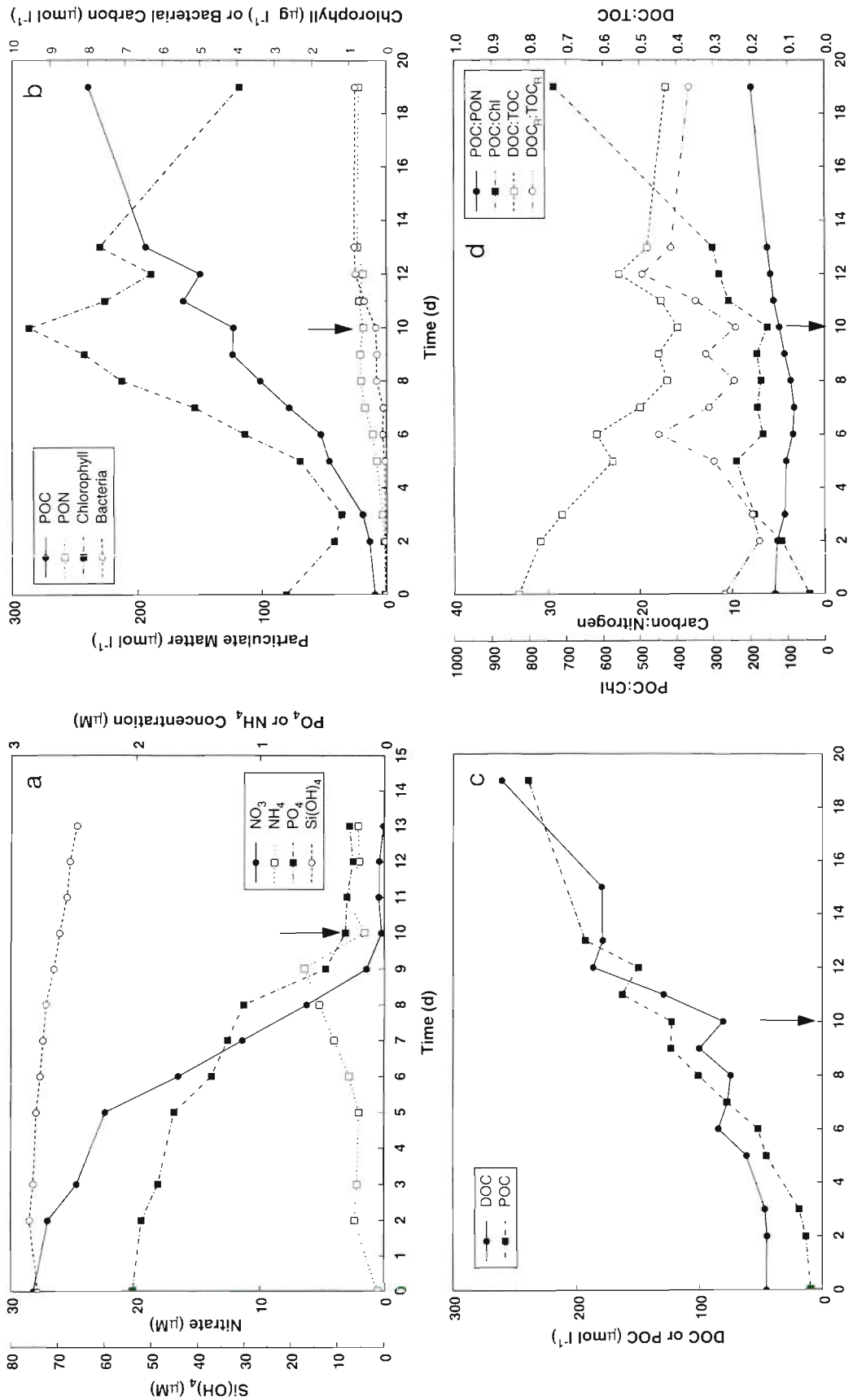


Fig. 2. Temporal changes in (a) concentrations of nitrate, ammonium, phosphate and silicic acid, (b) concentrations of particulate organic carbon, particulate organic nitrogen, chlorophyll, and bacterial carbon, (c) dissolved and particulate organic carbon concentrations, and (d) ratios of particulate organic carbon:particulate organic nitrogen, particular organic carbon:chlorophyll, dissolved organic carbon:total organic carbon (DOC:TOC) and recently produced DOC and total labile organic carbon ($DOC_R$:$TOC_R$) during the duration of GCE94-1. Vertical arrow indicates the time at which nitrate approached the limit of detection

respectively), although growth rates calculated from PON changes from Day 3 through 7 averaged 0.44 $d^{-1}$. For comparison, the predicted temperature-mediated growth rate is 0.52 $d^{-1}$ (Eppley 1972).

GCE94-2

The second experiment in 1994 was initiated on 25 November to assess the exponential growth phase of the bloom and was started with larger initial concentrations of chlorophyll and particulate matter. Nitrate decreased over 7 d from 27.3 to 15.0 µM (Fig. 3a), and phosphate decreased concomitantly. Silicic acid decreased by 2 µM. Chlorophyll decreased by 40% during the first 2 d, but increased thereafter to 4.21 µg $l^{-1}$, a net increase of 11% in 7 d (Fig. 3b). POC concentrations, on the other hand, increased throughout the experiment, and after 7 d had increased 7-fold to 83.3 µmol $l^{-1}$ (Fig. 3b). DOC concentrations increased from 43 to 58 µM, and bacterial carbon increased by 350% (Fig. 3c). Bacterial abundance was somewhat higher than in GCE94-1, and bacteria grew at 0.17 ± 0.02 $d^{-1}$ ($R^2$ = 0.91, n = 8) to a maximum concentration of 0.5 µmol C $l^{-1}$. Bacterial biomass again was always less than 1% of the total POC. The bacterial production rate increased from 0.02 to 0.34 µmol C $l^{-1}$ $d^{-1}$ in 8 d (1.5 to 12.4 pmol thymidine $l^{-1}$ $h^{-1}$). Over the course of the experiment, total cumulative bacterial production was equivalent to about 2% of the total primary production (calculated from hourly $^{14}C$ rates, assuming constant rates for primary production over each 24 h period).

Carbon:chlorophyll ratios increased dramatically during the experiment, but C:N ratios did not change systematically (Fig. 3d). The $DOC_R/TOC_R$ ratio was zero on Day 1 and ranged from 0.1 to 0.2 thereafter, whereas the DOC/TOC ratio decreased from 0.73 to 0.40, and then increased slightly. Growth rates were somewhat lower than observed in GCE94-1; rates calculated from particulate matter concentrations approached 0.25 $d^{-1}$ (Table 1), with the exception of chlorophyll-based rate, which was much lower. Nitrate-based rates also were low (0.08 $d^{-1}$; Table 1). The maximum sustained growth rate was observed from Day 1 through 4 and averaged 0.35 $d^{-1}$ (based on PON changes).

GCE95-1

This experiment was initiated on 28 December with a large biomass (7.4 µg $l^{-1}$ chl), with *Phaeocystis antarctica* again being the dominant species, although diatoms were also present. Nitrate concentrations decreased from 21.7 to <0.1 µM on Day 15, and silicic acid also decreased from 70.4 to 41.5 µM (Fig. 4a). Chlorophyll levels decreased to a minimum after 3 d (1.66 µg $l^{-1}$) but had increased by the end of the experiment to 11.1 µg $l^{-1}$, whereas POC increased throughout (from 29.7 to 124 µmol $l^{-1}$; Fig. 4b). C/N ratios remained constant, but POC/chl ratios increased from 45 to 325 (Fig. 4c). $DOC_R/TOC_R$ ratios again were low and did not exceed 0.13 at any time during the experiment, and DOC/TOC ratios were minimal at the end of the experiment (0.35). The initial bacterial biomass was about an order of magnitude greater than in 1994, and cells grew at 0.29 ± 0.02 $d^{-1}$ for the first 5 d ($R^2$ = 0.98, n = 5) to 1.6 µmol C $l^{-1}$. Bacterial production was much greater than in 1994, as expected from the higher biomass and faster growth rates. At the same time, primary production in the carboy (as in the field) was somewhat lower. In this experiment the cumulative bacterial production was equivalent to about 21% of the primary production integrated over 16 d. At the time this experiment was started, the bloom may have been in the early stages of senescence, as suggested by the large numbers of attached bacteria. Bacterial biomass as a percentage of POC reached a maximum of 3% in this experiment, most as attached forms.

Estimated phytoplankton growth rates were less than those predicted based on temperature (Table 1). Growth rates based on chlorophyll were negative, reflecting the net decrease in chlorophyll over the first 9 d. Nitrate-based growth rates were 0.22 $d^{-1}$, whereas those based on particulate carbon and nitrogen changes were both 0.14 $d^{-1}$. Maximum sustained growth rates (those which occurred for more than 3 d consecutively) were ca 0.25 $d^{-1}$.

## Field observations

The phytoplankton assemblages in 1994 along 76° 30' S were dominated numerically and in terms of carbon equivalents by *Phaeocystis antarctica*. The earliest occupation of the transect (November 12 to 16, 1994) was characterized by thin (ca 20 to 30 cm) ice cover, variable stratification (Fig. 5a), modest particulate carbon concentrations (surface levels averaged 7.91 and ranged from 2.30 to 21.1 µmol $l^{-1}$; Table 2) and chlorophyll concentrations, low bacterial abundances and carbon equivalents, and DOC concentrations at or slightly above deep water concentrations of 42 µM (Table 2). Nitrate concentrations were elevated, but showed a small reduction at the surface (Fig. 5b); silicic acid concentrations were uniformly high (Table 2). Although stratification was not significantly stronger during early December, 1995 (Fig. 6a), the ice cover was gone, and phytoplankton biomass was near its maximum (mean

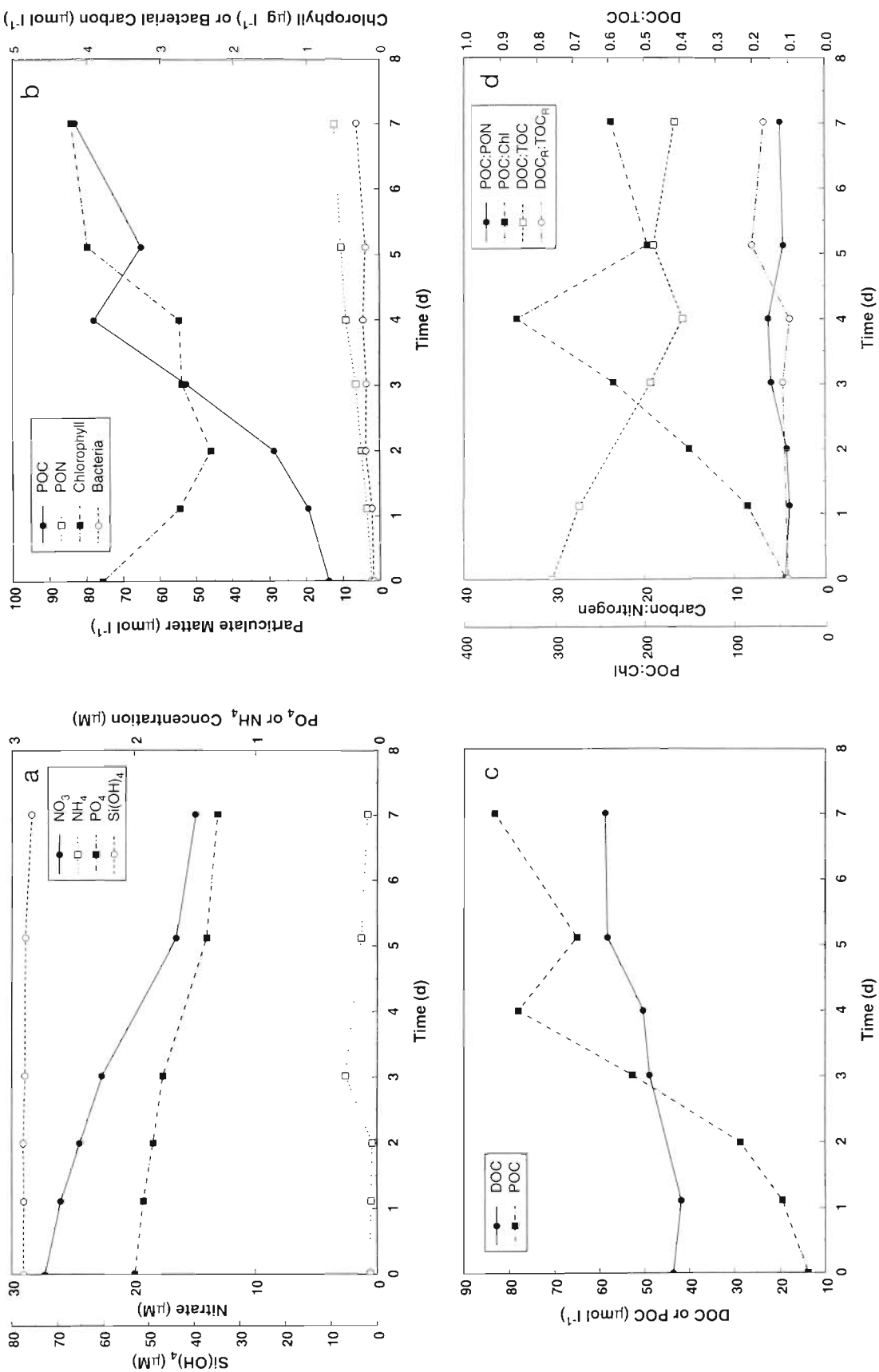


Fig. 3. Temporal changes in (a) concentrations of nitrate, ammonium, phosphate and silicic acid, (b) concentrations of particulate organic carbon, particulate organic nitrogen, chlorophyll, and bacterial carbon, (c) dissolved and particulate organic carbon concentrations, and (d) ratios of particulate organic carbon:particulate organic nitrogen, particulate organic carbon:chlorophyll, and dissolved organic carbon:total organic carbon (DOC:TOC) and recently produced DOC and total labile organic carbon ($DOC_R$:$TOC_R$) during the duration of GCE94-2

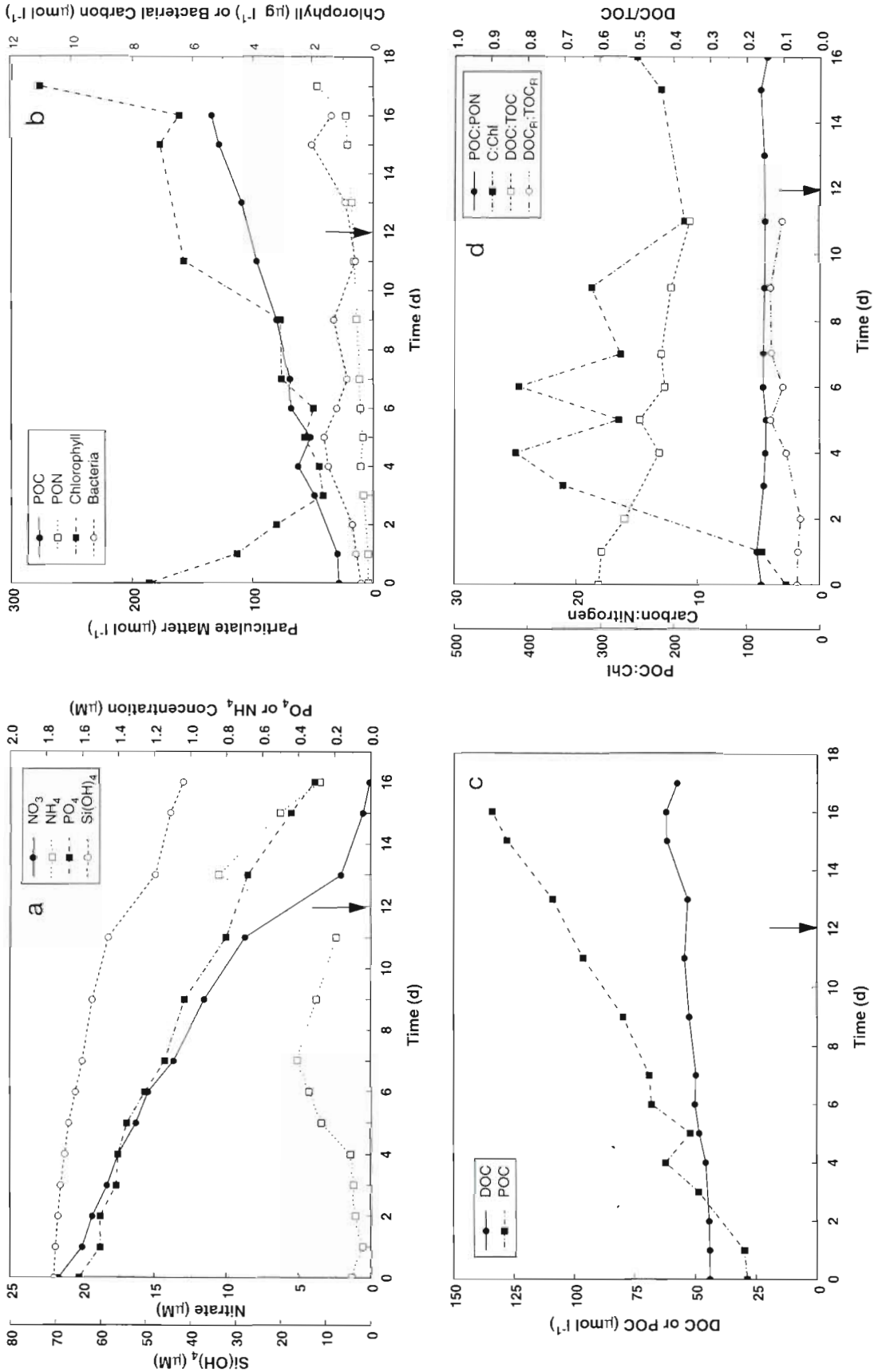


Fig. 4. Temporal changes in (a) concentrations of nitrate, ammonium, phosphate and silicic acid, (b) concentrations of particulate organic carbon, particulate organic nitrogen, chlorophyll, and bacterial carbon, (c) dissolved and particulate organic carbon concentrations, and (d) ratios of particulate organic carbon:particulate organic nitrogen, carbon:chlorophyll, dissolved organic carbon:total organic carbon (DOC:TOC) and recently produced DOC and total labile organic carbon ($DOC_R$:$TOC_R$) during the duration of GCE95-1. Vertical arrow indicates the time at which nitrate approached the limit of detection

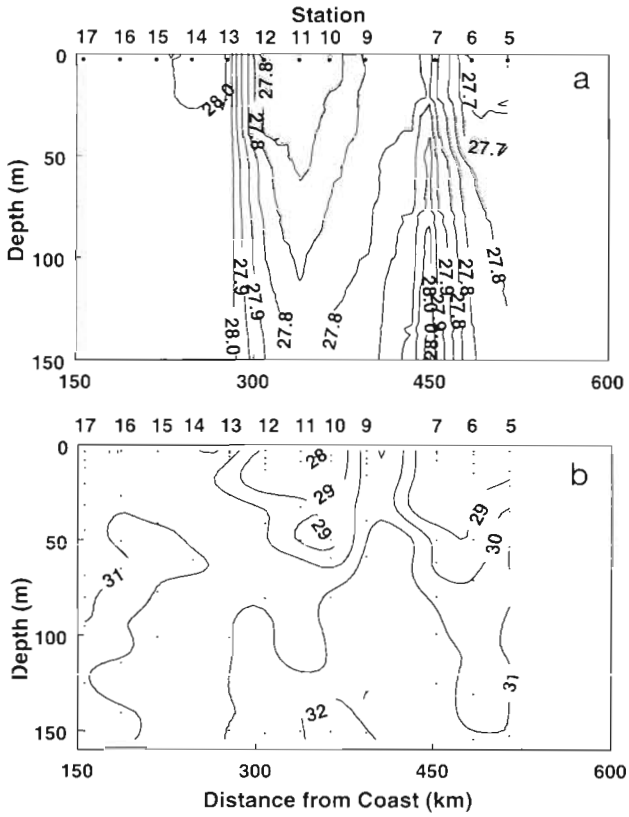


Fig. 5. Vertical distribution of (a) density (expressed as $\sigma_t$) and (b) nitrate (μM) during November 8 to 12, 1994

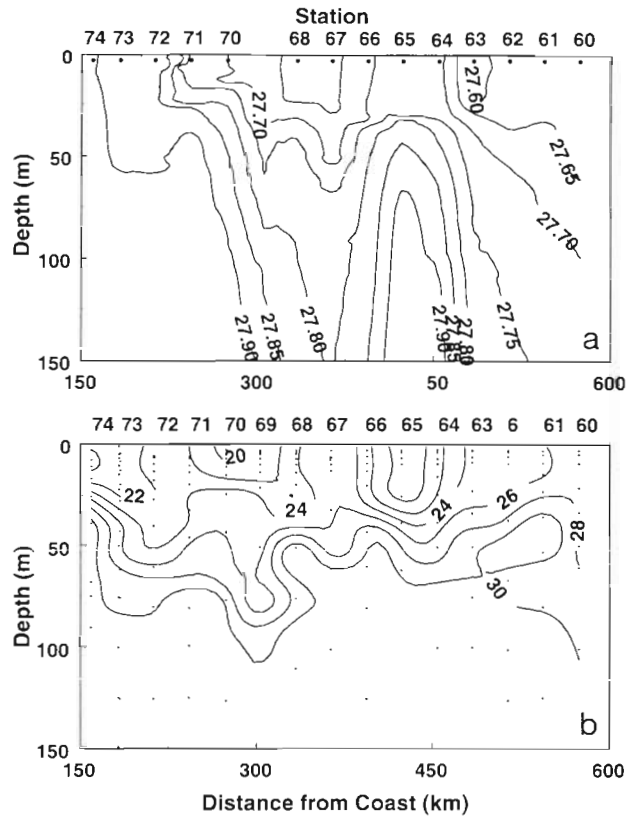


Fig. 6. Vertical distribution of (a) density (expressed as $\sigma_t$) and (b) nitrate (μM) during December 5 to 8, 1994

POC concentration = 23.0 μmol $l^{-1}$; Table 2). Bacterial abundance increased slightly, as did DOC concentrations (Table 2). Nitrate concentrations throughout the surface layer decreased substantially (Fig. 6b), and silicic acid still did not change greatly (Table 2).

The last occupation of the transect in 1995 showed marked stratification (Fig. 7a), decreased particulate matter concentrations, increased bacterial abundances, low DOC concentrations (Table 2), and substantially diminished nitrate levels (Fig. 7b). Chlorophyll levels were only 31% of the maximum values in 1994 (Table 2), and silicic acid concentrations had decreased slightly. The assemblage still had large numbers of *Phaeocystis antarctica* cells, but the abundance (absolute and relative) of diatoms also increased markedly.

The ratios of variables also changed significantly through time (Table 2). For example, the carbon:chlorophyll ratio increased from 64 to 126, and the bacterial carbon:particulate carbon ratio also increased substantially (from 6.3 and 11.0% in November and December to 58% in late January). The proportion of DOC relative to TOC decreased from 0.85 in mid-November to 0.68 and 0.71 in the 2 later cruises, and the percentage of recently produced DOC relative to total 'new' organic matter also decreased. N/P ratios were similar in all cruises and ranged from 13.4 to 14.0.

## DISCUSSION

### Enclosure experiments

The enclosure experiments provided insights into the carbon and nitrogen partitioning patterns of planktonic communities dominated by *Phaeocystis antarctica*. We had hypothesized that *P. antarctica* would produce and release large amounts of dissolved organic matter, similar to communities dominated by *P. pouchetii* in the North Sea (Lancelot & Mathot 1987). However, the enclosures did not produce exceptionally large DOC accumulations during exponential growth; indeed, DOC levels during the first experiment doubled by the time of nitrate depletion, and in the other 2 experiments only increased by 40 and 23%, respectively. These changes in DOC are within the range of seasonal variation seen in other regions (e.g. Carlson & Ducklow 1995, Peltzer & Hayward 1996). POC con-

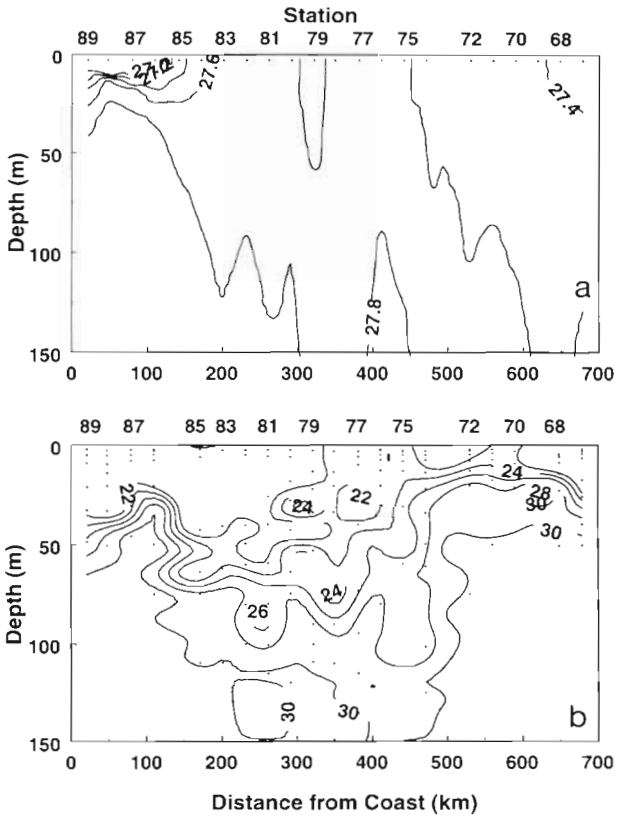


Fig. 7. Vertical distribution of (a) density (expressed as $\sigma_t$) and (b) nitrate (μM) during January 16 to 19, 1996

Table 2. Mean surface concentrations of various particulate and dissolved parameters within the 76° 30' S transect and their standard deviations. Range of observations in parentheses

| Variable | Nov 12–15, 1995 | Dec 8–12, 1995 | Jan 16–20, 1996 |
|---|---|---|---|
| Nitrate (μM) | 29.5 ± 1.04 (23.3 – 31.0) | 23.5 ± 3.1 (18.8 – 28.9) | 19.2 ± 0.44 (10.8 – 25.2) |
| Phosphate (μM) | 2.10 ± 0.05 (2.03 – 2.18) | 1.76 ± 0.15 (1.54 – 1.99) | 1.42 ± 0.33 (0.59 – 1.84) |
| Silicic acid (μM) | 77.1 ± 1.86 (72.3 – 78.9) | 73.5 ± 3.1 (68.3 – 77.1) | 60.3 ± 8.24 (34.2 – 68.5) |
| Ammonium (μM) | 0.09 ± 0.10 (0.00 – 0.44) | 0.10 ± 0.05 (0.03 – 0.23) | 0.30 ± 0.15 (0.10 – 0.66) |
| Chlorophyll (μg $l^{-1}$) | 1.49 ± 1.08 (0.15 – 2.88) | 5.75 ± 2.65 (1.17 – 11.5) | 1.77 ± 1.29 (0.31 – 4.68) |
| Particulate organic carbon (μmol $l^{-1}$) | 7.91 ± 5.08 (2.30 – 21.1) | 23.0 ± 12.9 (8.07 – 46.1) | 18.6 ± 5.44 (8.33 – 29.6) |
| Particulate organic nitrogen (μmol $l^{-1}$) | 1.05 ± 0.47 (0.32 – 1.77) | 3.86 ± 2.08 (1.41 – 7.81) | 2.99 ± 0.83 (1.37 – 4.90) |
| Bacterial carbon (μmol $l^{-1}$) | 0.50 ± 0.20 (0.29 – 1.00) | 2.50 ± 2.41 (0.43 – 8.91) | 10.7 ± 3.04 (3.83 – 14.2) |
| Dissolved organic carbon (μM) | 44.9 ± 2.10 (43.1 – 49.2) | 48.7 ± 10.3 (41.8 – 72.9) | 46.2 ± 2.40 (43.4 – 52.3) |
| POC:chl[a] (w/w) | 63.7 | 48.0 | 126 |
| POC:PON[a] (mol/mol) | 7.53 | 5.96 | 6.22 |
| DOC:TOC[a] (mol/mol) | 0.85 | 0.68 | 0.71 |
| $DOC_R$:$TOC_R$[a] (mol/mol) | 0.28 | 0.23 | 0.19 |

[a]Ratios derived from the means of each variable

centrations, on the other hand, increased by over an order of magnitude in the first experiment, and by 600 and 470% in the latter 2 experiments. Clearly most of the organic material being produced by photosynthesis was being partitioned to the particulate phase.

POC and DOC production continued unabated after nitrate depletion. POC concentrations doubled after Day 10 in GCE94-1 and DOC levels tripled (Fig. 2b, c). PON levels, however, did not increase, which suggests that carbon and nitrogen production and metabolism largely became uncoupled during this period. As a result, POC/PON ratios increased significantly upon nutrient depletion. We believe that upon nitrate depletion *Phaeocystis antarctica* continued to fix carbon and shunt much of the organic material into the mucoid sheath (Chrétiennot-Dinot et al. 1997), and protein and cellular synthesis largely ceased. Goldman et al. (1992) found that some laboratory cultures of diatoms also continued to fix carbon and release DOC, despite the absence of available nitrogen. Banse (1994) also found that carbon assimilation continued after nitrogen depletion in natural assemblages of phytoplankton, whereas Smith et al. (1995) found that particulate and total organic carbon leveled off upon nutrient depletion. The uncoupling of carbon fixation and nutrient acquisition we observed confounds the concept of carbon-based new production, since the organic carbon fixation which occurred in the absence of nitrogen assimilation represented a significant percentage of the total carbon production. Also, this carbon uptake relative to nutrient uptake clearly was not near the Redfield ratio, and material which might be removed from the surface would have greatly skewed elemental composition (Sambrotto et al. 1993). Further investigation on the significance of non-Redfieldian uptake is warranted in other Antarctic systems.

Chlorophyll was a poor indicator of phytoplankton biomass in the enclosures and responded rapidly to a changed irradiance environment. Although the original inocula were obtained from the surface layer, the sampled water column was mixed to a much greater depth (the mixed layer in general extended to at least the 5% isolume), and hence the *in situ* populations were likely exposed to variable irradiances through time. When maintained in a constant and high irradiance environment, *Phaeocystis antarctica* adapted its photosynthetic pigmentation by increasing the carbon:chlorophyll ratio. In 3 experiments the POC/chl ratio was initially ca 45, but within 24 h the ratio increased dramatically (at least doubling in all cases).

This parallels what generally is expected from culture and modeling experiments, where the amount of chlorophyll and photosynthetic reaction centers per unit of carbon decrease under high photon flux densities (e.g. Prézelin 1981, Kirk 1994). However, what is somewhat surprising is the extent to which *P. antarctica* assemblages modify this ratio. In all experiments prior to extreme colony disintegration (Day 19, GCE94-1), the ratio ranged from 237 to 316, which is much greater than is normally observed in temperate and tropical waters (e.g. Bannister & Laws 1983). It is, however, similar to those found in the Ross Sea previously (Smith & Nelson 1985, Smith et al. 1996), and consistent with pigment labeling experiments conducted in the same region (DiTullio & Smith 1996). High carbon:chlorophyll ratios also can result from substantial amounts of detrital material being present, but based on the C/N ratios we observed as well as microscopic observations, detrital (i.e. POC not associated with cells or colonies) contributions were exceedingly small, especially during exponential growth. Elevated POC/chl ratios appear to be consistent, ubiquitous adaptations of Ross Sea phytoplankton to the irradiance and/or nutrient fields present.

Bacteria grew exponentially at 0.17 to 0.29 $d^{-1}$ in the 3 experiments, all of which represented untreated (i.e. no removal of bacteriovores) water samples. Exponential growth at these substantial rates in 'whole' water suggests that bacterial growth was not strongly limited by bacterivory (Ducklow et al. 1992). If we assume that the bacterial growth efficiency was 15 to 20%, we can estimate that in GCE2-94 an amount of carbon equivalent to about 10 to 15% of the total primary production was metabolized by bacteria in the carboy. Phytoplankton biomass and DOC both increased throughout the experiment, except for a transient POC decline of ca 15 µmol C $l^{-1}$ on Days 3–4 (Fig. 3b, c). Bacteria must have been sustained by a flux of newly produced carbon, or by only minor utilization of existing pools. In 1995 the same assumption about growth efficiency would lead us to estimate that nearly all the primary production was metabolized by bacteria during the 16 d experiment. This is unlikely, and we suggest that bacterial growth efficiency was greater in this experiment, with higher growth rates and biomass accumulation resulting, compared to 1994.

Smith et al. (1995) conducted similar experiments in mesocosms initiated with water from off the coast of California, and they investigated the bacterial-diatom interactions in the resultant bloom. They did not observe that phytoplankton production and particulate/total organic carbon concentrations continued after nutrient depletion, but rather leveled off. They also found that bacterial carbon demand was estimated to be from 40 to 60% of the total carbon fixed during the bloom, in contrast to our estimation of 10 to 15% in GCE94-2. Attached bacteria within their bloom were suggested as being highly significant in solubilizing DOC from particles, despite their being a small percentage of total bacteria. We did find a variation in the relative proportion of attached bacteria in the water used to initiate the experiments, with GCE95-1 having the largest proportion of attached bacteria. We have no data on the relative activity of the bacterial fractions, but it certainly is possible that attached bacteria were active in oxidizing and utilizing the extracellular mucilage of *Phaeocystis antarctica*, and that this DOC production mechanism varies as a function of bloom development and physiological state.

Initial DOC/TOC ratios were high (approximately 0.75 in all experiments) and decreased as particulate matter generation proceeded. These ratios reflected the dominance of particulate production over dissolved production on the time scales of the experiment. Most systems have ratios of ca 0.9 (Hobson et al. 1976), implying that the largest organic carbon pool is usually DOC. In these enclosures this was not true during high biomass stages, where the particulate phase increased relative to DOC. Carlson et al. (1998) suggested that the DOC production mechanisms which dominate during a *Phaeocystis antarctica* bloom result in limited DOC production; furthermore, the DOC which is produced is readily mineralized by bacterioplankton, resulting in limited accumulation of the DOC pool. Van Rijssel et al. (1997) suggest that *P. globosa* (and by extension other *Phaeocystis* spp.) have an aqueous- rather than mucus-filled lumen in the colony, and that carbohydrate is just a small part of the colonial biomass. Our results of minor DOC production are consistent with this observation. The ratios of the recently produced pools of organic matter generated within the enclosures ($DOC_R$ and $TOC_R$) were also low, but increased slightly after nutrient depletion and with time. This suggests that the DOC being produced during senescence may have been slightly more refractory and accumulated in greater quantities than during exponential growth of phytoplankton, which in turn may imply that the material is highly enriched with carbon relative to nitrogen and hence is a 'poorer' substrate for bacterial catabolism.

Because the enclosures were closed systems, it is possible to construct a nitrogen budget and estimate the amount of DON produced during the course of the experiment (Fig. 8). More specifically, because the initial amounts of nitrate, nitrite, ammonium and particulate organic nitrogen are known, the sum of these pools should not change through time, and any 'disappearance' of nitrogen must (in the absence of denitrification) enter into the DON pool. Therefore, $DON_R$ (recently produced DON) produced during the experi-

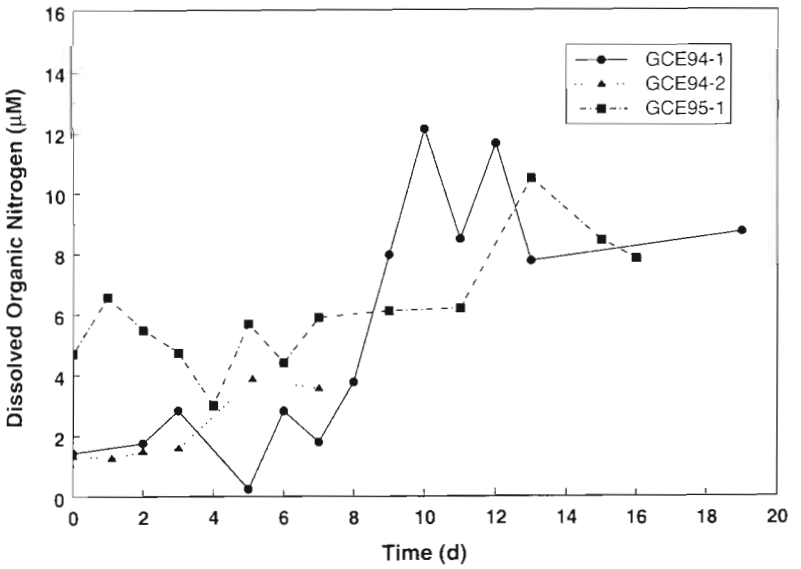


Fig. 8. Calculated (from Eq. 1) changes in recently produced dissolved organic nitrogen during the 3 enclosure experiments

ment can be calculated as

$$DON_R = 31.0 - (NO_3 + NO_2 + NH_4 + PON) \quad (1)$$

where 31.0 represents the baseline (i.e. sum of all dissolved nitrogen forms) value. During GCE94-1 DON accumulation was low and fairly constant during exponential growth, but rapidly began to increase as nitrate concentrations approached limiting levels. During senescence $DON_R$ pools exceeded 10 µM and did not change markedly thereafter. During GCE94-2 $DON_R$ did not exceed 3.9 µM, whereas in GCE95-1 $DON_R$ remained at low concentrations prior to nutrient depletion but again increased substantially as nitrate disappeared (Fig. 8). These results suggest that DON production in the Ross Sea is likely to be quantitatively minor, a finding corroborated by direct $DO^{15}N$ release measurements made by Hu & Smith (1998).

An alternate pathway for nitrogen in the enclosures would involve the generation of gaseous $N_2O$ during the process of nitrification. Although nitrification rates can be substantial in surface waters (e.g. Dore & Karl 1996), there are no data to suggest that these rates also occur in the cold, surface layer of the Southern Ocean. Furthermore, the sum of all nitrogen forms in the enclosures was constant through time, which strongly suggests that no gaseous forms of inorganic nitrogen were being generated during the course of the experiments.

### Comparison of experimental and field data

Many of the variables sampled in the field were markedly different from those observed in the enclosures, despite the overwhelming dominance of *Phaeocystis antarctica* in both. One of the most striking features was that nitrate never was depleted to the non-detectable levels found in the enclosures. The mean surface nitrate concentration in late January was 19.2 µM (Table 1), and studies completed later in the seasonal cycle suggest that although further nitrate uptake occurs, nitrate rarely declines below 10 µM (Smith et al. 1996). Phytoplankton do not deplete nitrate from the surface layer, and hence do not experience conditions which would stimulate large changes in their nitrogenous metabolism. It has been hypothesized that *in situ* concentrations of iron might limit phytoplankton growth and biomass in the Ross Sea (e.g. Sedwick & DiTullio 1997), and because our experiments were not intended to be free of trace-metal contaminants, they should be considered as trace-metal replete. PON levels in the surface layer were much less than those observed in the enclosures (reaching 21 µM in the enclosures but averaging 3.86 µM during the biomass maximum period in December; Table 2), as were POC levels (193 vs 23.0 µM). Chlorophyll levels, however, were similar in the two, with maximum chlorophyll levels in the field reaching 11.5 µg $l^{-1}$, whereas the maximum in the enclosures was 9.6 µg $l^{-1}$.

Bacteria generally grew faster and reached higher levels in the experimental enclosures than was observed in the field at the same time. For example, in 1994 bacteria in the upper 150 m of the water column grew at about 0.05 $d^{-1}$ and reached peak abundances of ca 0.5 to 1 × $10^9$ cells $l^{-1}$, which was about half of the maximum abundance seen in the enclosures. We suggest that in the experiments the combined effects of a greater photon flux and possibly the resulting nutrient depletion enhanced DOC production by *Phaeocystis* and other phytoplankton, and this in turn fostered faster bacterial growth rates and higher standing stocks. Bacterial production *in situ* was greater in 1995, so in this respect, the enclosures reflected the trends observed in the water column.

Field constituent ratios were also different than those found in enclosures. Average POC/chl ratios in the field ranged from 48.0 to 126, which were substantially lower than in the enclosure. We believe the difference represents the difference in the photoadaptative abilities of *Phaeocystis* as influenced by the nutrient and irradiance regime. Field populations always had excess nitrate available, whereas the enclosed populations did not. Furthermore, the enclo-

sures were incubated on deck in full sunlight (which averaged ca 50 µmol photons $m^{-2}$ $d^{-1}$; Hu & Smith in press), and hence the average irradiance experienced by the *in situ* populations was much less (probably by at least 2 orders of magnitude). The constant, high irradiance environment allowed the cells to adapt their photosynthetic machinery to high photon flux densities, and the elevated POC/chl ratios reflect that adaptation. Similarly, the mean molar POC/PON ratio at the surface during the 3 transects ranged from 5.96 to 7.53, whereas in the enclosures the ratios were generally much lower (between 3.5 and 5.0). The difference again may be adaptive, with *in situ* populations that are growing more slowly having relatively less protein than those growing at maximal rates. However, Lancelot et al. (1986) found little relationship between irradiance and protein synthesis for natural assemblages dominated by *Phaeocystis*, and Terry et al. (1983) found increased amounts of protein at low irradiances, although most of the variation was attributed to changes in other (non-nitrogenous) cellular constituents.

DOC concentrations in the field were also much lower than those which we found in the experimental enclosures. DOC levels averaged 44.9, 48.7, and 46.2 µM in the surface layer during the 3 transects, but reached 187 µM during GCE94-1 Similarly, although dissolved and particulate pools were strongly correlated in the enclosures, no such correlation was found in the surface layer. This suggests that the release rates of DOC in the field may have been lower than in the enclosures, and/or the bacterial populations were more capable of maintaining the lower DOC concentrations in the field. This latter explanation seems unlikely, since bacterial growth rates and biomass were enhanced in the experimental enclosures, but could not suppress DOC accumulation.

*Phaeocystis* blooms are regular occurrences in many regions of the world, including the North Sea, the Bering Sea continental shelf break, the Greenland Sea and other Antarctic coastal systems such as Prydz Bay (Lancelot et al. 1998). The North Sea environment appears radically different, in that the bloom is stimulated by coastal run-off and appears to become phosphorus limited in shallow waters. The copious DOC release found in the North Sea contrasts markedly with what has been observed in the Ross Sea (Carlson et al. 1998), but is much more similar to that found in the enclosures when nutrient limitation is reached. We suggest that the limitation of cell biomass production (in contrast to extracellular mucoid sheath production) induced by low ambient nutrient concentrations uncouples cellular production from carbon assimilation. As a result, overall carbon production continues, and approximately half of this production immediately enters the DOC pool (and larger amounts of DOC may ultimately be created through partial remineralization and solubilization of particles).

*Phaeocystis antarctica* is found throughout the waters surrounding Antarctica and often forms massive blooms early in the growing season. It generally is not grazed by mesozooplankton, and colonies in the Ross Sea appear to be grazed by microzooplankton at only low rates (Caron et al. unpubl.). As a result, its presence can greatly modify the local food web and surface layer carbon transformations. In addition, the dominant mechanism by which it exits the mixed layer is by sinking of large colonies and/or the formation of large aggregates from colonial material. These colonies and aggregates are thought to be largely degraded within the water column and hence represent only a seasonal sink for carbon rather than long-term removal within the carbon cycle. Some material does reach the sediments (Dunbar et al. 1998, Smith & Dunbar 1998), but quantitatively it is much less than in diatom assemblages where grazing produces rapidly sinking fecal material, which in large part is not degraded within the water column. Hence *P. antarctica* can markedly structure the carbon transformations in areas where it reaches substantial biomass levels. Our results suggest that the environmental influences on *Phaeocystis* growth and composition are significant, and that the fluxes of carbon between pools within *Phaeocystis*-dominated assemblages are often difficult to directly observe. Further understanding of the controls on *P. antarctica* growth and development will provide insights into the structure and function of polar continental systems and into the importance of the Southern Ocean within the global carbon cycle.

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